Habitat use, breeding biology, and effects of climate change on two endemic francolins in Ethiopia

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Declaration

I hereby declare that this thesis is my own work and that the work has not been submitted for any other degree or professional qualification. I certify that where reference has been made to the work of others in this thesis, appropriate credit has been given.

Erklärung

Ich erkläre hiermit, dass es sich bei dieser Arbeit um meine eigene Arbeit handelt und dass die Arbeit nicht für einen anderen Abschluss oder eine andere berufliche Qualifikation eingereicht wurde. Ich versichere, dass in dieser Arbeit auf die Arbeit anderer Personen Bezug genommen wurde und dass diese in angemessener Weise erwähnt wurde.

Bonn: ____________________ ____________

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Summary

The ecology, behavior, and conservation threats of endemic francolin species have been poorly documented in Ethiopia, despite their importance in providing appropriate species-specific conservation measures. Thus, this thesis aimed to make a substantial contribution to the knowledge of two allopatric francolin species (Harwood's Francolin *Pternistis harwoodi* and Moorland Francolin *Scleroptila psilolaema*) that are of exceptional conservation importance among the diverse birds of Ethiopia. Here, various field methods and advanced statistical analyses appropriate to the nature of the datasets were applied to draw reliable inferences and meaningful conclusions about the ecology and biology of these two endemic ground-dwelling pheasant species.

Using a camera trap approach and occupancy (static) modeling, I described the habitat use of Moorland Francolin across both relatively pristine and disturbed landscapes in the Afroalpine biome of Ethiopia for the first time. The occupancy (i.e., habitat use) of the species was higher in pristine than disturbed landscapes. The species was averse to predators and used roads and trails for feeding, connectivity and communication among conspecifics in pristine alpine habitat. The occupancy of the species was positively influenced by herb species richness. The detection probability of the species increased significantly as a function of sampling occasion and precipitation. Therefore, significant species-habitat associations in pristine habitats were likely related to the effects of conservation and management policies established by indigenous peoples, governments, and international organizations.

For Harwood’s Francolin, I applied dynamic occupancy modeling to determine spatiotemporal habitat use at fine and landscape scales. Direct observation and playback technique was used to collect the presence and absence data during two distinctive seasons, where the species was anticipated to use habitats differently. Occupancy probability decreased significantly with increasing Normalized Difference Vegetation Index (vegetation reflectance) and quadratic slope in the Upper Blue Nile Basin, suggesting that the species preferred sparsely vegetated habitat and flat to gentle slope gradient. Not surprisingly, anthropogenic disturbance had a significantly negative effect on species occupancy in the area. The detection probability of the species was recorded at habitats where average temperature was relatively higher. The dynamic parameters (colonization and extinction) showed no significant associations among covariates, but NDVI was slightly negatively influenced by colonization and anthropogenic disturbance positively influenced local extinction.

Furthermore, the study stressed to investigate the breeding biology of Harwood's Francolin for the first time in its native habitat. Direct field observations and camera traps were used to collect life history data. A non-lekking polygyny mating system was documented. Only female parents were responsible for nest site selection, nest building, and nest attendance. Such behavior was mainly linked to thwart risk of predation through, background matching, nest orientation and positioning, and reducing depositional odor trails. There were significant spatiotemporal differences in clutch size variation, as well as significant spatial differences in egg geometric variation, except for the shape index. Generally, Harwood’s Francolins show a uniparental care strategy with eggs being exclusively incubated and hatched by females, and nidifugous chicks being predominantly attended by their mothers. The results showed how breeding success could be attributed to nest site selection, nesting behavior, and parental care.

Because mountaintop endemic bird species are prone to climate change globally due their ecological specialization, particularly in the biodiversity hotspot regions of the tropics, this thesis also investigated the effect of climate change on the current and future habitat suitability of Moorland Francolin in the summits of the Ethiopian highlands. An ensemble model of six selected algorithms was used to analyze the geographical distribution of the species. Accordingly, annual mean temperature was the governing bioclimatic variable for the distribution of the species in the alpine and subalpine habitats, and to a lesser extent, other temperature variables, including mean diurnal range, temperature seasonality, and temperature annual range contributed to the current and future suitable habitat predictions. As a result, the target species is predicted to be at high risk of extinction in its current alpine habitat in the context of climate change. The assessment showed that the species could enter the IUCN Red List Vulnerable category.

Therefore, insights into the spatiotemporal patterns of habitat use, nesting behavior, and breeding success can contribute to better conservation strategy plans in the future by reducing habitat loss and hunting pressure on Harwood’s Francolin. In addition, I explored how integrating occupancy and climate change effects can add valuable suggestions for conservation action of Moorland Francolin, sympatric biodiversity and its alpine habitats in heterogonous landscapes. Captive breeding may be a reasonable conservation option for this species. Collectively, the results show that habitat management, habitat restoration, or law enforcement through a socio-ecological approach are crucial actions for species-specific conservation in this biodiversity host region.

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Abbreviations

AH	Afrotropical Highlands biome
AOO	Area of occurrence
AZE	Alliance for Zero Extinction
CBD	Convention on Biological Diversity
CHELSA	Climatologies at high resolution for the earth’s land surface areas
CTW	*Combretum-Terminalia* woodland and wooded grasslands
DAF	Dry evergreen Afromontane forest and grassland complex
DSR	Daily nest survival rates
EOO	Extent of occurrence
GCCA	Guassa Community Conservation Area
GeoCAT	Geospatial Conservation Assessment Tool
HDI	Human disturbance index
IBAs	Important Bird and Biodiversity Areas
IUCN	International Union for Conservation of Nature
KBAs	Key Biodiversity Areas
MESS	Multivariate Environmental Similarity Surface
NDVI	Normalized Difference Vegetation Index
PAs	Protected areas
SDMs	Species distribution models
SG	Sudan-Guinea Savanna biome
SSPs	Shared Socioeconomic Pathways
UBNB	Upper Blue Nile Basin
UNDP	United Nations Development Programme
UNESCO	United Nations Educational, Scientific and Cultural Organization
VU	Vulnerable

Chapter 1

General Introduction

Many species are experiencing rapid declines across their geographical ranges in the Anthropocene. Because the global distribution of biodiversity is highly uneven (e.g., Hole et al., 2011; Mittermeier et al., 2011), broad-scale conservation approaches (also known as conservation networks) are prioritized at the regional and landscape scales are being prioritized to prevent or mitigate the impacts of human-induced environmental problems on biodiversity and ecosystems. The three major important conservation targets related to my PhD work are Biodiversity Hotspots (Myers et al., 2000; Mittermeier et al., 2004), Endemic Bird Areas (Stattersfield et al., 1998), and Key Biodiversity Areas (KBAs) (IUCN, 2016). The first two targets essentially comprise of the popularly known Important Bird and Biodiversity Areas in Africa (Fishpool and Evans, 2001; BirdLife International, 2004). The other conservation networks, also nested within the above approaches, are part of the UNESCO World Heritage Site. Therefore, continued international funding for conservation and research in these areas has resulted in effective interventions for some target species and their sympatric biodiversity.

1.1. Biodiversity Hotspots of Ethiopia

The global biodiversity hotspots are considered to be of high conservation priority due to high levels of endemism and habitat loss (Myers et al., 2000; Mittermeier et al., 2004). Most importantly, human activities are the key menacing factors to the terrestrial biodiversity hotspots on a global scale (Bowler et al., 2020). Currently, there are 36 hotspots of biodiversity in the world (Hrdina and Romportl, 2017; Habel et al., 2019). Africa boasts eight of the world's biodiversity hotspots, two of which include Ethiopia: the Eastern Afromontane and the Horn of Africa (Mittermeier et al., 2011; Habel et al., 2019). Within the Ethiopian border, the centers of endemism occur in the Ethiopian highlands (also known as the mesic Roof of Africa) and the arid Horn of Africa (Fashing et al., 2022). These highlands are divided into the western and eastern highlands, which are intriguingly separated by the Ethiopian sector of the East African Rift Valley (Friis et al., 2010). They contain most of the high-elevational land (above 3000 m), typically known as Afroalpine

(Chignell et al., 2019; Groos et al., 2021). The evolution of the Ethiopian highlands is the result of uplift and volcanic processes (Abbate et al., 2015). This geological history, topography, and climate creates heterogeneous habitats suitable for diverse species groups characterized by high endemism (Antonelli et al., 2018). Therefore, the country's high endemic flora and fauna species could be explained by topographic variation (also signifying climatic conditions) and geographical isolations. For this reason, the Eastern Afromontane Biodiversity Hotspot, which includes the Ethiopian Highlands, ranks fourth by owning a high number of endemic plant and vertebrate families and genera (Mittermeier et al., 2004). As such, the country has conducive circumstances for testing many research questions related to evolution, ecology and conservation of floral and faunal assemblages (Fashing et al., 2022).

1.2. Protected Areas in Ethiopia

An increasing number of protected areas are being designated around the world in response to ongoing multifaceted threats, primarily human-induced pressures (e.g., Palomo et al., 2014; UNEP-WCMC, 2018). Protected areas (hereafter PAs) play a critical role in the conservation and preservation of biodiversity, and they have a crucial impact on the well-being of indigenous and local people through employment, ecotourism ventures, traditional natural resource use rights, and associated ecosystem services. Meanwhile, the purpose of PAs changed from an 'island' approach, which often limits people living near the protected areas in planning and using natural resources (Ervin et al., 2010) to a holistic or integrative approach, which reinforces mutual benefits and coexistence between nature and people in the ever-changing environment (Ervin et al., 2010; Palomo et al., 2014). Therefore, the effective and sustainable conservation of biological diversity and its ecological processes in PAs is dependent on a socio-ecological approach (Palomo et al., 2014; Moranta et al., 2021). However, most of Africa's PAs are "paper parks," which means that they lack effective management and interventions to lessen the exiting pressures (Dudley and Stolton, 1999).

Currently, most of Ethiopia's relatively pristine wildlife habitats are located in PAs. The main PAs are national parks, sanctuaries, wildlife reserves and control-hunting areas. Most of these protected areas have been identified and recognized as Important Bird and

Biodiversity Areas (hereafter IBAs) (Tilahun et al., 1996; Fishpool and Evans, 2001). All of the country's bird species are distributed from the lowest deserts to the highest mountaintops (up to 4600 m) in protected areas, IBAs and other unprotected areas, all of which generally fall within three biomes: the Afrotropical Highlands (further subclassified into Afroalpine and Afromontane), the Sudan-Guinea Savanna and the Somali-Masai biomes (Fishpool and Evans, 2001). Among these biomes, the Somali-Masai biome harbors the largest biome-restricted species richness in Ethiopia, while most endemic species are restricted to the Ethiopian highlands (e.g., Fishpool and Evans, 2001; de Klerk et al., 2002), especially the mountaintop habitats, also known as alpine habitats (Töpfer and Gedeon, 2020). Among 39 Endemic Bird Areas in Africa, three are in Ethiopia, including the Jubba and Shabeelle valleys, the South Ethiopia highlands and the Central Ethiopia highlands (Stattersfield et al., 1998; Fishpool and Evans, 2001). The magnitude and origin of environmental threats can be regional or global, and thus the combination of site-based (IBAs) and broad-scale (biomes, Endemic Bird Areas and biodiversity hotspots) approaches is used to conserve birds and their habitats (Fishpool and Evans, 2001).

1.3. Conservation impacts of IBAs

IBAs are sites that are critical for the conservation of birds and biodiversity on account of an internationally agreed set of criteria (BirdLife International, 2004; Waliczky et al., 2019; Donald et al., 2019). To tackle the growing human pressures (BirdLife International, 2004), the number of IBAs established worldwide has continued to grow since the 1970s, with more than 13,000 sites currently recognized worldwide (Waliczky et al., 2019; Donald et al., 2019). As such, IBAs have global impacts on conservation policy and planning and are used in the comprehensive frameworks of the Convention on Biological Diversity (CBD), the Ramsar Convention, the Convention on Migratory Species, the European Union, and other institutions (Waliczky et al., 2019).

There are nearly 70 IBAs identified during the first inventory in Ethiopia, and most are located outside PAs, with the exception of national parks, wildlife and private reserves, and national forest priority areas (Tilahun et al., 1996; Fishpool and Evans, 2001). Two national parks, including the Simien Mountains National Park and the recently inscribed

Bale Mountains National Park, are part of the World Heritage Site; evidencing a high level of global importance for biodiversity conservation through the active participation of various stakeholders. Interestingly, the achievement for the scenically remarkable Bale Mountains National Park is the result of unwavering strategic conservation efforts by local and international organizations. Conservation efforts also enhance ecosystem services that are valuable for both habitat and human well-being. Both parks are home to several unique plant and animal species. Unlike most PAs in the country, these parks and the Guassa Community Conservation Area (hereafter GCCA) are the pristine isolated habitats of the endangered flagship species, the Ethiopian wolf (*Canis simensis*) (Tefera and Sillero-Zubiri, 2006). The local community, in collaboration with national and international organizations, has effectively established exemplary conservation efforts to protect the species and its Ericaceous belt (which also holds moorland) and the adjacent Sub-Afroalpine belt in the Ethiopian highlands. Human pressures on the plateau of these three IBAs principally have been comparatively controlled, which directly contributes to the replenishment of herbaceous plants, which is key to the survival of rodent species and by this means, the endangered Ethiopian wolves get abundant rodents for predation in the natural habitats (Ashenafi et al., 2012; UNDP, 2012; Atickem and Stenseth, 2022). As such, the role of flagship species is well illustrated here, by directly leading to the conservation of the entire system in both geographically isolated national parks and GCCA.

In the history of natural resource conservation and management in Ethiopia, the governance of GCCA by the indigenous people (i.e., indigenous land use system also known as Qero system) has resulted in a deep-rooted responsibility and accountability for over four centuries (UNDP, 2012). The indigenous people have managed and used *Festuca* grasses (e.g., *Festuca macrophyhlla*, in Amharic: Guassa) to produce fodder and to make thatch, wall construction, whips, ropes, hats, brooms (mure) and raincoats (gesa). After a long history of traditional natural resource management, the socialist government's (Derg) agrarian reform and villagization policies collapsed the Qero system in 1975 (Ashenafi and Leader-Williams, 2005). Nevertheless, the government and international organizations such as the Frankfurt Zoological Society funded by the European Union, the Ethiopian Wolf Conservation Programme and the Darwin Initiative revived the Qero system in 2003. Its proximity to Addis Ababa makes it convenient and accessible to conservation organizations, researchers, and visitors. Although GCCA covers a small area (approximately 111 km^2) (Ashenafi & Leader-Williams, 2005; Nigussie et al., 2019), it is a pristine Afroalpine habitat and continuous to support several unique bird and mammal species. Among the most fascinating bird species richness distributed across the IBAs and their surrounding areas (Ash and Atkins, 2009; Gedeon et al., 2023, this thesis sheds light on two distinctive ground-dwelling or landfowl species of the Ethiopian highlands: Harwood's Francolin (*Pternistis harwoodi*) and Moorland Francolin (*Scleroptila psilolaema*). The central highlands of Ethiopia (also including the Upper Blue Nile Basin) are home to both endemic bird species. Specifically, Harwood's Francolin is restricted to two unprotected IBAs: the Jema and Jara valleys (sometimes spelled Jemma and Jara valleys), and the Mid-Abbay (Blue Nile) river basin while Moorland Francolin exits in GCCA, the Ankober-Debresina escarpment, the Entoto Natural Park and escarpment and the eastern highlands (previously the South Ethiopia highlands) in the Bale Mountains National Park (Tilahun et al., 1996; Fishpool and Evans, 2001). The most recent updated bird species checklist of Ethiopia reveals that both species occupy human-shaped landscapes over large geographical areas (Gedeon et al., 2023). In particular, this work has identified for the first time additional locations of Moorland Francolin adjacent to or far from the PAs and IBAs (Chapter 5).

1.4. Taxonomy and phylogenetic relationships of francolins

In this thesis, the English and scientific names of pheasants and related species mostly follow Gill et al. (2024). The order Galliformes (megapodes, guans, guineafowls, New Word quails, and pheasants and allies) is largely ground-dwelling birds (Winkler et al., 2015; Kimball et al., 2021; Gill et al., 2024). The family Phasianidae (pheasants and allies) comprises 188 extant species belonging to 54 genera, distributed globally across most terrestrial habitats (Gill et al., 2024). Following the updated taxonomic and phylogenetic studies of galliform species, there are currently seven endemic genera in Africa: *Xenoperdix*, *Afropavo*, *Peliperdix*, *Campocolinus*, *Scleroptila*, *Margaroperdix,* and *Pternistis* (Gill et al., 2024).

To date, only three of the ten Ethiopian francolin species (Harwood's Francolin, Erckel's Francolin *Pternistis erckelii*, and Chestnut-naped Francolin *P. castaneicollis*) have been studied to some extent with respect to their ecology and conservation (e.g., Robertson et al., 1997; Töpfer et al., 2014; Abrha et al., 2017; Gedeon et al., 2017b; Abrha et al., 2018). In the last decade, there have been significant advances in the taxonomy and phylogenetic relationships of francolins and spurfowls in Africa (Mandiwana-Neudani et al., 2019a, b; Hunter et al. 2021; Hustler 2021). In particular, Moorland Francolin has received special taxonomic attention (Hunter et al., 2019). It was previously thought to consist of two subspecies confined to the Afroalpine habitats of Ethiopia, western Kenya, and eastern Uganda (Madge and McGowan, 2002). However, based on vocalizations and plumage, both subspecies have been assigned species rank (Hunter et al., 2019; Gill et al., 2024). Currently, the Moorland Francolin is considered an endemic to the Ethiopian highlands (Hunter et al., 2019). In contrast, the taxonomic status of Harwood's Francolin is undebated monotypic. It is morphologically distinct from other species in the so-called "Northern Vermiculated spurfowls" group (Mandiwana-Neudani et al. 2019a). My thesis focuses on both endemic species of the Afrotropical Highlands (including the Afroalpine and Afromontane) and Sudan-Guinea Savanna biomes of Ethiopia. For ease of reference, I will use the original name "Harwood's Francolin" instead of "Harwood's Spurfowl", regardless of name inconsistencies in the literature. Indeed, all spurfowl species belonging to the genus *Pternistis* occur exclusively in Africa due to their distinctive morpho-vocalization characters (Mandiwana-Neudani et al. 2019a), yet there are still debating issues and gaps that require robust inference to understand the species diversity, delimitation and geographical distribution of the Galliformes in Africa (Hunter et al., 2021; Hustler, 2021; Crowe et al., 2022).

Following the most recent phylogenetic analyses, Harwood's Francolin is sister to Clapperton's Francolin (*Pternistis clappertoni clappertoni* and *P. c. sharpii*) (Mandiwana-Neudani et al., 2019a). Indeed, I have found that both species have very similar advertisement calls and morphologies compared to other francolin species. The only contiguous ranges for both species are recorded between Sayint and Simada districts south of the Lake Tana. An earlier report also supports this field observation (Urban et al., 1986). The closest relative of Moorland Francolin is Grey-winged Francolin (*Scleroptila* *afra)* of the Lesotho and South Africa, whereas the recently elevated Elgon Francolin (*S. elgonensis*) from Afroalpine habitats of Uganda and Kenya is closely related to both Finsch's Francolin (*S. finschi*) of central Africa and to Whyte's Francolin (*S. whytei*) of southeastern Democratic Republic of Congo to northern Zambia and northern Malawi (Mandiwana-Neudani et al., 2019b).

1.5. Morphology of francolins

Morphologically, many phasianids are sexually dimorphic (both sexual dimorphism and sexual dichromatism); typically, males have bright plumage and other features essential for elaborate ornamentation (del Hoyo et al., 1994; Winkler et al., 2015). Because these species are ground dwelling species, they have relatively stout legs, feet, and short and robust bills adapted for scratching the ground for feeding and nesting (Urban et al., 1986; del Hoyo et al., 1994; Winkler et al., 2015). The distinctive feature of most species is that adults have single or double spurs (del Hoyo et al., 1994; Winkler et al., 2015), as in the two Ethiopian francolins (Figure 1.1).

In living birds, melanins (black, brown, and pale yellow colors) and carotenoids (bright red, orange, and yellow colors) are the two main types of pigments derived from a variety of food sources, with the former being synthesized by animals and the latter by plants (Bostwick, 2016; Price-Waldman and Stoddard, 2021). Despite slight phenotypic differences between adult males and females of Harwood's Francolin, sexes are very similar (Redman et al., 2011), meaning that the species is sexually monochromatic and monomorphic. In support of this, my field measurements showed that adult females are slightly paler and adult males are slightly larger, with a mean body mass of 483.18 g (n = 29) for adult males and 391.95 g (n = 22) for adult females (unpublished report). Both adults have a red lower mandible and a black upper mandible with red at the base. However, the black upper mandible lacks red at the tip (Figure 1.1A), in contrast to a previous report (Urban et al., 1986). The color of the bare skin around the eyes, forehead, and legs (or tarsi) is red and brighter during the breeding season for both sexes. This could be due to the availability of diverse food during the rainy season, mainly plants responsible for carotenoid synthesis. Adult males have two horny spurs; the lower one is slightly longer, while females lack it completely. The lower spur of subadult males is considerably longer, suggesting the clue for aging in this species. In contrast, McGowan (1994) reported that females have much reduced spurs and the presence of 1-2 spurs only in males as mentioned by Mandiwana-Neudani et al. (2019a) seems imprecise. The spurs of this species grow in a gradual manner, with a lower one being visible in the immature stage. Interestingly, indigenous people identify the sexes of adults based on slight differences of body size and spur traits.

Figure 1.1. An adult male Harwood's Francolin (*Pternistis harwoodi*) has two spurs (top) and an adult male Moorland Francolin (*Scleroptila psilolaema*) has a single spur (bottom) and nostrils. Both species have brown eyes, slightly curved bills, and graduated tails. A complete photo of a female Moorland Francolin can be found in Chapter 2.

Moorland Francolin has similar plumage and coloration between adult males and females, but as with Harwood's Francolin, adult males are slightly larger than adult females (male = 417.11 g; n = 18 and female = 359.27 g, n = 11) (unpublished report). The species raises its crest feathers during communication (courtship and fear displays). The bill is blackish brown and pale at the base, and the tarsi are pale yellow to dull brown in adults. In addition, the species has nearly circular, light to dark brown ear patches (i.e., auricular feathers) covering the ear opening. This type of plumage has not been previously described in the literature. The species also has a finely spotted buff throat and the ventral side is marked with variable chestnut spots (Figure 1.1B).

1.6. Ecology of francolins: threats and ethno-ornithological relationship

Most, if not all, Galliformes are sedentary and have limited long flight, with the exception of quail and partridge (McGowan, 1994; Hosner et al., 2017). Although flight is the dominant tactic for escaping from predators in most birds (van den Hout et al., 2010), most pheasants prefer to escape by running and, to a lesser extent, fast and short flight when approached by predators (Urban et al., 1986; McGowan, 1994; Mandiwana-Neudani et al., 2019a, b). Ethiopian francolins and guineafowls live in groups. For example, Harwood's Francolins typically move in groups of 2 to 8 individuals (Abrha and Nigus, 2017), and Moorland Francolins show a similar pattern (Chapter 1).

Harwood’s Francolin demonstrates overlapping niches with Erckel's Francolin and Helmeted Guineafowl (*Numida m. meleagris*) in the central highlands of Ethiopia (Urban et al., 1986; Abrha et al., 2017; Abrha et al., 2018). Evidence from the Jema and Jara valleys IBAs shows distinct diurnal activity patterns of the species, which exhibits bimodality with peaks in the early morning and late in the afternoon (Abrha et al., 2018). Moorland Francolin shares its habitat with Erckel's Francolin in traditionally protected GCCA, officially protected and unprotected IBAs in the western highlands of Ethiopia, while its habitat overlaps with Chestnut-naped Francolin in Bale Mountains National Park in the eastern highlands (pers. obs.). Like other galliform species (Urban et al., 1986; del Hoyo et al., 1994), francolins in Ethiopia feed on seeds, tubers, insects, and litter-dwelling preys (worms) and occupy predominantly scrubland and bushland featured by grassy and steep slopes (McGowan, 1994; Ash and Atkins, 2009; Abrha and Nigus, 2017).

Archaeological evidence reveals that the oldest high-elevational human settlement in the world's history is recorded from the biodiversity hotspot region in Ethiopia (Ossendorf et al., 2019). The hunter-gatherers deliberately occupied the rock shelters of the highlands in the Afroalpine and Dry evergreen Afromontane forest and grassland complex (DAF) of

Ethiopia, where people relied on hunting wildlife and firewood collection (mainly charcoal) to survive in the cold conditions of the Late Pleistocene (Arthur et al., 2019; Ossendorf et al., 2019; Hensel et al., 2021; Bodin et al., 2024). Sporadic evidence from the contemporary paleoenvironmental data, particularly from the Afrotropical Highlands biome, shows that humans hunted ratites such as ostriches (Ossendorf et al., 2019) and cassowaries (Gaffney et al., 2021) and, remarkably, a volant galliform species (brushturkeys) (Gaffney et al., 2021). This therefore proves how humans have a long-standing relationship with Afroalpine and Afromontane bird species, other wildlife and their habitats in the Afrotropics. For example, the relationship between humans and Galliformes is also linked to food and cultural values (religious beliefs, paintings, writings, sports, etc.) (del Hoyo et al., 1994); this is likely to lead to overexploitation, threatening several species with extinction.

Ethno-ornithological relationship can be viewed as a multifaceted relationship between people, birds, and their ecosystems (Tidemann and Gosler, 2010). It focuses on people's indigenous knowledge of birds in terms of culture and spirit. People's perception of birds can be either positive or negative in terms of their values (Talukdar and Gupta, 2018). The positive knowledge and experience of local people towards wildlife is important for a successful conservation scenario (Brandon 1995; Talukdar and Gupta, 2018). In Ethiopia, people do not usually hunt birds for food because it is associated with religious beliefs (Ash and Gullick, 1989). Unfortunately, all pheasants are hunted in Ethiopia, including francolins, partridges, and guineafowls. For example, local people selectively hunt Harwood’s Francolin (locally known as Soren or Sorit: in Amharic and Sorene: in Afan Oromo, meaning red francolin) for household consumption and medicinal purposes (Robertson et al., 1997; Abrha et al., 2017). Consequently, the main conservation threats to francolins in the country are hunting and habitat loss (Töpfer et al., 2014; Abrha et al., 2017; Gedeon et al., 2017b). Most of the world's galliform species face related disturbances, mainly caused by human activities (Keane et al., 2005; McGowan et al., 2012).

Moorland Francolin occurs in both major blocks of the Ethiopian highlands (Ash and Atkins, 2009; Gedeon et al., 2017a; Gedeon et al., 2023). The population size, threat factors, and ecological niche of the species in different habitats remains elusive. Even then, little or nothing is known about the determinant factors, including biotic (vegetation traits and predators) and abiotic (climate, topography, etc.) attributes for such patterns. Hunting pressure on Erckel's Francolin is comparatively much more pronounced because of its larger size and the different perceptions of local people towards francolins. The vernacular name of Moorland Francolin is ‘Gagirt’ means ‘Satan’s spirit’ and it is also an insult used by the local people in North Shewa. Because the species is cryptic and shy, local people may approach it unknowingly and the bird may suddenly flee, producing a ghastly flapping sound. Consequently, the local people have two different attitudes towards Moorland Francolin, which is either perceived as a bad spirit or as being too small to catch, making it unattractive game prey (pers. obs.). For this reason, the species seems to have benefited from the perception of the indigenous people in some localities, especially in GCCA.

The menacing factors to Moorland Francolin are the loss of moorland and associated grassland habitats, and in this way, it is considered as Near Threatened (BirdLife International, 2024). The habitat use of the species is reported for the first time in this thesis (Chapter 2). Unlike Moorland Francolin, Harwood’s Francolin is only confined to the western highlands and has been comparatively well studied, regularly from the Jema and Jara valleys in Ethiopia (Robertson et al., 1997; Abrha and Nigus, 2017; Abrha et al., 2018). Herein, huge geographical ranges of both species are identified and species-habitat associations are determined over space and time (Chapters 3 and 3).

1.7. Breeding biology of pheasants

Understanding the breeding biology of avian species helps to produce successful conservation measures. At global level, knowledge of the breeding biology of avian species is not well known, particularly for tropical species (Xiao et al., 2017; Fierro-Calderón et al., 2021). In birds, nest site selection is the most important trait and is determined by nest material availability, condition of microhabitat, predation, and food availability (Hansell, 2000).

Compared to the sophisticated displays of males of several galliform species (Lovette, 2016), some male pheasant species, including francolins, lack exaggerated displays, but still rely on vocalization to attract females during the breeding season. For example, male

Harwood's Francolins mounted up commonly on stones and rocks, and sporadically on short snags, to produce territorial calls by pointing their heads upward (skyward), while females remained shy, cryptic, and crouched in their nests during the breeding season. This is essentially a dawn song in this species. Males also produce very distinctive low-pitched calls, especially during quiescence in the breeding season. This behavioral activity is frequently recorded between late morning and early afternoon (Abrha et al., 2018). By considering the timing and natural conditions, both francolin species respond to acoustic playback, making them easy to detect in low population densities and fragmented habitats (Chapters 2 and 3).

Bird nests are remarkably diverse in material composition and shape, and can be broadly classified into ground and tree (aerial) nests. The former include scrapes, domes, burrows, and mounds, while the latter include cups, globulars, and cavities, with platforms and other nests classified into both (Winkler, 2016). Birds build nests in ways that reduce the risk of predation through nest-site selection (considering factors like inaccessibility and shelter), as well as through camouflage and strategies to prevent overheating, all contributing to successful breeding (Mainwaring et al., 2014; Winkler, 2016). Nest-building behavior is critical to breeding success in many bird species (Mainwaring et al., 2014; Perez et al., 2023). Most, if not all, galliform species select nest sites on the ground to build scrape, burrow, and mound nests (e.g., Urban et al., 1986, del Hoyo et al., 1994, Madge and McGowan, 2002, Harris et al., 2014). On the other hand, some pheasants like tragopans (McGowan, 1994, Madge and McGowan, 2002) and guans (del Hoyo, 1994) are known to nest in trees. As with most bird species (Winkler, 2016), the breeding season of pheasants coincides with the rainy season when food is abundant (McGowan, 1994). Scarps in pheasants are used only for egg laying, incubation and hatching stages.

The breeding biology of many phasianids is characterized by the following four mutually inclusive life-history traits. 1) Reproductive skewness (Lislevand et al., 2009), where the mating system in many of these species is polygynous (Winkler et al., 2015), indicating reproduction dominated by a few adults in the population. Even though social monogamy is a typical mating system in most extant birds (Alcock, 2016; Gowaty, 2018), polygamous or promiscuous mating systems are assumed to occur disproportionately in galliform species (McGowan, 1994). 2) Low levels of cooperative breeding (Cockburn, 2006, Lislevand et al., 2009, Davies et al., 2012) or lack of alloparental care (Riedman, 1982; Ben Mocha et al., 2023). In other words, other than the parents, other individuals (i.e., conspecifics) do not provide care for the chicks. Cooperative breeding is reported in less than three percent of the world's bird species (Ligon, 2004). In general, the modes of parental care in birds are the use of geothermal heat in mound builders, brood parasitism, uniparental care (female-only care and male-only care), biparental care, and cooperative breeding (Cockburn, 2006). 3) Uniparental care (Cockburn, 2006). In most cases, only female pheasants are responsible for incubating and hatching the eggs (McGowan, 1994; Cockburn, 2006). 4) Precocial chicks (Cockburn, 2006), in which nidifugous chicks have considerably developed down at hatching and leave the nest immediately following their mothers to feed independently (McGowan, 1994; Hansell, 2000; Winkler et al., 2015).

In this thesis, I present the first study of the breeding biology of Harwood’s Francolins in the Sudan-Guinea Savanna and the Afrotropical Highlands biomes of the Upper Blue Nile Basin in Ethiopia (Chapter 4). The chapter details how the species successfully breeds in the context of prevalent stressors, such as human disturbances (including hunting), predation (natural), and associated threats.

1.8. Endemic birds and climate change in Ethiopia

Because the effect of future climate on mountaintop endemic species (insects: Rödder et al., 2021; McCain and Garfinke, 2021; amphibians: Cordier et al., 2020; reptiles: Biber et al., 2023; birds: Hoffmann et al., 2020; plants: Costion et al., 2015) and their habitats (Mata-Guel et al., 2023) in the tropics gets alarming concerns in the Anthropocene, this study also assesses on how Moorland Francolin persists in the ongoing climate change in the summits of the Ethiopian highlands.

In Ethiopia, limited species-level evidence shows that range-restricted birds are facing serious challenges due to habitat loss and climate change in the eastern Rift Valley. Endemic species of the Somali-Masai biome are particularly vulnerable. For instance, two endemic species in southern Ethiopia, Stresemann's Bushcrow (*Zavattariornis stresemanni*) and White-tailed Swallow (*Hirundo megaensis*), are predicted to vanish within the next half century due to climate change (Bladon et al., 2021). The endemic Black-fronted Francolin (*Pternistis atrifrons*) is on the brink of extinction from habitat loss, exacerbated by climate change, making it the most endangered galliform in Africa (Gedeon et al., 2017b; Gedeon et al., 2023). Additionally, the Liben Lark (*Heteromirafra archeri*), specialized to Liben and Jijiga rangelands, faces extinction mainly from grazing, bush encroachment, and agriculture (Spottiswoode et al., 2009; Mahamued et al., 2022). Overall, biodiversity and habitats in Ethiopia are threatened by climate change and other factors (Fashing et al., 2022). Conservation networks in Sub-Saharan Africa aim to maintain suitable climatic conditions despite future changes (Hole et al., 2011). However, there is insufficient species-level evidence for most mountaintop tropical birds regarding current and future climate change, necessitating urgent conservation assessments (Campos-Cerqueira et al., 2017). Understanding the impact of climate change on both francolins (Chapters 1 and 2) will enhance conservation efforts. To this end, model averaging (ensemble modeling) and Multivariate Environmental Similarity Surface (MESS) were employed to analyze suitable habitats and model uncertainties for Moorland Francolin (Chapter 5).

1.9. Aims and Scope

This thesis comprises studies of two endemic francolin species of the Ethiopian highlands. These studies aim to scrutinize occupancy (habitat use), breeding biology, and climate change impacts on francolin species to inform sound conservation measures in the Ethiopia highlands. In the second and third chapters, static and dynamic occupancy models (MacKenzie et al., 2018) were used to determine the associations between the target species and their habitats in Ethiopia. Here, I applied two different modeling approaches due to the nature of the data (i.e., response variable) collected from the field. The third chapter of this thesis highlights the nesting behavior, egg biometrics, and breeding biology of Harwood's Francolins in the Upper Blue Nile Basin (UBNB) of Ethiopia (Figure 1.2). The fourth chapter focuses on climate change effect on Moorland Francolin.

Specifically, the first objective focused on the occupancy of Moorland Francolin in pristine and human-shaped landscapes of the central highlands of Ethiopia. I collected presence/absence (popularly, detection/non-detection) data using camera traps in the Afroalpine biome. A single-season (static) occupancy model was used to model occupancy and detection probabilities while accounting for imperfect detection

(MacKenzie et al., 2002). Accordingly, I tested hypotheses derived from the stochastic biological and sampling processes to predict the occupancy and detectability of poorly known Moorland Francolins.

The second objective was to determine the dynamic (multi-season) occupancy modeling (MacKenzie et al., 2003) of Harwood's Francolin. I conducted both direct observation and playback techniques to collect detection/non-detection data in UBNB. Because the cryptic species went undetected, particularly in low-density populations and disturbed habitats - a potential source of false-negative detection - a combined approach is worthwhile to make robust inferences about true occupancy, detection, and dynamic parameters (colonization and extinction). Therefore, the influence of habitat covariates on these parameters was determined. The combination of multiple field methods produces overarching datasets and this helps fundamental inference for the conservation purpose of this threatened species (Chapter 3).

The third objective emphasized understanding the nesting behavior and breeding biology of Harwood's Francolins. This study pioneered the life history of the species, including reproductive, behavioral, and spatiotemporal variability of traits. Reproductive success is attributed to nest-site selection and parental nest building behavior in response to stressors in this species. The combination of direct field observations and camera trap data shapes also contributed to an understanding of how laying females select and build nests, incubate and hatch eggs, and care for nests and fledglings during the single breeding season (Chapter 4).

The fourth objective details the current and future habitat suitability of Moorland Francolin in the context of climate change and the determinants of such spatial distribution patterns. Due to model uncertainties, the results are obtained from model averaging; an ensemble-based model of individual competing models (Chapter 5).

I provide species-specific conservation approaches for both cryptic francolin species in Ethiopia (Figure 1.2).

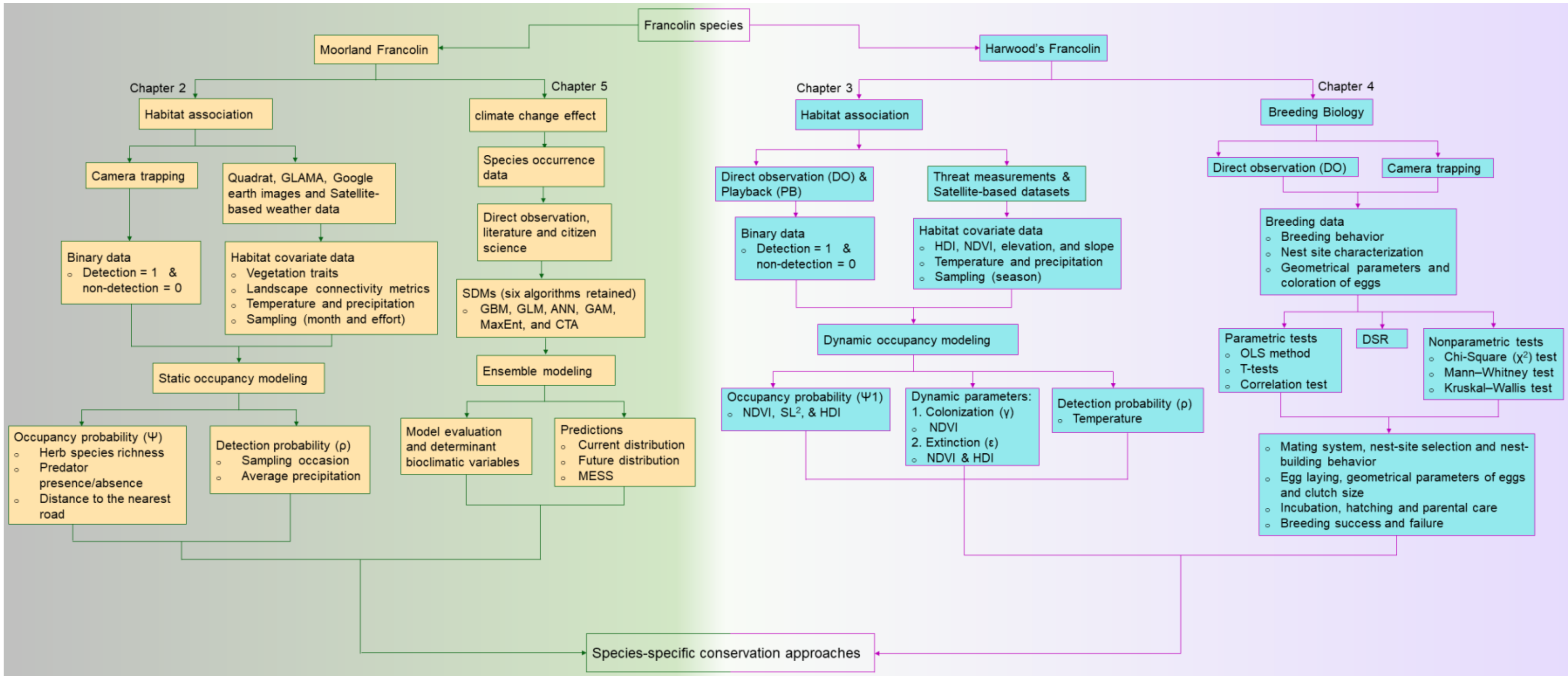

Figure 1.2. Thematic structure of the thesis.

Chapter 2

Occupancy of the Ethiopian endemic Moorland Francolin in pristine and degraded Afroalpine biome using a camera trap approach

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2.1. Abstract

Occupancy modeling is an essential tool for understanding species-habitat associations, thereby helping to plan the conservation of rare and threatened wildlife species. The conservation status and ecology of several avian species, particularly ground-dwelling birds, are poorly known in Ethiopia. We used camera-trap based occupancy modeling to investigate habitat covariate influence on occupancy (Ψ) and detection probability (ρ) estimates of Moorland Francolins *Scleroptila psilolaema* from spatially replicated surveys across both relatively pristine and disturbed landscapes in the Afroalpine biome of Ethiopia. Model-averaged estimate of $\hat{\psi}$ across all sites was 0.76 (SD = 0.28) and $\hat{\rho}$ was 0.77 (SD = 0.13) in pristine landscape. The $\hat{\psi}$ of the species in the disturbed landscape was 0.56 (SD = 0.19) and $\hat{\rho}$ was 0.48 (SD = 0.06). As hypothesized, based on our model-averaged beta coefficient estimates (β_{mean} ± SE), predators significantly negatively influenced the occupancy of Moorland Francolins in pristine habitat. We also found a significant positive association of occupancy with herb species richness. Contrary to our prediction, distance to road significantly negatively influence the occupancy of the species, suggesting that occupancy probability was highest in proximity to roadsides and trails in pristine habitat. There was no significant influence of habitat covariates on the occupancy of the species in the disturbed habitat. The most important covariates that significantly influence the detectability of the species in pristine habitat included sampling occasion and precipitation. The greater occupancy and detectability of this endemic species in pristine habitat could be linked with the particular conservation status and management of this biodiversity hotspot in the central highlands of Ethiopia. Our results suggest that strict legal enforcement is required sustainably to preserve Moorland Francolins and the ecological integrity of the entire Afroalpine biome. We recommend using camera traps in order to develop realistic and effective conservation and management strategies for rare, sensitive, cryptic, and ground-dwelling animals in the region.

Keywords: Afroalpine biome, camera trap, endemic, Moorland Francolin, occupancy, conservation

2.2. Introduction

Among the 34 Earth's biodiversity hotspots, the Eastern Afromontane hotspot, including the Ethiopian Highlands, ranks fourth by a number of endemic plant and vertebrate families and genera (Mittermeier et al., 2004). Next to the Guinea-Congo Forests biome, the second-highest number of biome-confined bird species are found in the Afrotropical Highlands biome (BirdLife International, 2004). In Ethiopia, all bird species subsist in three biomes: the Afrotropical Highlands (including the Afroalpine and Afromontane), the Sudan-Guinea Savanna, and the Somali-Masai biomes (Fishpool and Evans, 2001; Gedeon, Zewdie, & Töpfer, 2017). The Afroalpine biome of Ethiopia consists of a complex mosaic of grassland, moorland, bushland, and other habitat types, which are unique in terms of species distinctiveness. This biome harbors a considerable endemic flora and fauna and is home to a number of range-restricted bird species (Ash & Atkins, 2009; Gedeon, Zewdie, & Töpfer, 2017; Töpfer & Gedeon, 2020), as well as to rodents (Ashenafi et al., 2012; Bryja et al., 2019; Razgour et al., 2021), and medium and large-sized mammals (Ashenafi & Leader-Williams, 2005).

Historically, the oldest records of human high-elevational occupation worldwide are from the Afroalpine biome (Ossendorf et al., 2019), but today human population growth (Reber et al., 2018) is the key threat to wildlife in the Afroalpine and Afromontane (Asefa et al., 2017; Ashenafi et al., 2012; Razgour et al., 2021). Agricultural practices, human-induced climate change and other threats synergistically affect both the biomes' flora (Asefa et al., 2020) and fauna (Asefa et al., 2017; Razgour et al., 2021; Rodrigues et al., 2021).

Like in other tropical countries, the distribution of vegetation in Ethiopia reflects the interplay among altitudinal variation as well as climatic and other abiotic factors (Friis et al., 2010). The combination of different habitat characteristics, species traits and their interactions define the occurrence, occupancy and abundance of wildlife populations and influence their distribution patterns and detectability (Guillera-Arroita, 2017; Devarajan et al., 2020).

Most native bird species of Afroalpine and Afromontane habitats of Ethiopia are poorly studied in terms of their abundance, distribution and threats (Ash & Atkins, 2009; Gedeon, Zewdie, & Töpfer, 2017). One of them is the Moorland Francolin *Scleroptila psilolaema*

(Figure 2.1), an endemic species of the Ethiopian highlands (Gill et al., 2023; BirdLife International, 2023), where it inhabits both Afroalpine and Afromontane habitats (Töpfer & Gedeon, 2020). Knowledge on its breeding biology, home range size, population abundance, occupancy (i.e., habitat use), and other ecological patterns is still scant. Previous distributional data showed Moorland Francolins to occur in the eastern and western highlands (Ash & Atkins, 2009; Gedeon, Zewdie, & Töpfer, 2017). It is classified as Near Threatened due to the ever-increasing loss of moorland and grassland habitats (BirdLife International, 2023), but its population size and habitat association along its geographical range are insufficiently known.

Figure 2.1. An adult female Moorland Francolin *Scleroptila psilolaema* in the Afroalpine biome, Ethiopia. The feather patterns and colors contribute crypsis through background matching in this species (photo credit: Kai Gedeon).

In biodiversity-rich Sub-Saharan African countries such as Ethiopia, little attention is paid to camera trap-based research (Cordier et al., 2022). To fill this knowledge gap, our sampling protocol for Moorland Francolins occupancy estimates relies on data obtained using camera traps. Although this approach may disturb wildlife and alter their behavior (Wearn & Glover-Kapfer, 2017; 2019; Caravaggi et al., 2020), it is cost-effective and non-invasive to study ecological patterns such as population size and distribution of animals. The centerpiece in most occupancy-based camera trap studies are frequently applied on mammal species (e.g., Burton et al., 2015; Niedballa et al., 2015; Kays et al., 2019; Cremonesi et al., 2021; Wevers et al., 2021; Cordier et al., 2022), yet some studies are conducted on ground-dwelling bird species, mainly pheasants (e.g., O'Brien & Kinnaird, 2008; Zou et al., 2019; Tanwar et al., 2021; Sharief et al., 2022). Most importantly, camera traps are particularly useful to study elusive, cryptic and rare species (Winarni et al., 2005; O'Brien & Kinnaird, 2008; Si et al., 2014; Sharief et al., 2022) and thus represent the most promising approach to investigate Moorland Francolin. Camera trapping is more efficient than other methods such as traditional distance sampling (Suwanrat et al., 2015; Wearn & Glover-Kapfer, 2019). Moreover, it can provide valuable information to implement sound conservation strategies (O'Brien & Kinnaird, 2008; Si et al., 2014; Wearn & Glover-Kapfer, 2017; Sharief et al., 2022).

We attempt to draw an inference of baseline data on the ecology of Moorland Francolins using an occupancy modeling framework. We used presence/absence (i.e., detection/non-detection) data to analyze two stochastic processes: occupancy and detection probability. Occupancy is a dichotomous state variable that accounts for imperfect detection to minimize unreliable inferences of species distribution and range (Tyre et al., 2003; Kéry et al., 2010; Guillera-Arroita & Lahoz-Mohort, 2012; Bailey et al., 2014; MacKenzie et al., 2018). Occupancy models estimate the probability of a species' presence in a fraction of landscape units (MacKenzie et al., 2002, 2018) and help to understand habitat use within a landscape. They are applied across several animal taxa for the implementation of successful conservation and management strategies (MacKenzie et al., 2018; Burton et al., 2015; Steenweg et al., 2017). The objective of this study was to gain insight into the habitat use of Moorland Francolins in its native range for the first time and to investigate the effect of habitat covariates on occupancy and detection probability from spatially replicated surveys.

2.3. Materials and Methods

2.3.1. Study area

This study was performed in two areas (Figure 2.2): Guassa Community Conservation Area (hereafter GCCA) and an area encompassing the Sululta plain, Entoto Natural Park, Ankober-Debresina escarpment and a few sites between them (hereafter collectively abbreviated SEA). The study areas are part of Ethiopia's central highlands in which several Important Bird and Biodiversity Areas (IBAs) are designated (Tilahun et al. 1996). These highland areas consist of top mountain massifs and volcanic cones (Friis et al., 2010). Most of our study sites (93%) were located in IBAs, including GCCA, Entoto Natural Park, Ankober-Debresina escarpment, and Sululta plain. The remaining sites were located outside these IBAs in Angolela Tera, Assagirt, Sheno and Mendida districts. However, both IBAs and non-IBAs sites in SEA are under serious anthropogenic threat: farming, livestock grazing, settlement, monocultural plantations and recreational activities. For instance, ENP has shifted its purpose from conservation implementation (Tilahun et al., 1996) to recreational area where mass tourism (Asefa 2018; Tesema & Berhan 2019) and monocultural plantations (Tadesse & Tafere, 2017; Bahru et al., 2021) strongly affect the landscape. Both the Sululta plain and the Ankober-Debresina escarpment are mainly influenced by livestock grazing, farming and settlement expansions. Except for the Sululta plain, the other areas are dominated by exotic *Eucalyptus* plantations and African juniper *Juniperus procera* (Esayas & Bekelle, 2011). Therefore, we distinguished between the two study areas based on their different levels of human disturbance, topography, floristic structure and composition, and conservation status, considering GCCA a relatively pristine and SEA a strongly human-modified area.

GCCA (Figures 2.2 and 2.3) covers 78 km^2 (Steger et al., 2020), yet the total land area sums up to 111 km^2 if the adjoining villages and other land use types are included (Ashenafi & Leader-Williams, 2005; Nigussie et al., 2019). This area shows critically important habitat features for many wildlife species (Steger et al., 2020) and comprises both the Ericaceous belt (3000 – 3200 m a.s.l) and the Afroalpine belt (above 3200 m a.s.l) (Friis et al., 2010). The area has been managed by the local community through a management model called the Qero system (Ashenafi & Leader-Williams, 2005; Ashenafi et al., 2012). Unlike other IBAs of the study areas, the Qero system, coupled with the conservation initiatives of Frankfurt Zoological Society, The Darwin Initiative, European Union, and Ethiopian Wolf Conservation Program have significantly sustained the ecological integrity of GCCA since 2003. In this area, the Ethiopan Wolf *Canis simensis* is the flagship species (Tefera & Sillero-zubiri, 2006), generating income through ecotourism which is partly plowed back for the conservation of the species itself (Eshete et al., 2015; Estifanos et al., 2018).

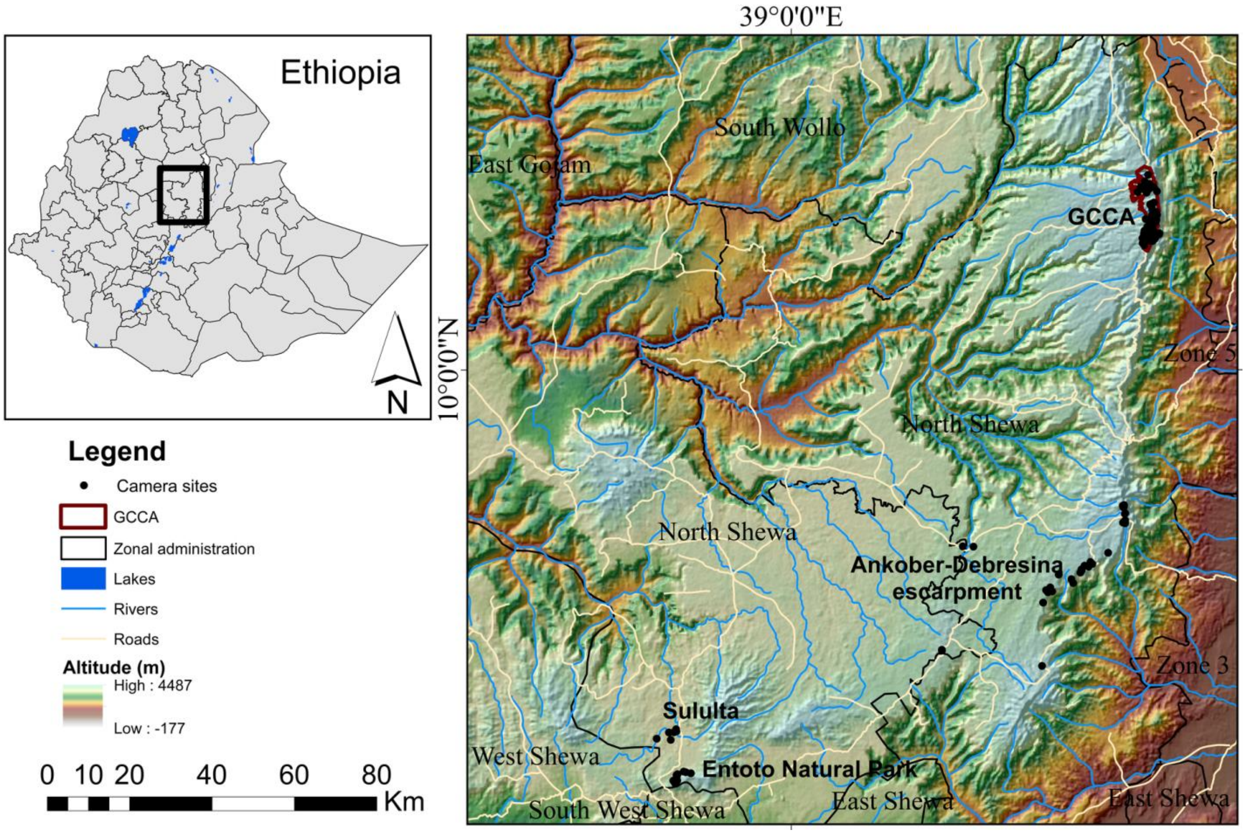

Figure 2.2. The two study areas (GCCA and SEA) and location of camera sites in the central highlands of Ethiopia. GCCA, Guassa Community Conservation Area. The southern areas (including Sululta, Entoto National Park, Ankober-Debresina escarpment, and other areas) form the second study area (SEA).

The second study area is SEA (Figures 2.2 and 2.3), forming part of the Afromontane with altitudes generally below 3000 m a.s.l. Very small patches of herbs, shrubs, scattered acacia trees, and exotic trees are common. Here, the Moorland Francolins persist in very small uncultivated and grassland patches of Afromontane habitats.

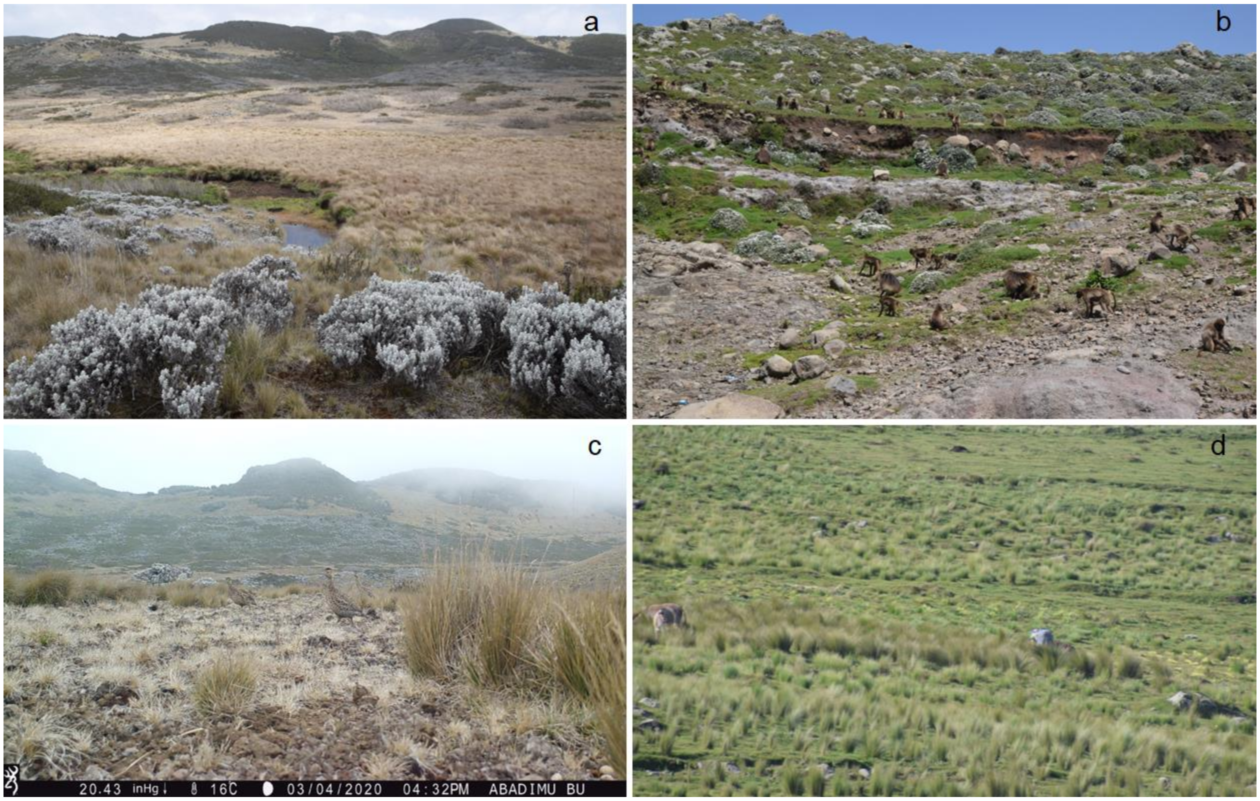

Figure 2.3. Afroalpine habitats in the central highlands of Ethiopia: GCCA with most habitat types (a) and the target species feeding in *Helichrysum-Festuca* grassland (c) and SEA with degraded rocky habitat (b) and grazing land (d).

These highland areas experience a bimodal rainfall pattern with main rain from June to September and smaller amount of rain from October to February (Mohammed et al., 2022). The distinctive habitat features of both of these areas are erratic climatic conditions and a very short dry season (ca. 2 months). The mean annual temperature of GCCA and SEA are 21.26 °C (± 0.95 SE) and 15.53 °C (± 0.55 SE), whereas the mean annual precipitation of GCCA and SEA were 2.65 mm (± 0.78 SD) and 2.69 mm (± 0.90 SD), respectively (Figure S1).

2.3.2. Sampling design

Site selection for this study was made randomly. Most sites were obtained through a distribution map from the IUCN, scientific literature, and citizen science data, whereas some sites were chosen without antecedent species records. Following the standard design procedure for allocating optimal sampling occasion (MacKenzie & Royle, 2005; MacKenzie et al., 2018), we initially attempted to conduct a total of 185 camera sites (or preferably sites) (*n* = 116 for GCCA and *n* = 69 for SEA) for a single-season design located in various habitat types. All camera sites were arranged in 39 line transects (*n* = 20 for GCCA and *n* = 19 for SEA), with an average transect length of 2.04 km (± 0.80 SD) across both study areas. In this study, we expected that the number of sites (*s*) and occasions (K) were sufficient to determine the stochastic processes. Then, the total survey is simply defined as $s \times K$ and the maximum survey occasion for each site was calculated by minimizing *s*, while taking a standard error of 0.05 for GCCA and 0.065 for SEA. Since both study areas are separated by approximately 150 km, independent camera trap data collections were conducted for 5 months for both areas. Along these geographical scales, specific habitat characteristics (i.e., covariates) predicted to influence the occupancy and detection rates of the target species were measured at each site (Table 2.1).

2.3.3. Camera trapping

In December 2019 and the first 3 weeks of January 2020, we made a pilot survey in both areas to assess the study species using camera traps and broadcast playback methods. A total of 20 cameras (Browning Trail Cameras and Bushnell Trophy Cam HD brands) were used for short-term deployments in this study. Since we had a small number of cameras, some adjoining habitats (see habitat covariates below) were simultaneously assessed and in both study areas cameras were deployed sequentially. Cameras were repositioned to other sites to cover the desired representative home range and to make the field survey more cost-effective. When small camera traps are available, repositioning to new sites is recommended to increase the spatial coverage of target species (Meek et al., 2014; Shannon et al., 2014; Si et al., 2014; Wearn & Glover-Kapfer, 2017).

Each camera trap was placed horizontally (i.e., camera alignment was perpendicular to the ground) within a 50 m radius (~ 0.8 ha) of plot or focal patch size to optimize detectability. Because some terrain settings were very difficult to conduct surveys, cameras were not fixed at the center of each plot instead they were placed approximately 10 – 30 m distance from the grid center, where freshly raked and possible feeding grounds were noticed. Single camera placement is employed to detect small-medium mammals and bird species (Ferreguetti et al., 2015; Lamelas-López & Salgado, 2021). The camera spacing in continuous habitats in GCCA was approximately 0.3 km (0.2-0.5 km), while in

SEA was approximately 0.5 km (0.3 – 0.8 km) to enhance detectability and to avoid spatial autocorrelation between camera traps. Though telemetry data collection was originally proposed to estimate the home range of the species which enables to estimate camera spacing, we assumed that the camera trapping space was sufficient and representative to study occupancy of this species based on available literature. If the average home range size of a target species is not known, it is recommended to infer spatial extent from congeneric or other related species (Niedballa et al., 2015). Mostly, camera trap spacing, based on home range, for pheasants ranges from 0.2 km (Zou et al., 2019) to 0.7 km (Suwanrat et al., 2015). Therefore, the camera spacing was higher than the home range diameter of the species, which was a similar approach as in other studies (Maffei & Noss, 2008; Niedballa et al., 2015). In our case, camera traps were unbaited but rather were providentially camouflaged with rocks, stones and Ericaceous heathlands of the study sites. Site selection for camera placement was randomly carried out across various habitats of both study areas, as was proposed by several other studies (e.g., Meek et al., 2014; Burton et al., 2015; Wearn & Glover-Kapfer, 2017; Tanwar et al., 2021; Cordier et al., 2022).

We placed camera traps on tree trunks, attached to thick coarser grasses (*Festuca* spp.) and shrubs, and on wooden stakes at approximately 30 – 60 cm above the ground, as this standard height is credible to trigger the motion sensor and it is reasonable to detect ground-dwelling bird species (Figure 2.3; Figure S2). Because some sites were in completely rocky areas, we also put cameras by arranging stacked stones that matched the background of the site. Most cameras had 16 GB memory and some cameras mounted on courser grasses and shrubs had 32 GB SanDisk memory card as they were easily triggered by the movement of vegetation during high wind velocity. However, to enhance good photographs and detectability, prudent vegetation removal was carried out in some sites to avoid false triggering mainly during windy conditions (Meek et al., 2014; Wearn & Glover-Kapfer, 2017). Our primary interest was to capture photos of the target species that can be easily pooled into detection/non-detection binary matrices. In most cases, the video function was discounted, yet some videos were collected from the field to understand the natural behavioral repertoire of the species and its interaction with other species (i.e., predators) in the habitats. Because both camera models had different setting options but similar functions, we set up cameras for the following typical important parameters: (1) camera traps were active for 24 h/day and programmed to capture 1 photo/trigger at 10 s intervals and some sites with more than one camera traps set to capture 20 s video/trigger, with subsequent videos delayed for 5 min; (2) the sensitivity of the infrared sensor was programmed to be medium or normal; and (3) the quality of photos were adjusted to be medium for both camera brands. The battery life of each camera was checked during data retrieval, storage, and repositioning of cameras. Extreme weather conditions (too hot or too cold) severely affected the sensitivity of sensors in our areas.

2.3.4. Habitat covariates

To include representative habitat types in GCCA, we adapted the habitat classifications of Ashenafi et al. (2012). The habitat types were Mima Mound, *Erica* Moorland, *Euryops-Alchemilla* shrubland, *Helichrysum-Festuca* grassland, and *Festuca* (Guassa) Grassland. In their classifications, swamp habitat which is typically characterized by woody vegetation (US definition) and reed swamp or forested fen (European definition) is now replaced by “peatland”. In this habitat, the wetland type is normally a moor surrounded by *Erica*, *Festuca* and other plant species and has permanent and ephemeral water fed by precipitation hence called “ombrothropic peatland”. Moreover, we identified and added montane forest to the classification as an important other habitat type for wildlife species in the area, though it was not included in the rodent-based study (Ashenafi et al., 2012). Because the sites in the SEA study area were human-dominated, the habitat types were homogenous and it was very hard to distinguish and classify in relation to vegetation patterns. Broadly, we categorized the habitats into *Eucalyptus*-*Juniperus* habitat and grazing lands. The latter class obviously incorporated agricultural lands. Overall, this area has been heavily transformed to *Eucalyptus* plantations to meet demand for wood products and improve the livelihoods of local communities (Tadesse & Tafere, 2017; Bahru et al., 2021).

At the sites, we collected 13 covariates derived from habitat features, landscape connectivity metrics, climatic factors, and sampling covariates which were predicted to influence the occupancy and detection probabilities of the target species. Occupancy was modeled as a function of site-specific covariates, including biotic factors (vegetation traits and predators) and landscape connectivity metrics, while detectability was modeled as a function of observational-specific covariates, including survey occasion (hereafter occasion) and climatic factors (precipitation and temperature). The occasion is defined as the total number of days for which each camera was active per site (Table 2.1).

Specific vegetation traits assumed to influence habitat use were collected from each site using different tools. Due to the occurrence of scattered trees within most sites (with the exception of montane forest adjoining to the moorland habitats and ENP) and complex landscapes varying with soil, climate, topographic, and other features, we used only two 20 × 20 m^2 randomly placed quadrats for tree species with DBH ≥ 10 cm in woody vegetation sites separated by at least 15 m between quadrat. Meanwhile, in each large quadrat, 5 × 5 m^2 for shrub and liana species with ≤ 10 cm were nested (Figure S2). Thus, the following vegetation traits were measured accordingly: (1) by placing five 1 × 1 m^2 quadrats (four in the corner and one in the center) in each nested quadrat; herb and fern species richness was identified and counted; (2) woody species richness and abundance were determined from the larger and nested plots; (3) woody species density (abundance of individual trees, shrubs and lianas/0.8 ha) was also estimated from each site; and (4) average tree canopy cover was estimated using GLAMA (Gap Light Analysis Mobile Application software) from vertically upward looking photos (approximately 8 photos/site) either directly collected in the field or retrieved photographs with a digital camera (Nikon D5300) from sampling sites (Gonsamo et al., 2011; Tichý, 2016).

Landscape connectivity metrics (landscape scale covariates), including elevation, distance to the nearest road (both paved and unpaved roads and trail with at least 1 m wide), distance to nearest water points and distance to nearest settlements were gauged either directly at the site using a handheld GPS and tape meter or indirectly using Google earth images. Nearest and accessible metrics to some sites were measured in the field. Average on-site ambient temperature and precipitation measurements would have been costly and very difficult to conduct in each site; instead, we obtained climatic data from NASA 2022 (https://power.larc.nasa.gov/data-access-viewer/) to understand species-habitat association.

Table 2.1. Habitat covariates predicted to affect occupancy and detection probabilities of Moorland Francolins in the central highlands of Ethiopia.

Covariate	Type of data	Measurement and scoring systems	Hypothesized relationship	References tested the effects
Occupancy covariates				
Fine-scale level covariates				
Herb species richness (Hsp)	Continuous	Number of herb species in each site	The species prefers herbaceous sites for feeding, breeding and concealment.	Jolli et al., 2012; Sukumal et al., 2017
Species richness (Sprich)[a]	Continuous	Plant species richness (i.e., alpha diversity) in each site	See Hsp	Atikah et al., 2021
Woody density (WD)	Continuous	Density of tree and shrub vegetation per 0.8 ha	The species is negatively influenced by birds of prey perched on trees and rocky areas.	Sukumal et al., 2017
Tree canopy cover (T_{caco})	Continuous	Tree canopy cover (CaCo) index estimated using mobile app or digital camera	Francolins avoid tree canopy cover due to the presence of human disturbance and birds of prey and other predators.	Sukumal et al., 2017; Chen et al., 2019; Atikah et al., 2021
Predator[b]	Binary	Presence of predator (1 = if predator/s was/were recorded and 0 otherwise).	Francolins are negatively influenced by predators.	Sukumal et al., 2017; Abrha et al., 2018
Landscape-scale covariates				
Elevation (Elev)	Continuous	The elevation of each site was measured in the field using GPS.	Elevation explains climate and vegetation variations that affect species survival and reproduction differently in both sites.	O'Brien & Kinnaird, 2008; Jolli et al., 2012; Pardo et al., 2017; Whitworth et al., 2018; Chen et al., 2019; Holzner et al., 2021; Wevers et al., 2021
Distance to roads (DR)[c]	Continuous	Distance from the center of each site to the nearest paved or unpaved roads	Proximity to road exposes the species to predators and other disturbances.	Whitworth et al., 2018; Dean et al., 2019; Semper-Pascual et al., 2020; Kroeger et al., 2022
Distance to settlements (DS)[c]	Continuous	Distance from the center of each site to the nearest settlement	Francolins avoid human settlements where several stressors, including human presence, grazing, mowing and others are common activities.	O'Brien & Kinnaird, 2008; Jolli et al., 2012; Nuttall et al., 2017; Pardo et al., 2017; Chen et al., 2019; Semper-Pascual et al., 2020
Distance to water point (DW)	Continuous	Distance from the center of each site to the nearest water point	Francolins use water points for food and cover in various habitats	Nuttall et al., 2017; Sukumal et al., 2017

		(wetlands, streams, madicolous, etc)		
Detection covariates				
Fine-scale level covariates				
Sampling month (M)[a]	Continuous	The survey month for both areas (SEA: Feb and Mar and GCCA: Apr-Jun) in 2020	Detection probability of Moorland Francolins varies between sampling months	Jolli et al., 2012; Holzner et al., 2021
Survey occasion (E)	Continuous	Number of days for which camera trap was active in each site per sampling occasion also called survey timing-how long?	The francolin detection increases with number of days of cameras deployed	Si et al., 2014; Semper-Pascual et al., 2020; Kays et al., 2019; Holzner et al., 2021; Wevers et al., 2021
Climate covariates				
Temperature (T)	Continuous	Temperature of each site while camera trap was active.	The francolin detection is influenced by temperature because francolins highly favor cold conditions and adapted to extreme low nocturnal temperature	Gedeon, Rödder, et al., 2017; Abrha et al., 2018
Precipitation (P)	Continuous	Precipitation of each site while camera trap was active.	Francolins have plenty of food resource to easily rake the wet ground and produce continuous calls for breeding during raining or wet season.	Gedeon, Rödder, et al., 2017; Abrha et al., 2018

Note: The first nine predictors are site-specific covariates, whereas the last four are observational-specific covariates.

[a] The spatiotemporal covariates are dropped due to high collinearity (Zuur et al., 2010; Dormann et al., 2013). This study selected herb species richness over total species richness (Sprich) in both study area. Herbaceous and shrubby vegetation were dominant in GCCA (> 80% ground vegetation cover) (Nigussie et al., 2019).

[b] Hunting was not considered as a threat for this species (See discussion).

[c] Human disturbance factors: grazing, mowing and farming are the major factors in the study sites (Ashenafi et al., 2012; Nigussie et al., 2019; Steger et al., 2020). *Festuca abyssinica and F. macrophyhlla* grasses (locally Guassa) intriguingly is valued for fodder for livestock (cut and carrying system and livestock grazing), thatching, wall building mix with mud, and help to make whip, rope, hat, broom (mure), and raincoats (gesa).

2.3.5. Data analysis

Single-season single species modeling framework was applied to understand the influence that habitat covariates have on occupancy and detectability while accounting for imperfect detection (Mackenzie et al., 2002, 2018). The detection history was derived from a sequence of species detection/non-detection dichotomous data (i.e., detection = 1 and non-detection = 0) that were pooled into occasions from consecutive camera-days for each site. For occupancy models, data collected by camera traps needs to be divided into sampling occasions (Sollmann, 2018). Such data treatment is important to maximize detectability, maintain spatiotemporal independence among occasions and thereby increases adequacy of model fit. Sensitive analysis was conducted without incorporating any covariates to evaluate the discrepancy of occupancy and detection estimates for different sampling intervals. Based on the input of the analysis, we chose the balance between high parameter estimates and small confidence intervals (see Table S1). Consequently, an occasion was defined as an interval of two camera days for both study areas.

Cameras were active for approximately six consecutive days ($n = 98$, 2-10 days) to obtain an average of three occasions per site at GCCA area. Whereas cameras at SEA area were active for approximately eight consecutive days ($n = 48$, 4-12 days) to obtain an average of four occasions per site. Number of camera days varied depending on the probability of detection of the species in the two different areas. Such study duration is recommended for high detectable species (Mackenzie & Royle, 2005; Guillera-Arroita et al., 2010). To account occupancy model assumptions (MacKenzie et al., 2002, 2018), each site was surveyed between one to five repeated occasions ($K_{\text{max}} = 5$; $K_{average} = 2.95$) in GCCA from March to June 2020, while in SEA each site was surveyed two to six repeated occasions ($K_{\text{max}} = 6$; $K_{average} = 3.46$) from February to March 2020. The discrepancy in number of occasions per site was due to accessibility, logistical constraints, security, weather conditions, and technical problems. We had missed observations in some sites meaning that sampling was not conducted at site *i* during time *t* and hence a missed observation represented by hyphen (−) was filled instead in the complete detection history (h_i). This also included data from malfunctioned cameras and blank photos in some cameras.

We used PRESENCE program v.2.13.39 (Hines, 2006) to model occupancy and detection estimates. The parameters were estimated using logit link and a maximum likelihood approach in the program (MacKenzie et al et al., 2018). Occupancy probability (Ψ) was modeled as a logit-link function of fine-scale level and landscape-scale covariates. The structure of the model framework of the occupancy probability of a site (i) in association with the site-specific covariates is expressed as:

$$logit(\Psi_i) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ldots + \alpha_u X_{iu}\,, \tag{1}$$

Likewise, the detection probability (ρ) was modeled as a logit-link function of observation-specific covariates. The general logit equation derived from the probability of detecting a species at site i, during survey j in association with the covariates is:

$$logit(\rho_{ij}) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ldots + \beta_u X_{iu} + \beta_{u+1} y_{ij1} \ldots \beta_{u+v} y_{ijv}\,, \tag{2}$$

where $X_{i1} \ldots X_{iu}$ refers to site covariates associated with the probability of a site *i* being occupied and $y_{ij1} \ldots y_{ijv}$ refers to sample covariates.

All continuous covariates were normalized by z score conversion (mean = 0 and SD = 1) to help convergence of the maximum likelihood algorithm prior to analysis (Schielzeth, 2010). Such data transformation produces better model performance and interpretability (Gelman & Hill, 2007; Schielzeth, 2010). Since we had spatial data, collinearity was assessed using variance inflation factor (VIF). Covariates with highest VIF were dropped in the analysis and covariates at threshold level VIF < 5 and Spearman's correlation ($r_s < 0.7$) were retained (Zuur et al., 2010; Dormann et al., 2013). Of the strongly correlated covariates, we retained ecologically important covariates based on field evidence and existed literature to understand their influence on occupancy and detectability. With a total of 11 covariates, the global model was run, and subsequently competing models were constructed based on plausible additive covariates. The null model (ψ(.),ρ(.)) was also constructed to compare with the relative weight of other additive models which included one or more covariates.

Since the ratio of effective sample size to the number of parameters (n/k) was small, model selection procedures were carried out using Akaike's Information Criterion for small sample bias adjustment (AIC_c) from the competing candidate set of models (Burnham & Anderson, 2002), where the most supported models are top-ranked models with $\Delta AIC_c \leq 2.0$ (Burnham & Anderson, 2002). Summed model weights of each covariate from each model were also calculated to rank the relative importance of the covariates (Burnham & Anderson, 2002). Then, in order to retain ecologically meaningful covariates, models with $\Delta AIC_c \leq 4.0$ were selected to drive model average estimates of occupancy and detection probabilities (Burnham et al., 2011) (Tables 2.2 and 2.3). Competitive models were used to estimate Ψ and ρ and calculated parameter estimates, standard errors (SEs), and level of significance based on 95% CI (zero-overlapped method) for each covariate. Uninformative parameters (Arnold, 2010; Leroux, 2019) were also assessed in our model sets. Estimates of the slopes (i.e., β coefficients) for covariates were used to determine the magnitude of their influence on Ψ and ρ.

We used a parametric bootstrap goodness of fit (GOF) using 10,000 permutations to assess the adequacy of fit of the global model (i.e., the most parameterized model) and Pearson's Chi-square test (χ^2) and non-Bayesian p-value were implemented to check overdispersion ($\hat{c}$) (MacKenzie & Bailey, 2004). The degree of overdispersion parameter estimate ($\hat{c}$) or variance inflation factor was assessed using chi-square (GOF) statistic. It was calculated by dividing the observed test statistic by the average of simulated test statistics.

We computed the number of occasions (K) to enhance the odds of detecting Moorland Francolins in a site. We considered a set of four levels of confidence (ρ^*): 0.7, 0.8, 0.9 and 0.99 by assuming that the species detection probability is always less than one. The occasion (K) was calculated from the detection probability (ρ) of the model averaging to determine the true absence of the species from a site (Pellet & Schmidt, 2005; Sewell et al., 2010; McGrath et al., 2015).

$$K = \frac{\log(1-\rho*)}{\log(1-\rho)}, \tag{3}$$

where ρ is the calculated detection probability and ρ* is the target detection probability as mentioned above.

Both original and square-root transformed data were used sequentially for normality assumption using Shapiro–Wilk and homoscedasticity tests. Consequently, we used one-way ANOVA to compare mean differences in photos captured among sampling months in GCCA, and a post-hoc testing procedure using Bonferroni error adjustment was applied for multiple comparisons. We also used the Mann–Whitney *U*-test to compare mean differences in photos and parameter estimates across spatiotemporal. Similarly, this test was used for occupancy probability estimates comparison in relation to predator presence and absence. This data was analyzed in IBM SPSS statistics (version 20). A two-tailed hypothesis test with an alpha value of 5% was considered.

2.4. Results

2.4.1. Camera trapping in GCCA and SEA

The deployed camera traps yielded 610 and 361 trap nights in GCCA and SEA, respectively. We failed to collect data from 21 (GCCA) and SEA (18) sites mostly due to battery failure and system malfunctioning. We found a significant difference in average photos captured among sampling months in GCCA ($F_{2, 95} = 11.775$, $p < 0.001$). There was no significant difference in average photos captured between sampling months in SEA (Mann–Whitney *U*-test = 277.5, $n = 48$, $p = 0.893$). Pooling the data across both study areas, the average photos captured in GCCA was approximately four units higher in comparison to SEA (Mann–Whitney *U*-test = 1365, $n = 146$, $p < 0.001$) (Figure S3). Likewise, model-averaged estimates of occupancy probability ($\hat{\psi}$) and detection probability ($\hat{\rho}$) parameters were significantly higher in pristine habitat than in the disturbed landscape (Figure 2.4).

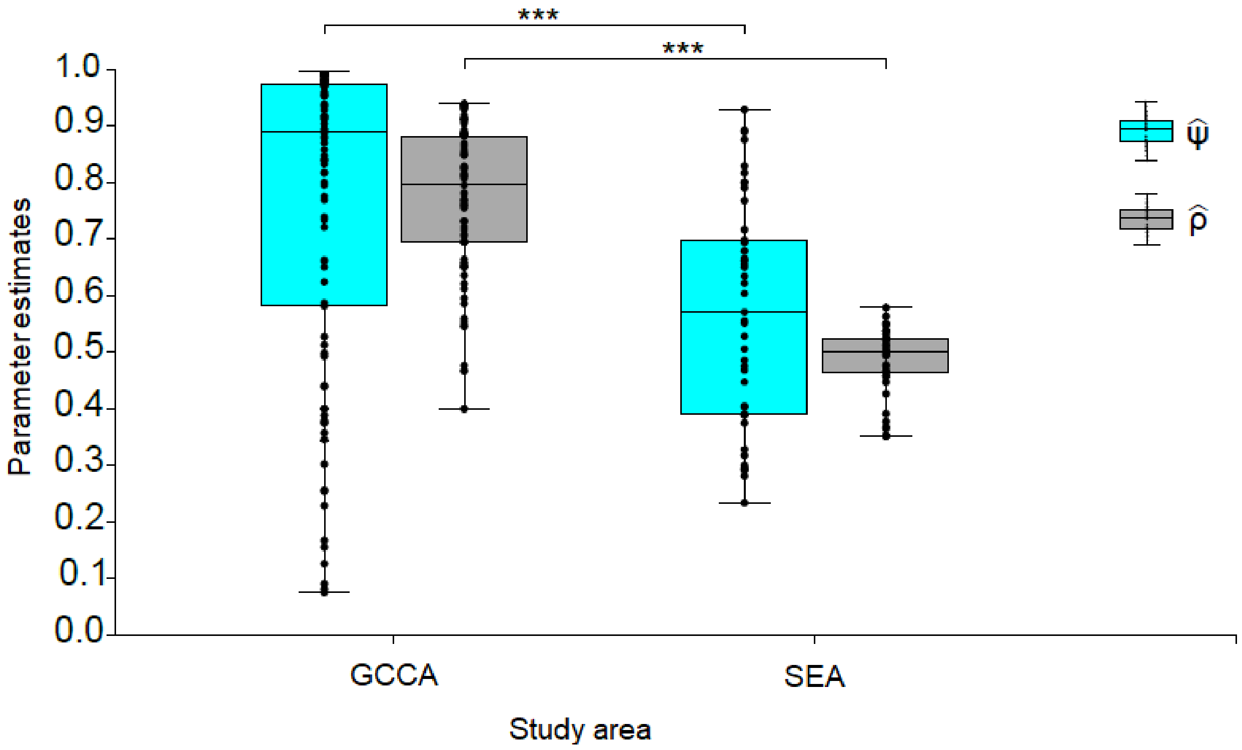

Figure 2.4. Parameter estimates (occupancy and detectability) of Moorland Francolin derived from model averaging. The asterisks (***) denote a strong statistically significant difference between parameter estimates in the study area at $p < 0.001$ level.

2.4.2. Habitat use modeling for traditionally managed habitat

We captured a total of 2632 photos (7–141 photos per site) from all sampling occasions in GCCA. Moorland Francolins were detected at 68 of 98 sites, which resulted in a naïve occupancy (proportion of sites that recorded at least one photograph on the whole camera sites) estimate of 0.69. In GCCA, at the habitat-specific level, the findings showed that the highest habitat use was obtained in Mima Mound, *Euryops-Alchemilla* shrubland, and *Helichrysum-Festuca* grassland. Conversely, the least was shown across the tree belt (i.e., montane forest and *Eucalyptus* plantations) (Figure S4).

The null model (ψ (.), ρ(.)) appeared to be the least important model to explain the stochastic processes (Table 2.2; Table S2). The Ψ for this model was 0.73 (SE = 0.05) with a 95% CI of 0.63–0.82 and ρ of 0.85 (SE = 0.03) with a 95% CI of 0.79–0.89. In GCCA, some evidence of breeding activity was observed from the camera traps, such as three juveniles being provisioned by both parents.

Table 2.2. Results of model selection for Moorland Francolins occupancy and detection probabilities in the central highlands of Ethiopia.

Model structure	AIC$_c$	ΔAIC$_c$	ω_i	*K*	-2l	$\hat{c}$
Traditionally protected landscape (GCCA)						
Ψ(Hsp + T$_{caco}$ + Pre + DR),p(E + T + P)	257.40	0.00	0.08	9	237.35	0.88
Ψ(Hsp + Pre + DR),p(E + T + P)	257.46	0.06	0.07	8	239.84	0.83
Ψ(Hsp + Pre + Elev + DR),p(E + T + P)	258.01	0.61	0.06	9	237.96	0.88
Ψ(WD + Hsp + Pre + DR),p(E + T + P)	258.07	0.67	0.05	9	238.02	0.80
Ψ(Hsp + T$_{caco}$ + Pre + DR),p(E + P)	258.16	0.76	0.05	8	240.54	0.81
Ψ(Hsp + Pre + Elev + DR),p(E + P)	258.39	0.99	0.05	8	240.77	0.83
Ψ(Hsp + Pre + DR),p(E + P)	258.44	1.04	0.05	7	243.20	0.84
Ψ(Hsp + T$_{caco}$ + Pre + Elev + DR),p(E + T + P)	258.47	1.07	0.04	10	235.94	0.82
Ψ(Hsp + Pre + Elev),p(E + T + P)	258.94	1.54	0.04	8	241.32	0.88
Ψ(WD + Hsp + Pre + DR),p(E + P)	258.96	1.56	0.03	8	241.34	0.83
Ψ(WD + Hsp + Pre + Elev + DR),p(E + T + P)	259.17	1.77	0.03	10	236.64	0.83
Ψ(WD + Hsp + T$_{caco}$ + Pre + DR),p(E + T + P)	259.18	1.78	0.03	10	236.65	0.80
Ψ(Hsp + T$_{caco}$ + Pre + DR + DW),p(E + T + P)	259.35	1.95	0.03	10	236.82	0.77
…						
Ψ(.),ρ(.)	298.28	40.88	0.00	2	294.15	1.09
Human-modified landscape (SEA)						
Ψ(Hsp+Tcaco+DR+DS),p(.)	182.77	0.00	0.07	6	168.72	0.99
Ψ(Hsp+DS),p(.)	183.32	0.55	0.06	4	174.39	1.14
Ψ(Tcaco+DS),p(.)	183.37	0.60	0.05	4	174.44	1.15
Ψ(Hsp+DR+DS),p(.)	183.62	0.85	0.05	5	172.19	0.97
Ψ(Hsp+Tcaco+DS),p(.)	183.75	0.98	0.04	5	172.32	1.15
Ψ(Tcaco+DS),p(E)	184.13	1.36	0.04	5	172.70	1.41
Ψ(Hsp+DS),p(T)	184.32	1.55	0.03	5	172.89	1.10
Ψ(Tcaco+DR+DS),p(.)	184.40	1.63	0.03	5	172.97	1.03
Ψ(Hsp+Tcaco+DR+DS),p(T)	184.45	1.68	0.03	7	167.65	0.95
Ψ(Hsp+DR+DS),p(T)	184.65	1.88	0.03	6	170.60	0.92
Ψ(Hsp+Tcaco+DR+DS),p(T)	184.68	1.91	0.03	7	167.88	1.04
Ψ(Tcaco),p(.)	184.76	1.99	0.03	3	178.21	1.15
…						
Ψ(.),ρ(.)	186.58	3.81	0.009	2	182.31	1.09

Note: Model rankings are based on the AIC*c* values; AIC*c* values compared to the top-ranked model (ΔAIC*c*); ΔAIC*c* scores ≤ 2.0 are the top-ranked model; model weight (ω*i*), and number of parameters (*K*), and -2l = -2LogeL. ĉ = overdispersion parameter to estimate lack of fit.

We constructed candidate sets without interactions between covariates to model Ψ and *p* in the order of parsimony models using ΔAIC$_c$. The bootstrapping procedure and χ^2 test revealed that the global model (ψ(WD + Hsp + T$_{caco}$ + Pre + Elev + DR + DS + DW),ρ(E + T + P)) lacks overdispersion ($\chi^2 = 35.95$; $p = 0.35$; $\hat{c} = 0.85$), showing independence among sites. Subsequently the combinations of occupancy and detection covariates of the top models were tested based on the lowest ΔAIC$_c$ values. The bootstrapped top 13 models also showed adequate model fit ($\hat{c} \sim 1$, Table 2.2). The summed weight of the top-ranked models ($\Delta AIC_c \leq 2.0$) was 0.61 and the most parsimonious model ($\psi(Hsp + T_{caco} + Pre + DR),\rho(E + T + P)$) had only 0.08 model weight, suggesting more plausible competing models existed to explain the occupancy and detection estimates (Table 2.2). We used model averaging to improve inference as the top model clearly showed model selection uncertainty (Symonds & Moussalli, 2011). Due to the ecological importance of individual covariates included in the top models, we discounted models with less than five ΔAIC_c to increase model weight (Richards, 2005) and we considered the top-ranked models with summed model weight of 0.95 (Symonds & Moussalli, 2011).

Model-averaged estimate of $\hat{\psi}$ across all sites was 0.76 (SD = 0.28) and $\hat{\rho}$ was 0.82 (SD = 0.05). The overall occupancy was 10% greater than the naïve occupancy estimates when detection probability is accounted for. As we hypothesized, predators negatively associated with the Ψ of Moorland Francolins in GCCA ($\beta_{mean} \pm SE = -2.12 \pm 0.84$; 95% CI: -3.76, -0.48) and the summed ω_i was 97% (Table 2.3). There was a higher average occupancy probability in the absence of predators in comparison to the presence of predators (Mann–Whitney *U*-test = 244.5, $n = 98$, $p < 0.001$) (Figure 2.5). These predators were avian and mammalian species. We observed Yellow-billed Kite *Milvus aegyptius*, Augur Buzzard *Buteo augur*, Verreaux's Eagle *Aquila verreauxii*, and Common Kestrel *Falco tinnunculus* to be common potential aerial predators of Moorland Francolins in the area. The most important potential mammalian predators were African Civet *Civettictis civetta*, Honey Badger *Mellivora capensis*, Black-backed Jackal *Canis mesomelas*, Serval *Leptailurus serval*, and White-tailed Mongoose *Ichneumia albicauda*.

We also found that herb species richness showed a significantly positive influence on the occupancy of the species based on model averaging estimates ($\beta_{mean} \pm SE = 1.40 \pm 0.68$, 95% CI: 0.07–2.74) and the summed ω_i was 97% (Table 2.3; Figure 2.6). Contrary to our prediction, distance to road was significantly negatively influenced the Ψ of the species and the model weight of the covariate was 78% ($\beta_{mean} \pm SE = -0.74 \pm 0.35$; 95% CI: -1.44, -0.05), suggesting that occupancy probability decreased as the distance to road increased in pristine habitat (Table 2.3; Figure 2.6).

As depicted in the top models, the ability to detect Moorland Francolins was modeled as a function of survey occasion, precipitation, and temperature with summed model weight of 0.95, 0.92, and 0.70, respectively. The most important covariates supported by our hypotheses, however, included sampling occasion (β_{mean} ± SE = 0.68 ± 0.23, 95% CI: 0.23–1.13) and precipitation (β_{mean} ± SE = 0.75 ± 0.36, 95% CI: 0.05–1.45), both of which significantly positively influenced the detectability of the species (Table 2.3; Figure 2.6). Although the detectability of the species was increasing with temperature, the beta coefficient estimate (β_{mean} ± SE = 0.40 ± 0.23; 95% CI: -0.04 to 0.84) overlapped zero which exhibited a positive association but non-significant difference with habitat use of the species.

Table 2.3. Summed model weight ($\Sigma\omega_i$) and influence of covariates calculated from model- averaged beta coefficient estimates and standard errors (β_{mean} ± SE).

Site	Covariate	$\Sigma\omega_i$	β_{mean} ± SE	95% CIs		*p*-Value
				Lower	Upper	
GCCA	Occupancy (Ψ)					
	Predator	0.97	-2.12 ± 0.84	-3.76	-0.48	0.011
	Herb species richness	0.97	1.40 ± 0.68	0.07	2.74	0.039
	Distance to road	0.78	-0.74 ± 0.35	-1.44	-0.05	0.034
	Tree canopy cover	0.46	-0.58 ± 0.37	-1.30	0.13	0.117
	Elevation	0.35	0.79 ± 0.60	-0.39	1.97	0.189
	Woody density	0.22	-0.46 ± 0.42	-1.29	0.37	0.277
	Distance to water	0.10	0.21 ± 0.41	-0.59	1.00	0.621
	Distance to settlement	0.06	0.36 ± 0.49	-0.60	1.33	0.472
	Detection (ρ)					
	Occasion	0.99	0.68 ± 0.23	0.23	1.13	0.003
	Precipitation	0.92	0.75 ± 0.36	0.05	1.45	0.037
	Temperature	0.70	0.40 ± 0.23	-0.04	0.84	0.082
SEA	Occupancy (Ψ)					
	Distance to settlement	0.76	0.74 ± 0.41	-0.07	1.55	0.071
	Tree canopy cover	0.72	-0.84 ± 0.48	-1.77	0.09	0.080
	Herb species richness	0.60	0.83 ± 0.48	-0.11	1.77	0.083
	Distance to road	0.37	0.62 ± 0.41	-0.18	1.42	0.131
	Predator	0.09	1.10 ± 1.23	-1.31	3.51	0.378
	Woody density	0.03	0.23 ± 0.44	-0.63	1.09	0.614
	Detection (ρ)					
	Occasion	0.26	0.39 ± 0.30	-0.19	0.98	0.195
	Temperature	0.23	0.34 ± 0.27	-0.19	0.86	0.210
	Precipitation	0.18	0.21 ± 0.21	-0.21	0.63	0.322

Note: Lower and upper 95% confidence intervals of the coefficients were constructed. Non-overlapping with zero (bold) shows significance values of β estimates.

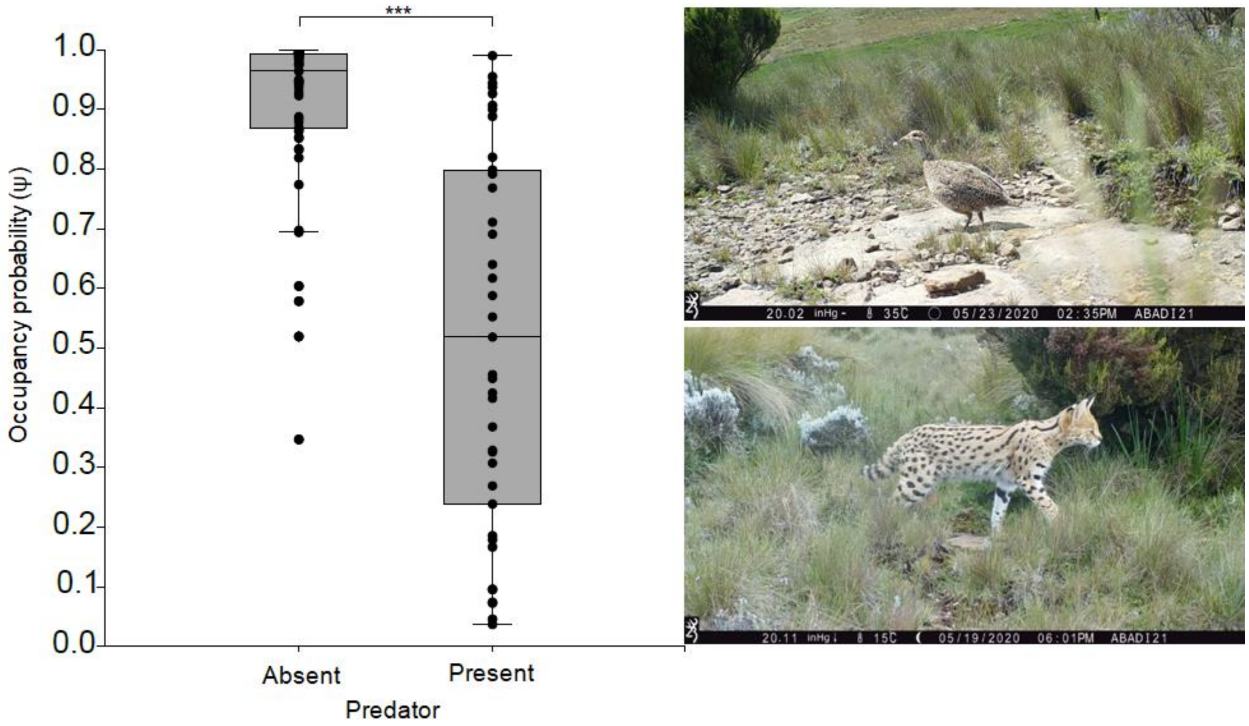

Figure 2.5. Occupancy probability of Moorland Francolin in association with predator presence/absence in GCCA. Cameras placed in woody plant species frequently had photos of predators like Serval *Leptailurus serval*. Error bars indicate standard errors of occupancy probability, *** $p < 0.001$.

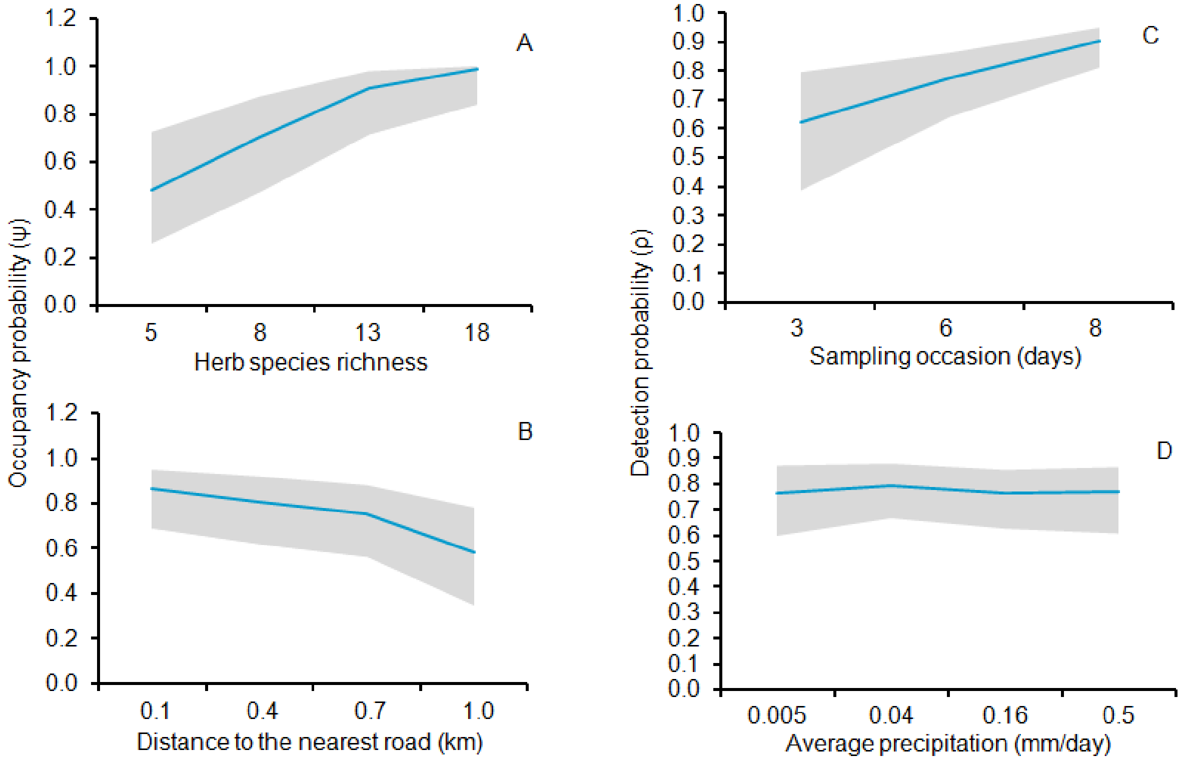

Figure 2.6. (A, B) Occupancy probability (ψ) of Moorland Francolin in association with herb species richness and distance to the nearest road (km) and (C, D) Detection probability (ρ) of the species in

association with sampling occasion and average precipitation (mm/day), respectively. The estimates for the parameters are created from the most parsimonious model that holds these covariates and the shaded area in each graph shows 95% confidence intervals.

2.4.3. Habitat use modeling for human-modified landscape

In the human-modified landscape, a total of 339 photos (2–29 photos per site) from 23 sites were trapped, yielding a naïve occupancy estimate of 0.48. The Ψ estimate without any covariate was 0.54 (SE = 0.08) with a 95% CI of 0.38–0.70 and ρ of 0.54 (SE = 0.06) with a 95% CI of 0.42–0.65. In this study area, based on the above considerations, the null model was included in the top important models with $\omega_i = 0.95$ to explain the stochastic processes. The global model (ψ(WD + Hsp + T_{caco} + Pre + Elev + DR + DS + DW),ρ(E+ T + P)) showed no evidence of lack of fit ($\chi^2 = 118.13$; $p = 0.35$; $\hat{c} = 1.07$). The most parsimonious model (Ψ(Sprich + T_{caco} + DR + DS),ρ(.)) had 0.07 model weight. Hence, all top models ($\Delta AIC_c \leq 2.0$) were equally supported to influence habitat use modeling in the case of SEA disturbed sites (Table 2.2; Table S2).

Model-averaged estimate of $\hat{\varphi}$ across all sites in SEA was 0.56 (SD = 0.19) and $\hat{\rho}$ was 0.48 (SD = 0.06). The overall occupancy was underestimated by approximately 17% when detection probability is not accounted for. Distance to settlement, tree canopy cover, herb species richness, distance to road, predator, and woody density appeared in the competing models to explain habitat use of the target species in this area. As predicted, distance to settlement ($\omega_i = 0.76$; $\beta_{mean} \pm SE = 0.74 \pm 0.41$; 95% CI: -0.07 to 1.55) positively associated with habitat use of the species, yet its respective 95% CIs overlapped zero. Other covariates also showed non-significant associations with occupancy of the species (Table 2.3).

In this study area, detectability was more supported without covariates based on the top models. Thus, the sample covariates predicted to influence detectability had relatively low summed weight and 95% of CIs overlapped zero. In this disturbed habitat, detection probability was not significantly affected by sample covariates but all covariates depicted positive association with detectability. The summed model weight of each covariate was below 0.30 (Table 2.3).

2.4.4. Recommended number of sampling occasions (*K*)

The sampling occasion (*K*) needed at GCCA was ranged from 1–3, this meaning that a single occasion (mean 0.86 and 1.14, respectively) was needed for a targeted confidence level of probabilities of 0.7 and 0.8 and two (mean 1.64) and three (mean 3.27) occasions sequentially were sufficient for 0.9 and 0.99 detection probabilities to estimate the true absence of the species at a given site. Similarly, we found that 2, 3, 4, and 7 occasions sequentially were needed at SEA.

2.5. Discussion

2.5.1. Occupancy and detection probability estimates using camera trap

Our study delivers the first insights into the habitat use of Moorland Francolins using a camera trap approach. Camera traps for this elusive and cryptic species helped us to avoid false-positive detection, which also corroborates the respective assumption for the occupancy model. The overall or true occupancy estimates in both study areas were greater than the naïve occupancy (ψ) estimates when detection probability is accounted for. These suggest that models incorporate imperfect detections to discount underestimating of overall occupancy (MacKenzie et al., 2018; Guillera-Arroita et al., 2014). Since we had small sample sizes and low density of individuals in SEA, we increased the sampling by one more occasion to minimize the effect of false-negative detections of the target species. Increasing of sampling occasion helps to increase the precision and accuracy of detectability of species (MacKenzie & Royle, 2005; Moore et al., 2014).

In many tropical African countries, the protected areas are called “paper parks”-existing in name only as they poorly counter habitat and species loss (Dudley & Stolton, 1999). However, GCCA as a traditionally protected area is exceptional in this case as the indigenous knowledge for conservation of natural resources, the Qero system, has supported several wildlife species for almost four centuries (Ashenafi & Leader-Williams, 2005; Nigussie et al., 2019). Occupancy and detection probability estimates of Moorland Francolins were higher in traditionally protected areas than in unprotected areas, suggesting the persistent and high conservation effort supporting the Ethiopian Wolf

(*Canis simensis*) by the local community in association with international organizations signifies the integrity and functionality of the whole community. Flagship species like this play a vital role in biodiversity conservation at local and global scales (Jarić et al., 2023), which is demonstrated by its positive side effects for Moorland Francolins and other species in GCCA, too. Unlike other carnivore species, this species is a rodent specialist (Vial et al., 2011; Ashenafi et al., 2012; Atickem & Stenseth, 2022).

2.5.2. Determinants of occupancy and detection probabilities

Based on beta estimates and moderate model weight, Moorland Francolins revealed an aversion to montane forest habitat due to the presence of predators in the tree canopies. The Afroalpine highlands are suitable habitats for predators (Clouet et al., 2000), and habitat use of many ground-dwelling birds is negatively influenced by the presence of predators in and around the forest habitats (Sukumal et al., 2017; Abrha et al., 2018). In concordance with these findings, our results confirm that predators (both aerial and ground predators) may strongly negatively influence the habitat use of Moorland Francolins in GCCA, although the main diet of several raptors is rodents (Clouet et al., 2000).

Though hunting pressure is one of the key factors for decreasing francolin populations nationwide (Töpfer et al., 2014; Abrha et al., 2017; Gedeon, Rödder, et al., 2017) and globally (McGowan et al., 2012), this threat was only of minor importance to Moorland Francolins in GCCA. However, in both study areas, but essentially in SEA, hunters preferably target to capture Erckel's Francolin *Pternistis erckelii* that usually subsist in habitats below the tree line in GCCA (Demis & Tesfaye, pers. comm.), and sympatrically with Moorland Francolins in SEA. Hunting pressure apparently is much more pronounced on *P*. *erckelii* due to its larger size and because of the different perceptions by the local communities toward both highland francolins.

Herb species richness was also supported based on model weight and top models. The protected grassland of GCCA covers almost 60% of its total area (Steger et al., 2020) and holds several range-restricted species (Ashenafi and Leader-Williams, 2005; Ashenafi et al., 2012). As expected, the occupancy probability of Moorland Francolins increased with herb species richness in GCCA, in line with other reports on pheasant species (Jolli et al., 2012; Sukumal et al., 2017). This vegetation type is widespread in the plateau of Afroalpine biome of Ethiopia (Nigussie et al., 2019; Steger et al., 2020) and it is the source of food and provides essential shelter for many grassland specialists (Töpfer & Gedeon, 2020). It had also a positive influence on the habitat use of Moorland Francolins at SEA, but the 95% confidence interval of the β-coefficient estimate overlapped zero showing less support for its influence on the species. This is because the area has been increasingly transformed into a monocultural plantation (Tadesse & Tafere, 2017; Bahru et al., 2021), and is subject to tourism activities (Asefa, 2018; Tesema & Berhan, 2019), overgrazing and other human-induced disturbances in the plateau of central highlands (Asefa et al., 2020). For instance, a recent report showed that the natural grassland of Entoto Natural Park has decreased over the last three decades and that the area is now dominated by *Eucalyptus* plantations (Tesema & Berhan, 2019). In such areas, Moorland Francolins showed a pronounced aversion toward modified habitat types. This implies that Afromontane grassland and shrubland specialists, especially Moorland Francolins might gradually become locally extinct.

Distance to road was also the other strongest covariate influencing the occupancy probability of Moorland Francolins, similar to other reports in ground-dwelling bird species (Whitworth et al., 2018). The occupancy probability of the species was higher along the edge of roadsides and trails than at sites located in remote in GCCA, in concordance with other reports on wildlife species (Kroeger et al., 2022; Paemelaere et al., 2023). This is unexpected because roads can attract hunters and predators, delivering also other human-induced perturbations (Dean et al., 2019; Kroeger et al., 2022). In GCCA, we observed that proximity to road attracts the species as there were food items mainly on the unpaved road, including grains and fruits thrown through window by passengers. Most roadsides have also dense native herbaceous vegetation, which may also help Moorland Francolins to survive. On the contrary, occupancy increased as the distance to road increased in SEA habitat but did not show a significant association with roads. This suggests that Moorland Francolins avoid roads and trails in a human-modified landscape. Thus, roads may have positive effects on bird species in more pristine habitats (Kroeger et al., 2022) and in areas where hunting pressure is controlled as a management strategy (Whitworth et al., 2018). Local low temperatures and high ground vegetation cover

(Nigussie et al., 2019; Steger et al., 2020) may lead the species to use the roadsides and trails: (1) to enhance foraging opportunities; (2) to stay more vigilant to avoid risk of predation; (3) as a heat source; (4) to facilitate mating, connectivity and communication.

Avoidance of human settlements is likely related to livestock grazing causing herb species richness to shrink at GCCA periphery (i.e., human occupation). Similarly, the effect of distance to settlement as a type of human disturbance posed a positive effect on Moorland Francolins in SEA. There was no significant difference for the covariate in this area, yet relatively high model-averaged beta coefficient estimate; model weight and confidence intervals reveal irregularity in association with the species, most presumably due to lack of habitat heterogeneity, a small sample size, limited number of cameras, and small sampling occasions, as compared to recommended occasions. Hence distance to settlement had a slightly significant positive influence on the species in SEA, agreeing with previous studies on pheasants (O'Brien & Kinnaird, 2008; Jolli et al., 2012; Nuttall et al., 2017; Chen et al., 2019), other bird (Pardo et al., 2017) and mammal species (Semper-Pascual et al., 2020; Paemelaere et al., 2023).

In line with our hypothesis, sampling occasion significantly positively influences the detectability of the species in GCCA. Conversely, in SEA, this covariate appeared in one of the most parsimonious models and it positively influenced detectability but it had low model weight and the beta coefficient estimates showed statistically non-significance association. The detectability may be affected by spatial variations and sample sizes. Our hypothesis that species detection increases with number of days of cameras deployed showed consistency with other findings in bird (Si et al., 2014; Paemelaere et al., 2023) and mammal species (Si et al., 2014; Shannon et al., 2014; Semper-Pascual et al., 2020; Holzner et al., 2021; Wevers et al., 2021). The magnitude of sampling occasion on detection probability estimate demonstrates species-specific response (Iannarilli et al., 2021).

In Ethiopia, after a long dry season, both a small and a main rain season occurs in most highland areas (Mohammed et al., 2022). Several francolin species are adapted to this seasonally changing precipitation regime (Gedeon, Rödder, et al., 2017; Abrha et al., 2018), which allows the areas to replenish food resources and ecosystem greenness vital for breeding (Abrha et al., 2018). This is because francolins may find plenty of food by easily raking and scratching the wet ground (Abrha et al., 2018). Moreover, during rain seasons, birds of prey soar less, and agro-pastoral encroachments seem lower compared to the dry season (pers. obs). Elsewhere in the tropics, the breeding season of birds is reported to be associated with the beginning of precipitation and this is linked to the abundance of food and cover resources (Jansen & Crowe, 2005; Cox et al., 2013; França et al., 2020). In our species, some camera traps have documented chicks being fed by their parents in GCCA, and this implies that the breeding season of the species may coincide with the short and mild precipitation distribution from February to June. Similarly, temperature positively influenced the detectability of the species, but there was little support for our hypothesis based on models. This may suggest that the species avoids extreme temperatures. Collectively, climate factors are very important for the detectability of the target species in the central highlands of Ethiopia.

2.5.3. Camera trapping for assessment of cryptic bird species

The Moorland Francolins, similar to other pheasants in the region, could potentially go visually undetected, particularly in areas of low population density and in disturbed habitats. Extreme weather conditions, seasonality, expert experience, and other factors may also obscure the ability to detect the species. This is because the birds usually remain silent, hidden, and squatted when people approach them. Thus, false-negative detection could bias inferences about the occupancy and detection probability estimates and other parameters. However, the deployment of non-invasive modern approaches like remotely triggered camera traps can avoid such ecological concerns. This approach also helps to discover new geographical ranges, other wildlife species (including predators) and thereby helping to understand the interactions of the Moorland Francolins in its natural habitat. Another positive feature of the camera trapping technique is that it is cost and time-effective. Our results strongly support the deployment of camera traps for the detection of cryptic and little-known species in a topographically complex region. Camera traps provide reliable comprehension and precision of the occupancy of Moorland Francolins in the Afroalpine Biome. Such camera trap data (Wearn & Glover-Kapfer, 2017; O'Brien & Kinnaird, 2008; Si et al., 2014; Steenweg et al., 2017; Sharief et al., 2022) ultimately promotes the proper conservation of the target species.

2.6. Conclusions

The findings demonstrate that habitat use of Moorland Francolins is higher in the more pristine habitats compared to the strongly human-influenced in SEA. This suggests that a community-based conservation area (i.e., GCCA) is a crucial remnant habitat of endangered and data-deficient wildlife species in Ethiopia. Since such community-based conservation approaches obviously support sustainable species-habitat conservation, strengthening the existing Qero system and expanding the model to other potential hotspot sites and/or IBAs is strongly recommended to circumvent the mounting anthropogenic disturbances in the region (Asefa et al., 2017; Razgour et al., 2021; Rodrigues et al., 2021; Chengere et al., 2022).

Our results also show that the species uses various herb species, roadsides and trails for resting, hiding, survival, and reproduction. Conversely, predators threatened the francolins predominantly in native and plantation forests, thus Moorland Francolins tend to avoid tree canopy cover and human settlements in both study areas. In the human-modified SEA areas, most covariates had a weak influence on the occupancy and detection estimates of our target species because habitats are dominated by *Eucalyptus* plantations, fragmented meadow hill patches, and farmlands, unlike the heterogeneous and protected habitats in the GCCA.

We confirm that camera trap deployment corroborates the presence or absence of shy ground-dwelling birds not only in known areas but also in understudied areas. The detectability of francolins was determined by the sampling occasion and precipitation. Further research using single or multi-season modeling is required to understand the influence of habitat covariates, seasonal colonization, and local extinction from spatiotemporally replicated surveys.

Author contributions

Abadi Mehari Abrha: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); project administration (equal); software (lead); validation(equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). Kai Gedeon: Conceptualization (equal); funding acquisition (equal); methodology (supporting); project administration (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (equal). Lars Podsiadlowski: Methodology (supporting); project administration (supporting); supervision (equal); writing – review and editing (equal). Demis Mamo Weldesilasie: Data curation (supporting); project administration (supporting); writing – original draft (supporting); writing – review and editing (supporting). Till Töpfer: Conceptualization (equal); funding acquisition (equal); methodology (supporting); project administration (equal); supervision (equal); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal).

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Conflict of interest statement

The authors declare that they have no conflict of interest.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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2.7. References

Abrha, A. M., Nigus, H. K., Weldetnsae, B. G., Tilahun, M., Nigusse, A. G., & Deribew, K. T. (2017). Effects of human disturbances on two sympatric francolin species in the Central Highlands of Ethiopia. *Podoces, 12*(1), 13−21.

Abrha, A. M., Zelelew, S. A., Nigus, H. K., & Alelign, A. (2018). Diurnal activity patterns of Harwood's Spurfowl *Pternistis harwoodi* in relation to habitat types and climatic conditions in the Central Highlands of Ethiopia. *Ostrich*, *89*(2), 195−201.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management*, *74*(6), 1175−1178.

Asefa, A., Davies, A. B., McKechnie, A. E., Kinahan, A. A., & van Rensburg, B. J. (2017). Effects of anthropogenic disturbance on bird diversity in Ethiopian montane forests. *The Condor: Ornithological Applications*, *119*(3), 416−430.

Asefa, A. (2018). Avifauna of Entoto Mountain Forest, Ethiopia: Diversity and Potential for Tourism Development. *Journal of Science and Sustainable Development*, *6*(2), 16−28.

Asefa, M., Cao, M., He, Y., Mekonnen, E., Song, X., & Yang, J. (2020). Ethiopian vegetation types, climate and topography. *Plant Diversity*, *42*(4), 302−311.

Ash, J., & Atkins, J. (2009). *Birds of Ethiopia and Eritrea: an atlas of distribution*. Bloomsbury Publishing.

Ashenafi, Z. T., & N. Leader-Williams (2005). Indigenous common property resources management in the Central Highlands of Ethiopia. *Human Ecology, 33*(4), 539−563.

Ashenafi, Z. T., Leader-Williams, N., & Coulson, T. (2012). Consequences of human land use for an Afro-alpine ecological community in Ethiopia. *Conservation and Society*, *10*(3), 209−216.

Atickem, A., & Stenseth, N.C. (2022). The role of rodents in the conservation of endangered species in the Ethiopian highlands. *Therya*, *13*(1), 73−77.

Atikah, S. N., Yahya, M. S., Norhisham, A. R., Kamarudin, N., Sanusi, R., & Azhar, B. (2021). Effects of vegetation structure on avian biodiversity in a selectively logged hill dipterocarp forest. *Global Ecology and Conservation*, *28*, e01660.

Bahru, T., Kidane, B., & Tolessa, A. (2021). Prioritization and selection of high fuelwood producing plant species at Boset District, Central Ethiopia: an ethnobotanical approach. *Journal of Ethnobiology and Ethnomedicine*, *17*, 1−15.

Bailey, L. L., MacKenzie, D. I., & Nichols, J. D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution*, *5*(12), 1269−1279.

BirdLife International, (2004) *State of the world's birds 2004: indicators for our changing world. Cambridge*, UK: BirdLife International.

BirdLife International, (2023). Species factsheet: *Scleroptila psilolaema*. Downloaded from http://www.birdlife.org on 28/04/2023

Bryja, J., Meheretu, Y., Šumbera, R., & Lavrenchenko, L. A. (2019). Annotated checklist, taxonomy and distribution of rodents in Ethiopia. *Folia zoologica*, *68*(3), 117−213.

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information−Theoretic Approach*. Second Edition. New York: Springer-Verlag

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral ecology and sociobiology*, *65*, 23−35.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., ...& Boutin, S. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675−685.

Caravaggi, A., Burton, A. C., Clark, D. A., Fisher, J. T., Grass, A., Green, S., ...& Rivet, D. (2020). A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conservation Science and Practice*, *2*(8), e239.

Chen, L., Shu, Z., Yao, W., Ma, Y., Xiao, W., & Huang, X. (2019). Combined effects of habitat and interspecific interaction define co-occurrence patterns of sympatric Galliformes. *Avian Research*, *10*(1), 1−13.

Chengere, S. A., Steger, C., Gebrehiwot, K., Nemomissa, S., & Dullo, B. W. (2022). Modeling Cultural Keystone Species for the Conservation of Biocultural Diversity in the Afroalpine. *Environments*, *9*(12), 156.

Clouet, M., Barrau, C., & Goar, J. L. (2000). The diurnal Afro−alpine raptor community of the Ethiopian Balé Highlands. *Ostrich*, *71*(3−4), 380−384.

Cordier, C. P., Smith, D. A. E., Smith, Y. E., & Downs, C. T. (2022). Camera trap research in Africa: A systematic review to show trends in wildlife monitoring and its value as a research tool. *Global Ecology and Conservation*, e02326.

Cox, D. T., Brandt, M. J., McGregor, R., Ottosson, U., Stevens, M. C., & Cresswell, W. (2013). The seasonality of breeding in savannah birds of West Africa assessed from brood patch and juvenile occurrence. *Journal of Ornithology*, *154*, 671−683.

Cremonesi, G., Bisi, F., Gaffi, L., Zaw, T., Naing, H., Moe, K., ...& Martinoli, A. (2021). Camera trapping to assess status and composition of mammal communities in a biodiversity hotspot in Myanmar. *Animals*, *11*(3), 880.

Dean, W. R. J., Seymour, C. L., Joseph, G. S., & Foord, S. H. (2019). A review of the impacts of roads on wildlife in semi-arid regions. *Diversity*, *11*(5), 81.

Devarajan, K., Morelli, T. L., & Tenan, S. (2020). Multi-species occupancy models: Review, roadmap, and recommendations. *Ecography*, *43*(11), 1612−1624.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ...& Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27−46.

Dudley, N., & Stolton, S. (1999). *Conversion of paper parks to effective management: developing a target*.

Esayas, K., & Bekele, A. (2011). Species composition, relative abundance and distribution of the avian fauna of Entoto Natural Park and Escarpment, Addis Ababa. *SINET: Ethiopian Journal of Science*, *34*(2), 113−122.

Eshete, G., Tesfay, G., Bauer, H., Ashenafi, Z.T., de Iongh, H., & Marino, J. (2015). Community resource uses and Ethiopian wolf conservation in Mount Abune Yosef. *Environmental Management*, *56*, 684−694.

Estifanos, T., Polyakov, M., Pandit, R., Hailu A., Burton, M. (2018). *Protection of the Ethiopian Wolf: What are tourists willing to pay for?* Working Paper 1803, Agricultural and Resource Economics, the University of Western Australia, Crawley, Australia.

França, L. F., Figueiredo-Paixão, V. H., Duarte-Silva, T. A., & Santos, K. B. D. (2020). The effects of rainfall and arthropod abundance on breeding season of insectivorous birds, in a semi−arid neotropical environment. *Zoologia*, *37,* 1−7.

Ferreguetti, Á. C., Tomás, W. M., & Bergallo, H. G. (2015). Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil. *Journal of Mammalogy*, *96*(6), 1245−1254.

Fishpool, L.D.C., & Evans, M. I. (eds). (2001). *Important Bird Areas of Africa and associated islands: priority sites for conservation*. Newbury/Cambridge, UK: Pisces Publications/BirdLife International.

Friis, I., Demissew S., & van Breugel, P. (2010). Atlas of the potential vegetation of Ethiopia. *Biologiske Skrifter, 58,* 1−307*.*

Gedeon, K., Roedder, D., Zewdie, C., & Toepfer, T. (2017). Evaluating the conservation status of the Black-fronted Francolin *Pternistis atrifrons*. *Bird Conservation International*, *28*(4), 653−661.

Gedeon, K., Zewdie, C., & Töpfer, T. (2017). The birds (Aves) of Oromia, Ethiopia–an annotated checklist. *European Journal of Taxonomy*, *306*, 1−69.

Gelman, A., & Hill, J. (2007). *Data Analysis Using Regression and Hierarchical/Multilevel Models*. New York: Cambridge University Press.

Gill, F., Donsker, D., & Rasmussen, P. (Eds.) (2023). IOC World Bird List (v 13.1). Doi 10.14344/IOC.ML.13.1. http://www.worldbirdnames.org/

Gonsamo, A., Walter, J. M. N., & Pellikka, P. (2011). CIMES: A package of programs for determining canopy geometry and solar radiation regimes through hemispherical photographs. *Computers and electronics in agriculture*, *79*(2), 207−215.

Guillera-Arroita, G., Ridout, M. S., & Morgan, B. J. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, *1*(2), 131−139.

Guillera-Arroita, G., & Lahoz-Monfort, J. J. (2012). Designing studies to detect differences in species occupancy: power analysis under imperfect detection. *Methods in Ecology and Evolution*, *3*(5), 860−869.

Guillera-Arroita, G., Lahoz-Monfort, J. J., MacKenzie, D. I., Wintle, B. A., & McCarthy, M. A. (2014). Ignoring imperfect detection in biological surveys is dangerous: A response to 'fitting and interpreting occupancy models'. *PloS One*, *9*(7), e99571.

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography*, *40*(2), 281−295.

Hines, J. E. (2006). *PRESENCE-Software to estimate patch occupancy and related parameters*. USGS-PWRC Available: http://www.mbr−pwrc.usgs.gov/software/presence.html

Holzner, A., Rayan, D. M., Moore, J., Tan, C. K. W., Clart, L., Kulik, L., ...& Widdig, A. (2021). Occupancy of wild southern pig−tailed macaques in intact and degraded forests in Peninsular Malaysia. *PeerJ*, *9*, e12462.

Iannarilli, F., Erb, J., Arnold, T. W., & Fieberg, J. R. (2021). Evaluating species-specific responses to camera-trap survey designs. *Wildlife Biology*, *2021*(1), 1−12.

Jansen, R., & Crowe, T. M. (2005). Relationship between breeding activity and rainfall for Swainson's Spurfowl, *Pternistis swainsonii*, within southern Africa, with specific reference to the Springbok Flats, Limpopo Province, South Africa. *Ostrich-Journal of African Ornithology*, *76*(3−4), 190−194.

Jarić, I., Normande, I. C., Arbieu, U., Courchamp, F., Crowley, S. L., Jeschke, J. M., ...& Ladle, R. J. (2023). Flagship individuals in biodiversity conservation. *Frontiers in Ecology and the Environment*.

Jolli, V., Srivastav, A., & Thakur, S. (2012). Patch occupancy for cheer pheasant *Catreus wallichii* in the Great Himalayan national park conservation area. *International Journal of Galliformes Conservation,* 2, 74−81.

Kays, R., Arbogast, B. S., Baker-Whatton, M., Beirne, C., Boone, H. M., Bowler, M., ...& Spironello, W. R. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution,* 11(6), 700−713.

Kéry, M., Gardner, B., & Monnerat, C. (2010). Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography, 37*(10), 1851−1862.

Kroeger, S. B., Hanslin, H. M., Lennartsson, T., D'Amico, M., Kollmann, J., Fischer, C., ...& Speed, J. D. (2022). Impacts of roads on bird species richness: A meta−analysis considering road types, habitats and feeding guilds. *Science of The Total Environment*, 812, 151478.

Lamelas-López, L., & Salgado, I. (2021). Applying camera traps to detect and monitor introduced mammals on oceanic islands. *Oryx*, *55*(2):181–188.

Leroux, S. J. (2019). On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. *PLoS One*, *14*(2), e0206711.

MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, *9*, 300−318.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248−2255.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2018). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier.

MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of applied Ecology*, *42*(6), 1105−1114.

Maffei, L., & Noss, A. J. (2008). How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. *Biotropica*, *40*(1), 71−75.

McGrath, T., Guillera-Arroita, G., Lahoz-Monfort, J. J., Osborne, W., Hunter, D., & Sarre, S. D. (2015). Accounting for detectability when surveying for rare or declining reptiles: turning rocks to find the grassland earless dragon in Australia. *Biological Conservation*, *182*, 53−62.

McGowan, P. J. K., Owens, L. L., & Grainger, M. J. (2012). Galliformes science and species extinctions: what we know and what we need to know. *Animal Biodiversity and Conservation*, *35*(2), 321−331.

Meek, P. D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., ...& Townsend, S. (2014). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and conservation*, *23*, 2321−2343.

Mittermeier, R. A., Robles-Gil, P., Hoffmann, M., Pilgrim, J. D., Brooks, T. B., Mittermeier, C. G., Lamoreux, J. L. & Fonseca, G. A. B. (2004). *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions*. CEMEX, Mexico City, Mexico.

Mohammed, J. A., Gashaw, T., Tefera, G. W., Dile, Y. T., Worqlul, A. W., & Addisu, S. (2022). Changes in observed rainfall and temperature extremes in the Upper Blue Nile Basin of Ethiopia. *Weather and Climate Extremes*, *37*, 100468.

Moore, A. L., McCarthy, M. A., Parris, K. M., & Moore, J. L. (2014). The optimal number of surveys when detectability varies. *PLoS One*, *9*(12), e115345.

Niedballa, J., Sollmann, R., Mohamed, A. B., Bender, J., & Wilting, A. (2015). Defining habitat covariates in camera-trap based occupancy studies. *Scientific Reports*, *5*(1), 17041.

Nigussie, G., Fekadu, M., Demissew, S., & Warkineh, B. (2019). Impact of conservation management on land change: a case study in Guassa Community Conservation Area for the last 31 years (1986–2015). *Modeling Earth Systems and Environment*, *5*, 1495−1504.

Nuttall, M., Nut, M., Ung, V., & O'Kelly, H. (2017). Abundance estimates for the endangered green peafowl *Pavo muticus* in Cambodia: Identification of a globally important site for conservation. *Bird Conservation International*, 27, 127– 139.

O'Brien, T. G., & Kinnaird, M. F. (2008). A picture is worth a thousand words: the application of camera trapping to the study of birds. *Bird Conservation International*, *18*(S1), S144−S162.

Ossendorf, G., Groos, A. R., Bromm, T., Tekelemariam, M. G., Glaser, B., Lesur, J., ...& Miehe, G. (2019). Middle Stone Age foragers resided in high elevations of the glaciated Bale Mountains, Ethiopia. *Science*, *365*(6453), 583−587.

Paemelaere, E. A., Mejía, A., Quintero, S., Hallett, M., Li, F., Wilson, A., ... & Melville, J. (2023). The road towards wildlife friendlier infrastructure: Mitigation planning through landscape-level priority settings and species connectivity frameworks. *Environmental Impact Assessment Review*, *99*, 107010.

Pardo, L. E., Lafleur, L., Spinola, R. M., Saenz, J., & Cove, M. (2017). Camera traps provide valuable data to assess the occurrence of the Great Curassow *Crax rubra* in northeastern Costa Rica. *Neotropical Biodiversity*, *3*(1), 182−188.

Pellet, J., & Schmidt, B. R. (2005). Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. *Biological Conservation*, *123*(1), 27−35.

Razgour, O., Kasso, M., Santos, H., & Juste, J. (2021). Up in the air: Threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian Highlands bat. *Evolutionary Applications*, *14*(3), 794−806.

Reber, D., Fekadu, M., Detsch, F., Vogelsang, R., Bekele, T., Nauss, T., & Miehe, G. (2018). High-altitude rock shelters and settlements in an African alpine ecosystem: The Bale Mountains national park, Ethiopia. *Human Ecology*, *46(*4*)*, 587−600.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, *86*(10), 2805−2814.

Rodrigues, P., Dorresteijn, I., Guilherme, J. L., Hanspach, J., De Beenhouwer, M., Hylander, K., ...& Nimmo, D. (2021). Predicting the impacts of human population growth on forest mammals in the highlands of southwestern Ethiopia. *Biological Conservation*, *256*, 109046.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103−113.

Semper-Pascual, A., Decarre, J., Baumann, M., Camino, M., Di Blanco, Y., Gómez−Valencia, B., & Kuemmerle, T. (2020). Using occupancy models to assess the direct and indirect impacts of agricultural expansion on species' populations. *Biodiversity and Conservation*, *29*, 3669−3688.

Sewell, D., Beebee, T. J., & Griffiths, R. A. (2010). Optimising biodiversity assessments by volunteers: the application of occupancy modelling to large-scale amphibian surveys. *Biological Conservation*, *143*(9), 2102−2110.

Shannon, G., Lewis, J. S., & Gerber, B. D. (2014). Recommended survey designs for occupancy modelling using motion-activated cameras: insights from empirical wildlife data. *PeerJ*, *2*, e532.

Sharief, A., Singh, H., Joshi, B. D., Singh, I., Mukherjee, T., Chandra, K., ...& Sharma, L. K. (2022). Understanding distribution and occupancy of Himalayan monal in Uttarkashi district, Uttarakhand for conservation and management planning. *Wildlife Biology*, *2022*(2), e01013.

Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. *PeerJ*, *2*, e374.

Sollmann, R. (2018). A gentle introduction to camera−trap data analysis. *African Journal of Ecology*, *56*(4), 740−749.

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., ...& Rich, L. N. (2017). Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, *15*(1), 26−34.

Steger, C., Nigussie, G., Alonzo, M., Warkineh, B., Van Den Hoek, J., Fekadu, M., ...& Klein, J. A. (2020). Knowledge coproduction improves understanding of environmental change in the Ethiopian highlands. *Ecology and Society*, *25*(2); 1−19.

Sukumal, N., Dowell, S. D., & Savini, T. (2017). Micro-habitat selection and population recovery of the Endangered Green Peafowl *Pavo muticus* in western Thailand: implications for conservation guidance. *Bird Conservation International*, *27*(3), 414−430.

Suwanrat, S., Ngoprasert, D., Sutherland, C., Suwanwaree, P., & Savini, T. (2015). Estimating density of secretive terrestrial birds (Siamese Fireback) in pristine and degraded forest using camera traps and distance sampling. *Global Ecology and Conservation*, *3*, 596−606.

Symonds, M. R., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral ecology and sociobiology*, *65*, 13−21.

Tadesse, S. A., & Tafere, S. M. (2017). Local people's knowledge on the adverse impacts and their attitudes towards growing *Eucalyptus* woodlot in Gudo Beret Kebele, Basona Worena district, Ethiopia. *Ecological Processes*, *6*(1), 1−13.

Tanwar, K. S., Sadhu, A., & Jhala, Y. V. (2021). Camera trap placement for evaluating species richness, abundance, and activity. *Scientific Reports*, *11*(1), 23050.

Tefera, Z., & Sillero-Zubiri, C. (2006). A flagship species for Afroalpine conservation: An overview of the status and conservation of the Ethiopian wolf. *Walia*, 25, 13−21.

Tesema, A. D. & Berhan, G. (2019). Assessment of biodiversity conservation in Entoto Natural Park, Ethiopia for ecotourism development. *Asian Journal of Ethnobiology*, *2*(1), 22−37.

Tichý, L (2016). Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. *Journal of Vegetation Science,* 27, 427–435.

Tilahun, S., Edwards, S., & Gebregziabher, T. (eds) (1996). *Important Bird Areas of Ethiopia: a first inventory*. Addis Ababa: Ethiopian Wildlife & Natural History Society.

Töpfer, T., Podsiadlowski, L., & Gedeon, K. (2014). Rediscovery of the Black−fronted Francolin *Pternistis (castaneicollis) atrifrons* (Conover, 1930)(Aves: Galliformes: Phasianidae) with notes on biology, taxonomy and conservation. *Vertebrate Zoology*, *64*(2), 261−71.

Töpfer, T., & Gedeon, K (2020). *Alpine Birds of Africa*. Encyclopedia of the World's Biomes, Volume 1, 505−516.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications, 13*, 1790−1801.

Vial, F., Macdonald, D. W., & Haydon, D. T. (2011). Limits to exploitation: dynamic food web models predict the impact of livestock grazing on Ethiopian wolves *Canis simensis* and their prey. *Journal of Applied Ecology*, *48*(2), 340−347.

Wearn, O. R., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: a guide to best−practices. *WWF conservation technology series*, *1*(1), 181.

Wearn, O. R., & Glover-Kapfer, P. (2019). Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *Royal Society open science*, *6*(3), 181748.

Wevers, J., Beenaerts, N., Casaer, J., Zimmermann, F., Artois, T., & Fattebert, J. (2021). Modelling species distribution from camera trap by−catch using a scale−optimized occupancy approach. *Remote Sensing in Ecology and Conservation*, *7*(3), 534−549.

Whitworth, A., Beirne, C., Flatt, E., Pillco Huarcaya, R., Cruz Diaz, J. C., Forsyth, A., ...& Vargas Soto, J. S. (2018). Secondary forest is utilized by Great Curassows (*Crax rubra*) and Great Tinamous (*Tinamus major*) in the absence of hunting. *The Condor: Ornithological Applications*, *120*(4), 852−862.

Winarni, N. L., Carroll, J. P., & O'Brien, T. G. (2005). The application of camera traps to the study of Galliformes in southern Sumatra, Indonesia. In *Galliformes 2004: Proceedings of the 3rd International Galliformes Symposium (RA Fuller and SJ Browne, Editors).* World Pheasant Association, Fordingbridge, UK, pp: 109−121.

Zou, F., Zhang, Q., Zhang, M., Lee, M. B., Wang, X., Gong, Y., & Yang, C. (2019). Temporal patterns of three sympatric pheasant species in the Nanling Mountains: N−mixture modeling applied to detect abundance. *Avian Research*, *10*, 1−10.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, *1*(1), 3−14.

2.8. Supplementary information

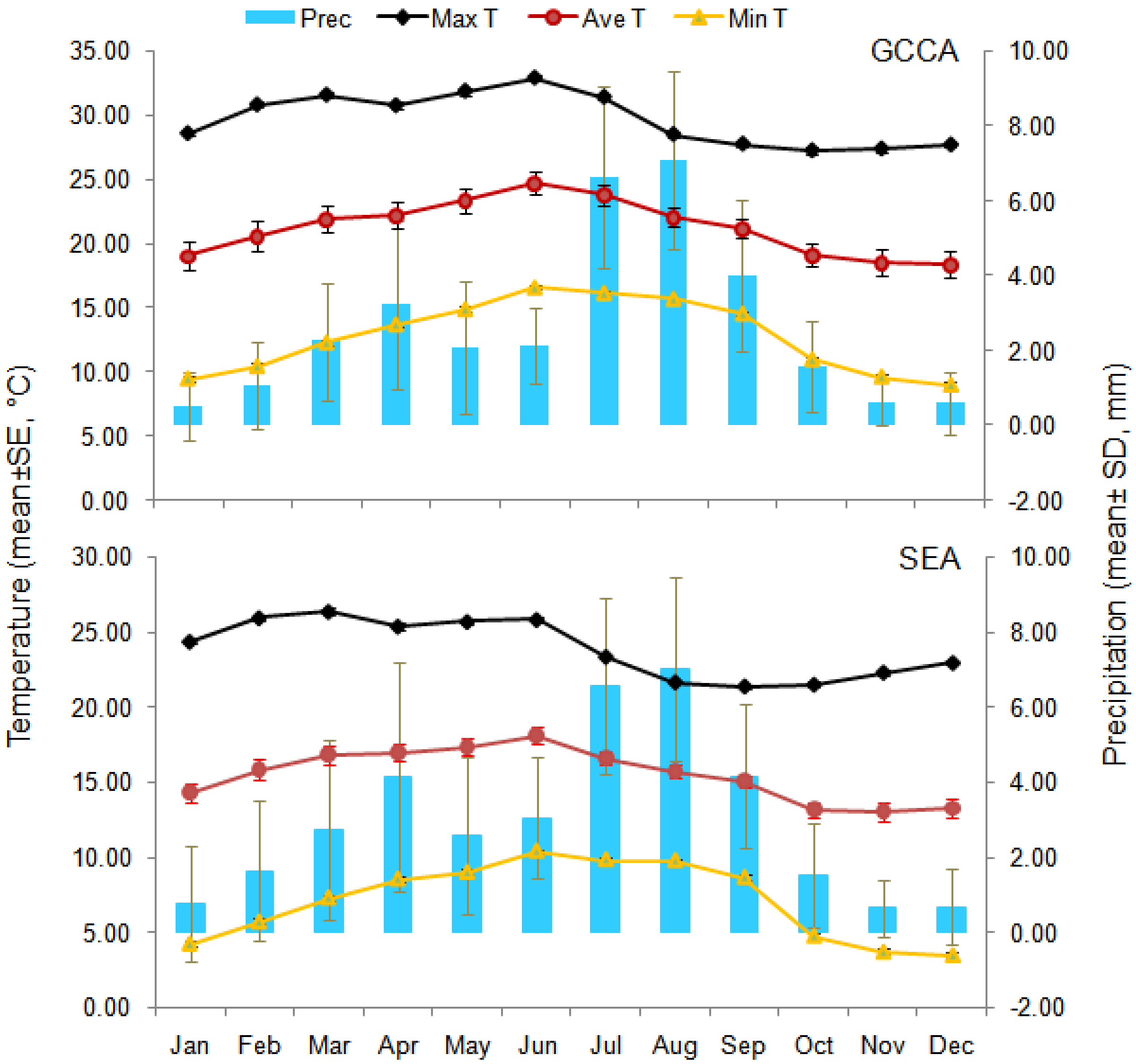

Figure S1. Climatic conditions of GCCA and SEA from 1981-2020 (https://power.larc.nasa.gov/data-access-viewer). Temperature (°C) and precipitation (mm) values are based on mean monthly data for each year (mean maximum, average and mean minimum temperatures).

Table S1. Sensitive analyses for the constant model (null model) using different sampling occasions for GCCA and SEA study areas. The middle sampling occasion was opted over the lowest and highest estimates. Abbreviations: *k*-parameter; ψ-occupancy probability; ρ-detection probability, and n-effective sample size.

Study area		Sampling occasion											
		Output 1				Output 2			Output 3				
	k	Estimate	SE	95% CI	n	Estimate	SE	95% CI	n	Estimate	SE	95% CI	n
GCCA	ψ	0.72	0.05	0.61-0.80	98	0.73	0.05	0.63-0.82	98	0.77	0.05	0.66-0.85	94
	ρ	0.63	0.02	0.59-0.68	98	0.85	0.02	0.79-0.89	98	0.86	0.03	0.79-0.91	94
SEA	ψ	0.51	0.08	0.36-0.65	48	0.54	0.08	0.38-0.70	48	0.54	0.08	0.37-0.69	48
	ρ	0.38	0.04	0.31-0.46	48	0.54	0.06	0.42-0.65	48	0.65	0.07	0.50-0.77	48

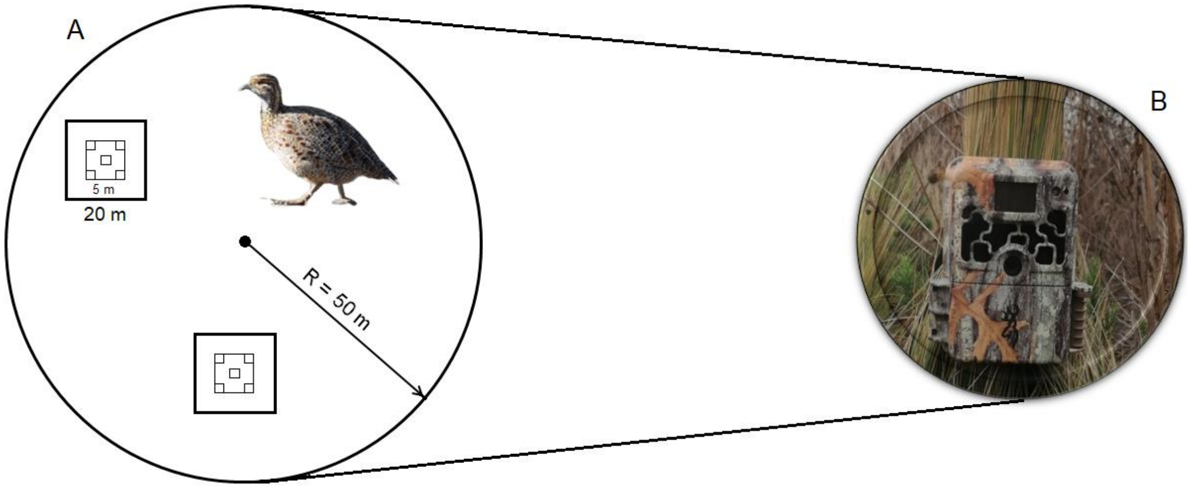

Figure S2. Schematic illustration of quadrant and camera placement in each circular plot (c. 0.8 ha). All quadrats for woody and herbaceous plant species (A) and camera trap mounted on coarser grass species (B) are shown.

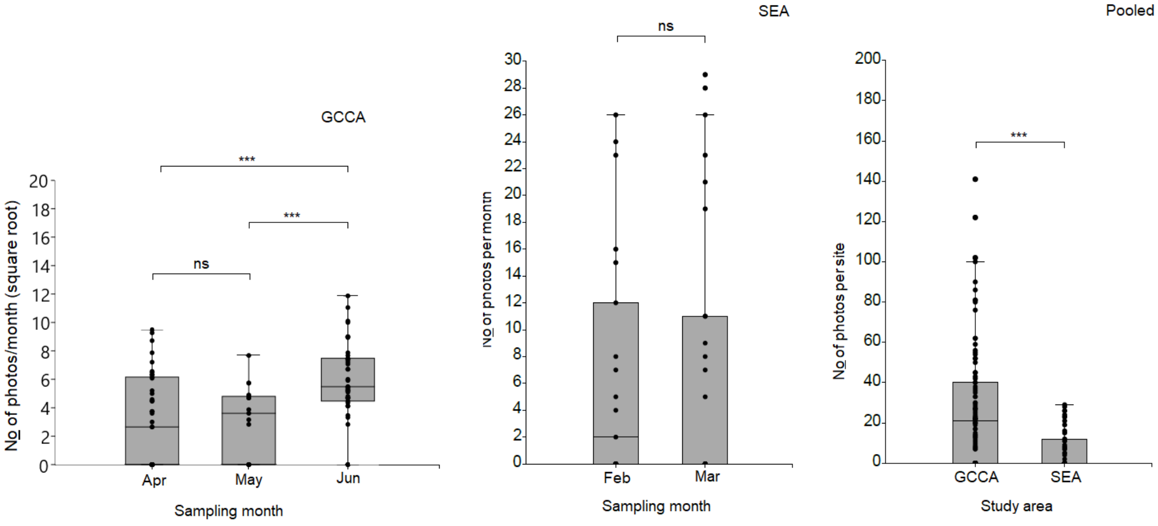

Figure S3. Number of photos captured in different sampling months and across study area. The asterisks (***) denote $p < 0.001$ level.

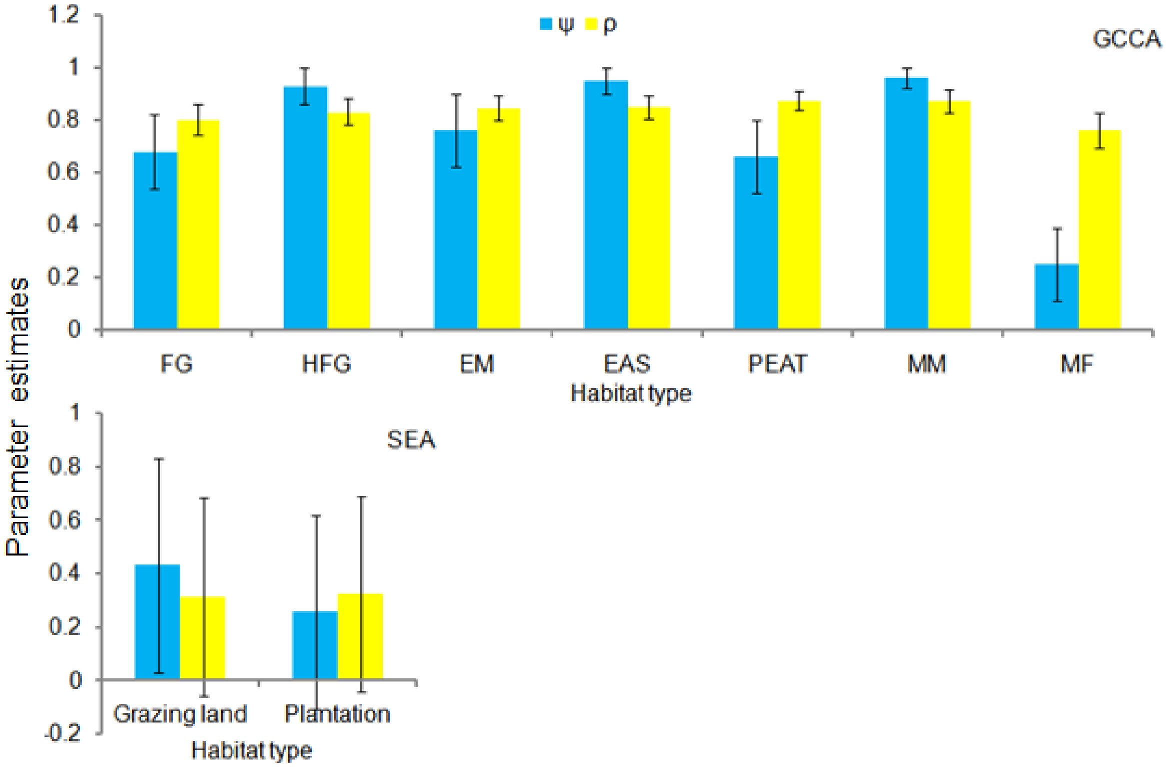

Figure S4. Occupancy and detection probability estimates of Moorland Francolin in different habitat types in central highlands of Ethiopia. Both parameter estimates were derived from model average estimates and error bars represent SEs. Abbreviations: FG-*Festuca* Grassland; HFG-*Helichrysum-Festuca* Grassland; EM-Erica Moorland; EAS-*Euryops-Alchemilla* Shrubland; Peat-Peatland; MM-Mima Mound and MF-Montane Forest.

Table S2. Model outputs for GCCA and SEA study areas.

GCCA					
Model	AIC_c	ΔAIC_c	ω_i	K	-2L
psi(Hsp+Tcaco+Pre+DR),p(E+T+P)	257.40	0.00	0.0801	9	237.35
psi(Hsp+Pre+DR),p(E+T+P)	257.46	0.06	0.0777	8	239.84
psi(Hsp+Pre+Elev+DR),p(E+T+P)	258.01	0.61	0.0590	9	237.96
psi(WD+Hsp+Pre+DR),p(E+T+P)	258.07	0.67	0.0573	9	238.02
psi(Hsp+Tcaco+Pre+DR),p(E+P)	258.16	0.76	0.0548	8	240.54
psi(Hsp+Pre+Elev+DR),p(E+P)	258.39	0.99	0.0488	8	240.77
psi(Hsp+Pre+DR),p(E+P)	258.44	1.04	0.0476	7	243.20
psi(Hsp+Tcaco+Pre+Elev+DR),p(E+T+P)	258.47	1.07	0.0469	10	235.94
psi(Hsp+Pre+Elev),p(E+T+P)	258.94	1.54	0.0371	8	241.32
psi(WD+Hsp+Pre+DR),p(E+P)	258.96	1.56	0.0367	8	241.34
psi(WD+Hsp+Pre+Elev+DR),p(E+T+P)	259.17	1.77	0.0331	10	236.64
psi(WD+Hsp+Tcaco+Pre+DR),p(E+T+P)	259.18	1.78	0.0329	10	236.65
psi(Hsp+Tcaco+Pre+DR+DW),p(E+T+P)	259.35	1.95	0.0302	10	236.82
psi(Tcaco+Pre+Elev+DR),p(E)	259.45	2.05	0.0287	7	244.21
psi(Hsp+Pre+Elev),p(E+P)	259.48	2.08	0.0283	7	244.24
psi(Hsp+Tcaco+Pre+Elev),p(E+T+P)	259.81	2.41	0.0240	9	239.76
psi(Hsp+Pre+DR),p(E)	259.84	2.44	0.0237	6	246.92
psi(Hsp+Tcaco+Pre),p(E+T+P)	259.87	2.47	0.0233	8	242.25
psi(Hsp+Pre+DR+DW),p(E+T+P)	259.89	2.49	0.0231	9	239.84
psi(Hsp+Pre),p(E+T+P)	260.12	2.72	0.0206	7	244.88
psi(Hsp+Tcaco+Pre+DR),p(E)	260.20	2.80	0.0198	7	244.96
psi(WD+Hsp+Tcaco+Pre+Elev+DR),p(E+T+P)	260.46	3.06	0.0173	11	235.39
psi(Hsp+Tcaco+DR),p(E+T+P)	260.52	3.12	0.0168	8	242.90
psi(WD+Hsp+Pre+DR+DW),p(E+T+P)	260.54	3.14	0.0167	10	238.01
psi(Hsp+Tcaco+Pre+Elev+DR+DW),p(E+T+P)	260.76	3.36	0.0149	11	235.69
psi(WD+Hsp+Pre+Elev),p(E+T+P)	260.88	3.48	0.0141	9	240.83
psi(Hsp+Tcaco+Pre),p(E+P)	260.92	3.52	0.0138	7	245.68
psi(Hsp+Tcaco+Pre+Elev+DR+DS),p(E+T+P)	261.00	3.60	0.0132	11	235.93
psi(Hsp+Pre+DS),p(E+T+P)	261.02	3.62	0.0131	8	243.40
psi(Hsp+Tcaco+Pre+DR+DW+DS),p(E+T+P)	261.20	3.80	0.0120	11	236.13
psi(Hsp+Tcaco+Pre+DW),p(E+T+P)	261.24	3.84	0.0117	9	241.19
psi(Hsp+Pre),p(E+P)	261.29	3.89	0.0115	6	248.37
psi(Hsp+Tcaco+DR+DS),p(E+T+P)	261.35	3.95	0.0111	9	241.30
psi(.),p(.)	298.28	40.88	0.0000	2	294.15
SEA					
Model	AIC_c	ΔAIC_c	ω_i	K	-2L
psi(Hsp+Tcaco+DR+DS),p(.)	182.77	0.00	0.07	1.00	6
psi(Hsp+DS),p(.)	183.32	0.55	0.06	0.76	4

psi(Tcaco+DS),p(.)	183.37	0.60	0.05	0.74	4
psi(Hsp+DR+DS),p(.)	183.62	0.85	0.05	0.65	5
psi(Hsp+Tcaco+DS),p(.)	183.75	0.98	0.04	0.61	5
psi(Tcaco+DS),p(E)	184.13	1.36	0.04	0.51	5
psi(Hsp+DS),p(T)	184.32	1.55	0.03	0.46	5
psi(Tcaco+DR+DS),p(.)	184.40	1.63	0.03	0.44	5
psi(Hsp+Tcaco+DR+DS),p(T)	184.45	1.68	0.03	0.43	7
psi(Hsp+DR+DS),p(T)	184.65	1.88	0.03	0.39	6
psi(Hsp+Tcaco+DR+DS),p(P)	184.68	1.91	0.03	0.38	7
psi(Tcaco),p(.)	184.76	1.99	0.03	0.37	3
psi(Tcaco),p(E)	184.94	2.17	0.02	0.34	4
psi(Tcaco+DS),p(P)	184.98	2.21	0.02	0.33	5
psi(Pre+Tcaco+DS),p(.)	185.11	2.34	0.02	0.31	5
psi(Hsp),p(.)	185.12	2.35	0.02	0.31	3
psi(Hsp+DR+DS),p(P)	185.22	2.45	0.02	0.29	6
psi(Hsp+Tcaco+DS),p(P)	185.30	2.53	0.02	0.28	6
psi(Hsp+Tcaco+DR+DS),p(E)	185.33	2.56	0.02	0.28	7
psi(Hsp+Tcaco),p(.)	185.37	2.60	0.02	0.27	4
psi(Hsp+Tcaco+DS),p(E)	185.39	2.62	0.02	0.27	6
psi(Hsp+Tcaco+DS),p(T)	185.40	2.63	0.02	0.27	6
psi(Hsp+DS),p(E)	185.41	2.64	0.02	0.27	5
psi(Tcaco+DS),p(E+T)	185.43	2.66	0.02	0.26	6
psi(Tcaco),p(E+T)	185.44	2.67	0.02	0.26	5
psi(Hsp+DR),p(.)	185.52	2.75	0.02	0.25	4
psi(Tcaco+Pre+DR+DS),p(.)	185.58	2.81	0.02	0.25	6
psi(WD+Tcaco+DS),p(.)	185.63	2.86	0.02	0.24	5
psi(Hsp+DS),p(E+T)	185.65	2.88	0.02	0.24	6
psi(Tcaco+DS),p(E+P)	185.68	2.91	0.02	0.23	6
psi(Pre+Tcaco),p(.)	185.82	3.05	0.02	0.22	4
psi(Tcaco+DR+DS),p(E)	185.86	3.09	0.02	0.21	6
psi(Hsp+Pre+Tcaco+DS),p(.)	186.00	3.23	0.01	0.20	6
psi(Hsp+DR+DS),p(E	186.19	3.42	0.01	0.18	6
psi(Hsp+DR),p(T)	186.23	3.46	0.01	0.18	5
psi(Hsp+Tcaco+DR+DS),p(T+P)	186.25	3.48	0.01	0.18	8
psi(Tcaco),p(P)	186.34	3.57	0.01	0.17	4
psi(Tcaco),p(E+T+P)	186.35	3.58	0.01	0.17	6
psi(Tcaco),p(E+P)	186.41	3.64	0.01	0.16	5
psi(.),p(.)	186.58	3.81	0.01	0.15	2
psi(Hsp+Tcaco+DS),p(E+T)	186.62	3.85	0.01	0.15	7
psi(WD+Tcaco+DR+DS),p(.)	186.72	3.95	0.01	0.14	6

Chapter 3

Dynamic occupancy modeling of a cryptic ground-dwelling pheasant species in the Upper Blue Nile Basin in Ethiopia

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3.1. Abstract

Modeling the occupancy of species in the context of habitat components is a crucial step to deliver an appropriate conservation strategy. Accounting for imperfect detection in occupancy models helps to conclude on true species distribution and occupancy. We used dynamic occupancy modeling to investigate the influence of habitat covariates on occupancy dynamics of the Near Threatened Harwood's Francolin (*Pternistis harwoodi*) in the Upper Blue Nile Basin in Ethiopia. We used direct observation and playback technique to collect presence/absence data during both a wet and a dry season in 2019 and 2020. By accounting for species' imperfect detection, the model averaged estimates of occupancy probabilities (mean ± SE) across respective seasons were 0.81 ± 0.08 and 0.79 ± 0.07 and detection probabilities were 0.47 ± 0.08 and 0.62 ± 0.06. The colonization and local extinction probability estimates between seasons were 0.59 ± 0.20 and 0.12 ± 0.07, respectively. We demonstrate that occupancy probability significantly decreased with increasing both Normalized Difference Vegetation Index (NDVI: $\beta_{mean} \pm SE = -1.83 \pm 0.66$; 95% CI: -3.12, -0.54) and quadratic term of slope ($SL^2 = -1.51 \pm 0.62$; 95% CI: -2.73, -0.29) in the study area. Furthermore, human disturbance index (HDI: = -1.06 ± 0.54; 95% CI: -2.12, -0.004) significantly negatively influenced the occupancy of the species. As we hypothesized, the detection probability increased significantly as a function of average temperature (0.37 ± 0.13; 95% CI: 0.12, 0.63). There were no statistically significant associations among covariates and the dynamic parameters, yet important covariates such as NDVI slightly negatively influenced colonization, whereas HDI positively influenced local extinction. The aversion of the species towards human disturbance and its persistence at lower NDVI and lower slopes has important implications for conservation strategy in the area. The current study demonstrates empirical evidence of dynamic occupancy modeling for a cryptic ground-dwelling pheasant species in the Upper Blue Nile Basin. Further study is recommended to understand spatiotemporal species-habitat association at fine and landscape scales.

Keywords: Harwood's Francolin, NDVI, Occupancy, Colonization, Local extinction, Conservation

3.2. Introduction

Occupancy modeling of a species in the context of habitat components is critically important for successful conservation and management of ecological systems (Lahoz-Monfort et al., 2014; MacKenzie et al., 2018). The species-habitat associations and distributions are commonly modeled using species distribution models (SDMs) (e.g., Elith et al., 2006; Phillips et al., 2006; Elith and Leathwick, 2009). These models integrate occurrence or count data of species with habitat covariate (i.e., environmental covariate) data to make ecological inferences on species distribution (Elith et al., 2006; Elith et al., 2011). Nevertheless, most of these conventional SDMs use presence-background, true absence or pseudo-absence data without accounting for imperfect detection to predict species distributions (e.g., Guisan and Zimmermann, 2000; Elith et al., 2006; Elith et al., 2011). Such type of models generates biased estimates of true distribution of species as a function of habitat covariates (Kéry et al., 2010). The consideration of imperfect detection for species occupancy and distributions in ecological data is essential to create robust inferences (MacKenzie et al., 2003, 2018; Lahoz-Monfort et al., 2014; Guillera-Arroita et al., 2014; Guillera-Arroita, 2017).

Unlike conventional models such as the popular presence-only models, occupancy models are ‘data hungry models’ and perform better (Jha et al., 2022). Occupancy models need accurate and precise presence/absence data and environmental factors to produce sound conservation and management strategies for wildlife species (MacKenzie et al., 2002, 2018). These factors determine species-habitat associations (Kearney, 2006; Morrison et al., 2012) and are generally classified into resources, risks and conditions (Matthiopoulos et al., 2020). Among these factors, Normalized Difference Vegetation Index (NDVI) as a surrogate for vegetation or ecosystem greenness (Leveau et al., 2018; Green et al., 2019; Debela et al., 2021; Wu et al., 2021), topography (Burner et al., 2019; Campos-Cerqueira et al., 2021; Debela et al., 2021; Jean-Pierre et al., 2022), anthropogenic disturbances (Ramesh and Downs, 2014; McGowan et al., 2012; Abrha et al., 2017; Devarajan et al., 2020), disease (Bailey et al., 2014; Blanco et al., 2019; Chaudhary et al., 2020; Keesing and Ostfeld, 2021), climatic conditions (Debela et al., 2021; Jean-Pierre et al., 2022) and others affect species in spatiotemporal dynamics (Devarajan et al., 2020).

Harwood's Francolin (other name: Harwood's Spurfowl) *Pternistis harwoodi* is an endemic and Near Threatened pheasant species in Ethiopia (BirdLife International, 2018). In Ethiopia, most pheasants, especially francolins, are highly threatened bird species due to hunting and habitat loss (Töpfer et al., 2014; Abrha et al., 2017; Gedeon, et al., 2017). Galliformes face multiple anthropogenic threats (Keane et al., 2005; McGowan et al., 2012; Tian et al., 2018) with hunting (Keane et al., 2005; McGowan et al., 2012), livestock grazing (Wang et al., 2021) and other habitat losses (Bagaria et al., 2021) and climate change (Zahoor et al., 2022; Liu et al., 2023) being the key menacing factors globally. For instance, around 66% of galliform species are threatened by these synergetic effects (McGowan et al., 2012).

Harwood's Francolin was first discovered in 1899 at Ahiya Fej at south of Jama district in the central highlands of Ethiopia. The subsequent field expeditions that focused on identification of new localities for the species were conducted in Kalo Ford (Cheeseman and Sclater, 1935; Urban et al., 1986), near Bichana, and Muger River sub-basins (Urban et al., 1986). The most recent study on the ecology of the species has been frequently reported from Jema and Jara sub-basins (Robertson et al., 1997; Ash and Atkins, 2009; Abrha and Nigus, 2017; Abrha et al., 2017, 2018). Most of these earlier studies were limited by time and research funds. There is a scarcity of information about the mechanisms explaining the distribution and spatiotemporal habitat use dynamics of Harwood's Francolins so far. Currently, the conservation status of the species is downlisted from the 'Vulnerable' to the 'Near Threatened' category on the IUCN Red List (BirdLife International, 2018); yet empirical evidence supports spacious geographical range and conservation action that has practically reduced the threats of the target species at site level are lacking. The species is one of the three endemic bird species that could be prioritized for future flagship conservation and management action plans in Ethiopia (Ash and Atkins, 2009).

Even though most studies on ground-dwelling birds of Africa are derived from static occupancy modeling (e.g., Ramesh and Downs, 2014; Maseko et al., 2017; Smith et al., 2017; Gumede et al., 2022; Abrha et al., 2023; Bitani et al., 2023), studies using dynamic occupancy modelling are lacking, in particular on habitat use of galliform species from Ethiopia. Here, we collected presence/absence data of Harwood's Francolins using a combination of techniques from two-season surveys, which ranged from Mida Woremo to Amuru, Yaso and Bure districts in the Upper Blue Nile Basin (UBNB). We also collected some spatiotemporal sets of covariates from ground truthing (i.e., field surveyed) and remotely sensed levels in the area. Using dynamic (multi-season) occupancy modeling (MacKenzie et al., 2003), we modeled occupancy and associated parameters governing the processes of the system to draw inferences about the occupancy dynamics of the target species in its native range. Therefore, the objective was to determine factors influencing probabilities of occupancy, seasonal colonization, local extinction and detection of the target species across large spatiotemporal scales in UBNB.

3.3. Materials and Methods

3.3.1. Study area

Ethiopia harbors two large blocks of highlands: the Western and Eastern highlands segmented by the East African Rift Valley. The study area is part of the Western highland, which stretches from Mida Woremo district in north Shewa zone of Amhara to the junction among Amuru, Yaso and Bure districts of Oromia, Benishangul-Gumuz and Amhara regions, respectively. The elevation of the study area ranges from 840 to 2520 m a.s.l (Figure 3.1). The dominant habitat vegetation types (for simplicity habitat types) are *Combretum-Terminalia* woodland and wooded grasslands (CTW), Dry evergreen Afromontane forest and grassland complex (DAF), riparian vegetation (RV) and farmland mosaics (Friis et al., 2010). We also included mixed plantations (commonly different fruits and vegetables) scattered along the course of the Jema, Wenchit and Jara Rivers as an additional habitat type in this study.

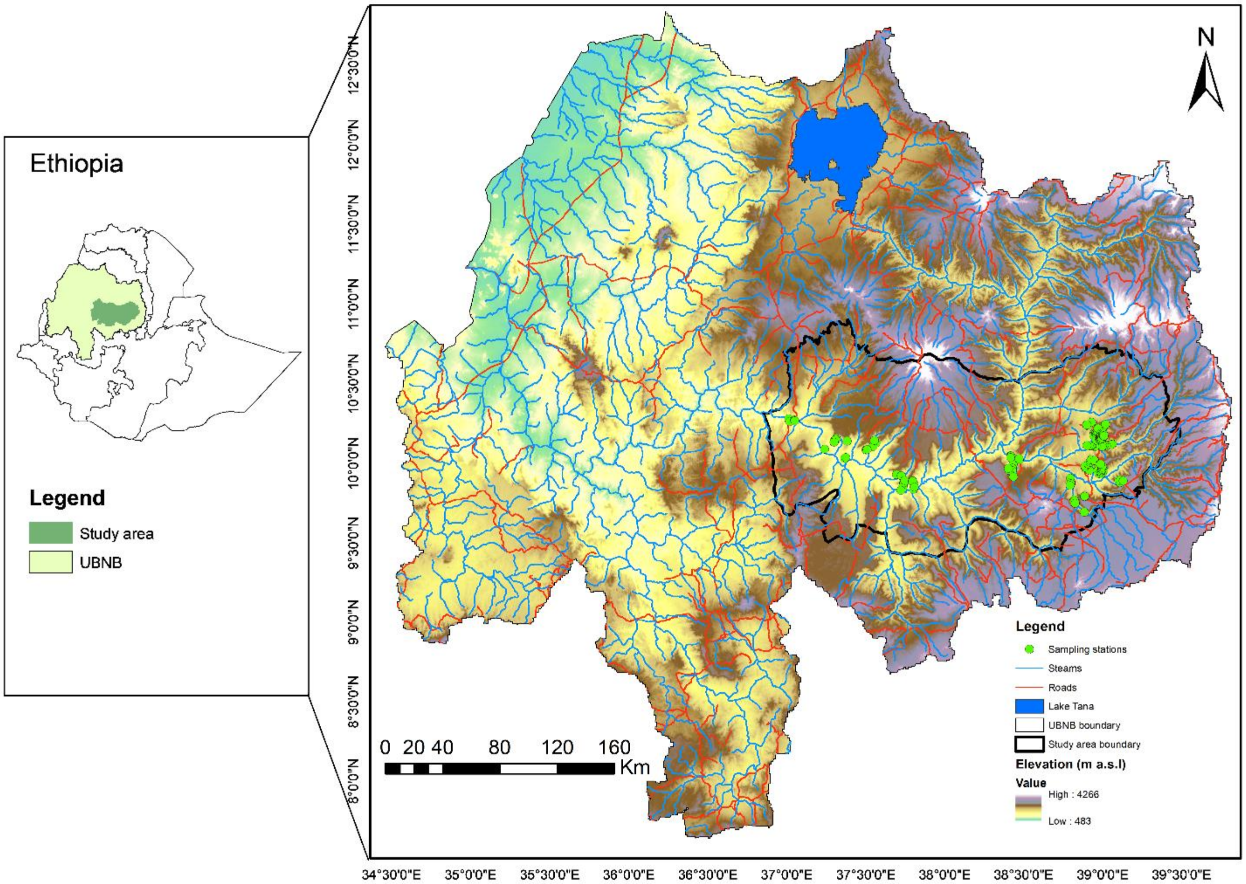

Figure 3.1. Study area in the Upper Blue Nile Basin (UBNB) based on digital elevation model (DEM) (SRTM Global elevation data- https://earthexplorer.usgs.gov). All sampling stations (n = 144) are included in the map.

In UBNB, two Important Bird and Biodiversity Areas (hereafter IBAs) including the Mid-Abbay (Blue Nile) River Basin and Jema and Jara valleys are designated particularly because of the occurrence of endemic species, including Harwood's Francolin (Tilahun et al., 1996; BirdLife International, 2023). According to the biome classification of Fishpool and Evans (2001), the Mid-Abbay is part of the Sudan-Guinea Savanna biome, whereas the Jema and Jara valleys belong to the Afrotropical Highlands biome. Multifaceted anthropogenic disturbances are common phenomena across the Ethiopia highlands (Nyssen et al., 2004), particularly in the habitat of the target species (Robertson et al., 1997; Abrha et al., 2017). Generally, the dominant land cover type of UBNB is farmland mosaics (Tekleab et al., 2013). The mean annual temperature of Jema and Jara valleys and the Mid-Abbay IBAs is 18.61°C (± 0.09 SE) and 20.34°C (± 0.11 SE), and the mean annual precipitation is 3.45 mm (± 4.57 SD) and 5.36 mm (± 8.54 SD), respectively. The area is characterized by a high degree of rainfall variability, with the main rain season from June to September (Mohammed et al., 2022).

3.3.2. Sampling design

3.3.2.1. Presence/Absence data

Field surveys were conducted during two periods, reflecting a dry (26 October 2019 to 29 March 2020) and a wet season (26 August to 14 November 2020). We conducted direct observation approach (Buckland et al., 2004; Sutherland, 2006) to collect presence/absence data in UBNB. It is a valuable field approach for occupancy modeling studies, particularly bird monitoring (Zamora-Marín et al., 2021; Zwerts et al., 2021). We also conducted indirect observations such as auditory detections with stimulus and molted feather occurrences. Including indirect methods helps to produce robust estimates of occupancy and associated parameters for cryptic, shy and rare species (MacKenzie et al., 2018; De Rosa et al., 2022; Goldman et al., 2023), such as Harwood's Francolin.

Sampling stations (hereafter stations) (Figure 3.1) were selected randomly from predetermined line transects across five habitat types in UBNB. We had 61 line transects (average = 2.1 km ± 1.2 SD) and along these transects a total of 144 stations were allocated. Each station was a 50 meter-radius with a minimum distance of 0.7 km between them. The number of stations (i.e., effective sample size) allocated across habitat types was based on the standard design procedure (excluding survey cost) for multi-season occupancy study (MacKenzie and Royle, 2005; MacKenzie et al., 2018). Thus stations were selected according to proportion of each habitat size and habitat preferences of the Harwood's Francolins in UBNB (CTW = 42, DAF = 44, farmland = 32, plantations = 12 and RV = 14). The evergreen scrub vegetation habitat is part of DAF in this study (Friis et al., 2010). Four trained field observers participated and each observer assigned to visit new stations during the entire study to avoid potential observer effect. Data collections were mostly performed in the morning (6:00-10:00) and in the late afternoon (15:00-18:00) as the species exhibit optimum activity patterns in both time blocks (Abrha and Nigus, 2017; Abrha et al., 2018) and this could potentially help to minimize false negative detections. In each station, the observers spent 10-minute bouts to record presence/absence (i.e., detection/non-detection) of Harwood's Francolins.

The same stations were surveyed in both non-consecutive seasons. The distance between stations in the continuous habitat ranged from 0.7 to 3.0 km along transects to maintain independence among stations and minimize spatial autocorrelation. Sampling effort was between one to three repeated surveys with an average survey ($K_{average}$) of 1.95 and 2.56 in both seasons, respectively. Repeated surveys in each site were conducted in alternate order based on morning and late afternoon time blocks. Thus, data were collected in an interval of 4-7 days at each station. The total number of surveys (s stations surveyed K times) was 864. However, due to logistic and time constraints, adverse weather conditions, COVID and security reasons, we only visited 581 stations.

Because direct observation produces low data quality for cryptic and shy species (Zwerts et al., 2021), we used a playback technique (De Rosa et al., 2022) at some of the stations to ascertain the presence of elusive Harwood's Francolins. The target species could remain silent and go undetected due to its behavior essentially in some low-density populations as well as highly disturbed habitat types. In such conditions, we applied a playback call using a Sony speaker (Sony SRS-XB10 portable wireless speaker, Sony Electronics Inc.) immediately after having failed to observe visually. We confirmed that Harwood's Francolins are easily attracted by a playback call during a preliminary assessment survey in 2018 (Gedeon and Abrha, pers. obs). We conducted the survey with an alternation of a 5 s playback call followed by 1 min of silence to aurally detect the target species. This call survey was repeated three times until the target species was lured by the stimulus. The device was held at about 2 m high and rotated for 360° until the target species responded to the stimulus. We applied it carefully to lure the target species by minimizing unnecessary disturbance on the behavior of the species and the entire community. We did not perform playback when there was an obvious reaction towards our presence or an anti-predator behavior by congenerics, other bird and mammal species in the area. Playback was used during morning and late afternoon time block to match with the normal time for calling and the amplitude of the loudspeaker was adjusted to be low to medium depending on the proximity to the center of the station; medium amplitude was adjusted when observers were at the edge of the stations and there was no disturbance on the nearest station.

We combined direct and indirect observations to minimize false absence of the target species. Data were recorded as detection history of a sequence of binary spatial occupancy patterns (detection = 1 and 0 otherwise).

3.3.3. Habitat covariates

We considered habitat covariates both at fine scale and landscape scale levels and climatic conditions. Because fine-scale data have limited spatiotemporal coverage and accessibility (Cisneros-Araujo et al., 2021), most of our covariates were accessed from remotely sensed data (Table 3.1). Our key interests in considering some covariates were mainly derived from previous studies on anthropogenic disturbances (Robertson et al., 1997; Abrha et al., 2017), activity patterns in the context of climate factors (Abrha et al., 2018), and habitat preferences (Abrha and Nigus, 2017) of the target species. We also incorporated ecologically significant climate covariates from previous studies on congeneric species in Ethiopia (Gedeon et al., 2017). Accordingly, six covariates were collected from each station to model occupancy, detection and dynamic parameters (i.e., colonization and extinction).

In our datasets, we used two remotely sensed spatiotemporal covariates (https://earthexplorer.usgs.gov/, accessed on 31 August 2022) including: 1) time-series Normalized Difference Vegetation Index (NDVI; per station at 30 m resolution and 16-day frequency) derived from Landsat 8 OLI/TIRS images (raster band 4 and 5) for the periods of 2019 and 2020. Thus, NDVI = (NIR-RED)/(NIR+RED), where NIR and RED imply near-infrared and red (visible) spectral reflectance, respectively (Kriegler et al., 1969). 2) Elevation and slope were derived from Digital Elevation Model (DEM) of Shuttle Radar and Topography Mission (SRTM-DEM) of 1 arc-second for global coverage (~30m resolution). We downloaded NDVI by minimizing the aerosols and cloud cover noises. Even though elevation was recorded from ground truthing data using handheld Global Positioning System (GPS, with accuracy ~ ± 3m, Garmin eTrex 30), we ultimately took it from the STRM-DEM data for consistency purpose. All remotely sensed data were derived for each station and the satellite-based vegetation index (i.e., NDVI) was extracted for both seasons. The average NDVI for each station was computed. We calculated all these habitat covariates in QGIS (version 3.26.1) software (http://www.qgis.org/). Enhanced

Vegetation Index (EVI) may be preferred over NDVI (Qiu et al., 2018) due to its capability to enhance vegetation monitoring and consider adjustments to reduce the effect of soil and atmospheric noises (Huete et al., 1997; Tuanmu and Jetz, 2015), yet it is not encouraged to apply it in topographically complex area (Matsushita et al., 2007), like the Ethiopian Highlands. NDVI has been extensively used in Ethiopia as a surrogate for aboveground net primary productivity or ecosystem greenness (Muir et al., 2021) and forage availability (Worku et al., 2023), particularly for UBNB (Merga et al., 2022; Moisa et al., 2022). Elevation, slope and average temperature (hereafter temperature) covariates were also in quadratic terms to test the nonlinear influence on occupancy and dynamic parameters.

Following the procedure of Abrha et al. (2017) on the same species, the average human disturbance index (HDI) was determined from each station. HDI covariate was measured after the detection/non-detection data was completed in each station, as this field activity could hamper species detection and impose unnecessary disturbance. The type of human disturbances were classified as: 1) vegetation influence based on local people (VIP) which included cutting, debarking, mowing and thatching; 2) vegetation influence based on livestock grazing pressure (LG); 3) vegetation influence based on fire introduction (VIF) for charcoal preparation, farming activities and honey production and 4) hunting practices (HP). In this study, other minimal anthropogenic disturbances (Abrha et al., 2017) and natural predation effects were not measured due to logistical constraints. Some of these threats were also site-specific in the basin. The HDI covariate of each station was calculated as:

$$HDI = VIP \times 0.4 + LG \times 0.3 + HP \times 0.25 + VIF \times 0.15 \ldots\ldots\ldots\ldots\ldots\ldots \text{ equation 1}$$

The extent of disturbance weight for each disturbance class was assigned based on the previous research findings in the Jema valley sub-basin (Abrha et al., 2017). We followed the protocol of Barber-Meyer et al. (2013) for quantifying and assigning of HDI weight for dynamic occupancy modeling of Harwood’s Francolins.

We obtained remotely sensed climatic data such as temperature and precipitation from National Aeronautics and Space Administration/Prediction of World Wide Energy Resources (NASA/POWER) satellite-based weather system (https://power.larc.nasa.gov/data-access-viewer/, accessed on 27 August 2022). Because meteorological stations were absent near to the stations, with exception close to Gohatsion (Mohammed et al., 2022), we preferred remotely sensed data. Both data were extracted based on daily average values exactly corresponding to the Julian day of repeated surveys in each station. We lacked ground truthing climatic data and there was no literature related to our focus in Ethiopia to perform bias correction for our data.

We modeled initial occupancy probability (ψ_1) as a function of site-specific covariates including NDVI, slope, elevation, and HDI and the quadratic terms of both topographic covariates. Detection probability (ρ) was modeled as a function of sample covariates such as temperature and its quadratic term, precipitation and season. In addition, detection probability was modeled as a function of NDVI and HDI. Here, seasonal variation in ecosystem or vegetation greenness (i.e., NDVI) and HDI were also hypothesized to influence the detectability of Harwood's Francolins. Accordingly, we tested the influence of covariates on occupancy, detection, local colonization and extinction parameters (Table 3.1).

Table 3.1. Description of habitat covariates influencing initial occupancy probability (ψ_1), colonization probability (γ), extinction probability (ε), and detection probability (ρ). Some empty cells in the table indicate that the value of coefficients (i.e., beta-β) was not checked for some parameters.

Covariate	Units	Description and source	Predicted effect on dependent variable				Hypotheses and references
			ψ_1	γ	ε	ρ	
NDVI	Dimensionless	Extracted for each station from Landsat 8 Operational Land Imager (OLI) / Thermal Infrared Sensor (TIRS) images. Downloaded from: https://earthexplorer.usgs.gov/	-	-	+	-	Ecosystem greenness influences the occurrence of bird species (Leveau et al., 2018; Green et al., 2019; Debela et al., 2021; Wu et al., 2021). Harwood's Francolins prefer shrubs, herbs and sparse trees in and around farmlands (Abrha and Nigus, 2017) where food sources are available.
Elevation	m	Extracted for each station from Digital Elevation Model (DEM) of Shuttle Radar and Topography Mission (SRTM-DEM). Downloaded from: https://earthexplorer.usgs.gov/	+	+	-		Elevation influences the occupancy of bird species (Burner et al., 2019; Campos-Cerqueira et al., 2021; Jean-Pierre et al., 2022). Harwood's Francolins' occupancy increases with elevation because increasing elevation may decrease human disturbance in most parts of the area.
Slope	Percent	See elevation	+	+	-		Topographic variables such as slope affect bird species (Debela et al., 2021). The target species avoids extremely steep slopes in various habitat types (Abrha and Nigus, 2017).
HDI	Dimensionless	The index of human disturbance across stations (i.e., at fine scale level)	-	-	+	-	Anthropogenic disturbances influence occupancy of bird species (Abrha et al., 2017; Devarajan et al., 2020).
Season	Julian date	The dry and wet seasons during data collection				+/-	Seasons influence detectability of Harwood's Francolins due to seasonal variation in food availability.
Temperature	°C	Daily temperature extracted for each station from NASA/POWER) satellite-based weather system. Downloaded from: https://power.larc.nasa.gov/data-access-viewer/				+	Temperature and precipitation influence detectability of Harwood's Francolins (Abrha et al., 2018), since these factors affect reproductive success of bird species (Skagen and Adams, 2012; Mares et al., 2017). Hence, the odds of detecting the target species may increase.
Precipitation	mm	See temperature				+	

3.3.4. Data analyses

The dynamic occupancy modeling was performed using the program PRESENCE 12.38 (Hines, 2006). The modeling (MacKenzie et al., 2003) was used to determine the effect of habitat covariates on each parameter estimate (ψ_1, γ, ε, and ρ) of Harwood's Francolins. This modeling approach explicitly integrates changes in an occupancy rate of a site over time with dynamic parameters: colonization and local extinction probabilities. The colonization probability (γ) is defined as that an unoccupied station in season t is occupied by the species in season $t + 1$; and extinction (ε) is defined as the probability that a station occupied in season t is unoccupied by the species in season $t + 1$ (MacKenzie et al., 2003, 2018). The assumptions of this modeling approach (MacKenzie et al., 2003; 2018) are: 1) No unmodeled heterogeneity in all parameters, 2) Occupancy state is static within a season, 3) Independence of detection of species and detection history in each station, and 4) Absence of false positive detections.

Prior to analyses, all continuous covariate data were normalized to increase the software performance. We used Pearson's correlation coefficients (r) and variance inflation factor (VIF) to assess for multicollinearity between independent covariates in IBM SPSS statistics (version 20) (Table S1). All covariates did not show a strong correlation ($r < 0.7$) (Dormann et al., 2013). Because the VIF values were less than three, there were no confounding effects between independent covariates. Hence, all covariates were retained for the subsequent competing model sets. Then, based on previous ecological studies on francolin species (Robertson et al., 1997; Abrha and Nigus, 2017, Abrha et al., 2017; Gedeon et al., 2017; Abrha et al., 2018), we tested combinations of habitat covariates effect on each parameter. The null model ($\psi_1(.),\gamma(.),\varepsilon(.),\rho(.)$) was also analyzed for comparison in the candidate sets.

The ratio of effective sample size (n) to the number of parameters (K) (i.e., n/K) was determined. Then we used Akaike's information criteria corrected for small sample sizes (AIC_c) as $n/K \leq 40$ (Burnham and Anderson, 2002). This procedure helped with model selection by producing competing modeling with combinations of covariates of interest in the order of parsimony and cumulative model weight of each covariate (Burnham and Anderson, 2002). We built a total of 33 models depending on biological and ecological hypotheses about habitat preference, threat, and behavior of Harwood's Francolins. Because most candidate models revealed similar levels of support, our models did not show a "better" representation of the data (MacKenzie et al., 2018). Meanwhile, we incorporated competing models constituted from the top to the bottom, i.e., continuing the list until the cumulative Akaike Weight (ωi) of all models was at least 0.95 (Symonds and Moussalli, 2011). The level of significance was based on 95% CI (zero-overlapping method) and beta (β) coefficient estimates were used to understand the magnitude and effect of covariates on initial occupancy, colonization, local extinction and detectability. We also checked the presence of uninformative parameters using information criterion (IC) in the candidate model sets (Arnold, 2010; Leroux, 2019). Finally, model averaging approach was employed to calculate averaged β coefficient estimates ($\beta_{mean} \pm SE$) (Burnham and Anderson, 2002; Symonds and Moussalli, 2011).

3.4. Results

3.4.1. Spatiotemporal patterns in occupancy and dynamic parameters

Harwood's Francolins were detected at 71 and 93 stations throughout the three sampling efforts in the first and second seasons, respectively. This yielded naïve occupancy estimates of 0.49 and 0.65 without correcting for imperfect detection. Based on the null model $((\psi_1(.),\gamma(.),\varepsilon(.),\rho(.))$, initial occupancy, detection, colonization, and extinction probability estimates were 0.76 (95%: 0.64–0.86), 0.58 (95%: 0.52–0.63), 0.50 (95% 0.25–0.75), and 0.12 (0.04–0.28), respectively (Table S2). By accounting for imperfect detection, the average estimates of initial occupancy across seasons were greater than the naïve occupancy. Following the inclusion of covariates in the models, the estimates of initial occupancy across habitat types were similar across habitats, except for plantations. The detection probability was similar across the habitats. The colonization estimates were similar in most habitat types but were lower in plantations. The local extinction estimates were similar in most habitats but slightly greater in plantations (Figure 3.2).

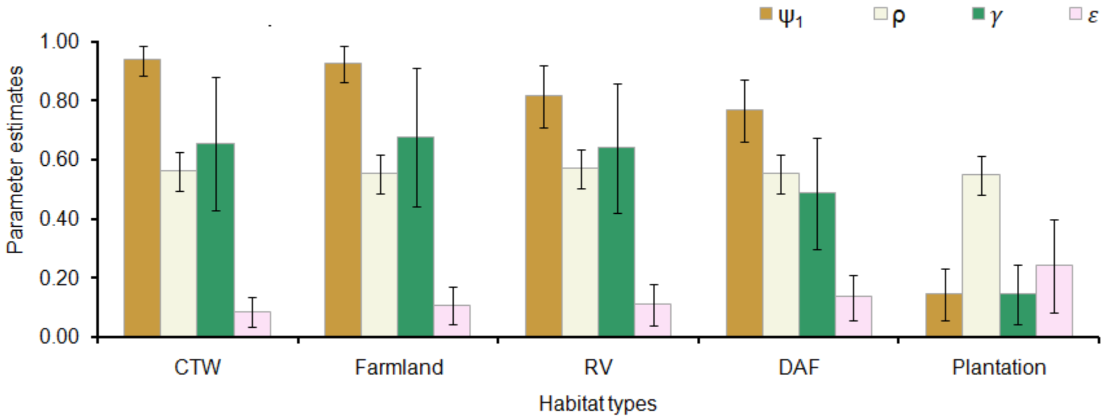

Figure 3.2. Average estimates of initial occupancy probability (ψ_1), detection probability (ρ), colonization probability (γ) and extinction probability (ε) across different habitat types in the Upper Blue Nile Basin (estimation calculated from models with $\Delta AIC_c<4.00$). Error values are standard errors. Abbreviations: CTW-*Combretum-Terminalia* woodland and wooded grasslands; DAF-Dry evergreen Afromontane forest and grassland complex and RV-riparian vegetation.

The averaged estimates of occupancy probability ($\hat{\psi}$) Harwood's Francolins across seasons were 0.81 ± 0.08 and 0.79 ± 0.07, respectively and averaged detection probability ($\hat{\rho}$) estimates were 0.47 ± 0.07 and 0.62 ± 0.06, respectively. The average detectability increased by 32% from 0.47 in 2019 to 0.62 in 2020 (Figure 3.3A). The seasonal colonization and local extinction probability estimates during study seasons were 0.59 ± 0.20 and 0.12 ± 0.07, respectively (Figure 3.3B).

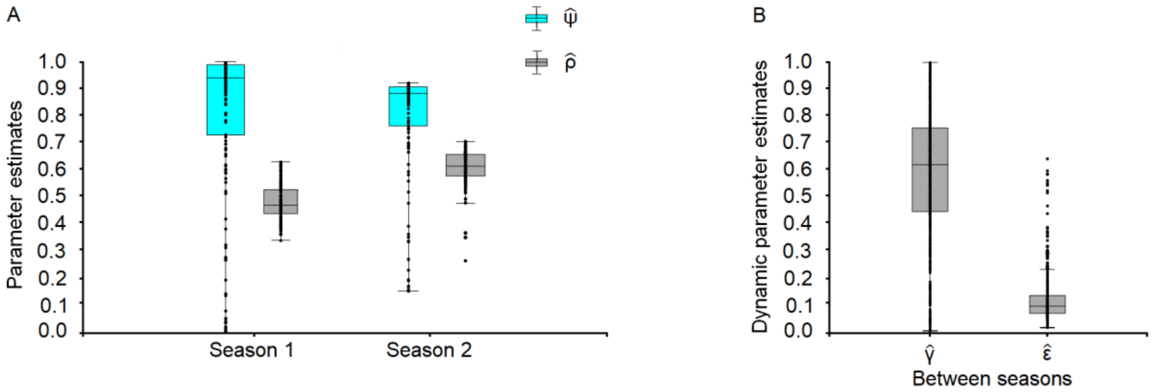

Figure 3.3. Model averaged estimates of occupancy probability ($\hat{\psi}$) and detection probability ($\hat{\rho}$) (A) across seasons and dynamic parameters ($\hat{\gamma}$-colonization and $\hat{\varepsilon}$-extinction) (B) between seasons. Estimations were calculated from top models with $\Delta AIC_c < 4.00$.

The null model was not included among the top candidate sets. In the top-ranked models HDI, NDVI, slope and its quadratic term, temperature and the effect of seasons were incorporated. These competing models were largely built without interactions (except for quadratic fit of elevation, slope and temperature) to model underlying dynamic processes and are ranked in the order of the lowest ΔAIC_c. The cumulative weight ($\Sigma\omega_i$) of the top-ranked models ($\Delta AIC \leq 2.0$) was 0.53 and the first-ranked model ($\psi_1(HDI+NDVI+SL+SL^2),\gamma(NDVI),\varepsilon(.),\rho(S+T)$) received 0.11 model weight separately which reasonably imply the presence of other competing models to draw inferences about the occupancy and underlying dynamic processes (Table 3.2). In other words, our competing models showed model selection uncertainty and hence weak support for the research questions. Therefore, to improve the representation of our data, we applied model averaging, which contained all competing models with $\Delta AIC_c < 4.00$ to produce the strongest statistical inferences following the recommendation of Symonds and Moussalli (2011). Moreover, the model weight (ω_i) of covariates that appeared in the top-ranked models was increased by removing other models with ΔAIC_c less than six (Richards, 2005; Richards et al., 2011).

Table 3.2. Model selection with covariates for dynamic occupancy analysis. Model rankings are based on the Akaike information criterion (AIC) corrected for small sample size (AIC_c) values and only candidate models with $\Delta AIC_c < 2.00$ and null model are reported. Model weight (ω_i), number of parameters (K), and twice the negative log-likelihood (-2l) are reported.

Model	AIC_c	ΔAIC_c	ω_i	K	-2l
$\psi_1(HDI+NDVI+SL+SL^2)$, $\gamma(NDVI)$, $\varepsilon(.),\rho(S+T)$	727.85	0.00	0.11	15	694.10
$\psi_1(HDI+NDVI+SL+SL^2)$, $\gamma(NDVI)$, $\varepsilon(.),\rho(NDVI+S+T)$	728.42	0.57	0.08	16	692.14
$\psi_1(HDI+NDVI+SL+SL^2)$, $\gamma(NDVI)$, $\varepsilon(NDVI),\rho(S+T)$	728.75	0.90	0.07	16	692.47
$\psi_1(HDI+NDVI+SL+SL^2)$, $\gamma(NDVI)$, $\varepsilon(.),\rho(HDI+S+T)$	728.90	1.05	0.06	16	692.62
$\psi_1(HDI+NDVI+SL+SL^2)$, $\gamma(.),\varepsilon(.),\rho(NDVI+S+T)$	729.05	1.20	0.06	15	695.30
$\psi_1(HDI+NDVI+SL+SL^2)$, $\gamma(.),\varepsilon(.),\rho(S+T)$	729.35	1.50	0.05	14	698.09
$\psi_1(HDI+NDVI+SL+SL^2)$, $\gamma(NDVI)$, $\varepsilon(HDI),\rho(NDVI+S+T)$	729.46	1.61	0.05	17	690.60
$\psi_1(HDI+NDVI+SL^2)$, $\gamma(NDVI)$, ε $(.),\rho(S+T)$	729.51	1.66	0.05	14	698.25
…					
$\psi_1(.),\gamma(.),\varepsilon$ $(.),\rho$ $(.)$	772.65	44.80	0.00	4	764.36

Abbreviations: ψ_1(psi) = initial occupancy probability, γ = colonization probability, ε = extinction probability, and ρ = detection probability, HDI = human disturbance index, NDVI = Normalized Difference Vegetation Index, SL= slope, SL^2 = quadratic term of slope, S = season and T = temperature.

3.4.2. Influence of habitat covariates on Harwood’s Francolins

As we hypothesized, NDVI correlated significantly negatively with the initial occupancy probability of Harwood’s Francolins at the stations in UBNB ($\beta_{mean} \pm SE = -1.83 \pm 0.66$; 95% CI: -3.12, -0.54). Thus, the occupancy probability estimates decreased by 76% with increasing NDVI. The habitat use of the target species was also decreased with increasing quadratic slope, suggesting that the species revealed avoidance towards steep and extremely steep slopes (β_{mean} ± SE = -1.51 ± 0.62; 95% CI: -2.73, -0.29). We also observed that the occupancy probability decreased by 47% across the quadratic slope gradient. The occupancy probability of Harwood's Francolins significantly decreased with increasing HDI (β_{mean} ± SE = -1.06 ± 0.54; 95% CI: -2.12, -0.004) and was decreased by 17% across HDI gradient (Table 3.3 and Figure 3.4).

Table 3.3. Cumulative model weight ($\Sigma\omega_i$) and influence of covariates calculated from model-averaged beta coefficient estimates and standard errors (β_{mean} ± SE). β estimates values are shown with 95% confidence intervals and p values. Zero overlapping shows non-significant values. Only fixed influences are included.

Covariate	$\Sigma\omega_i$	β_{mean} ± SE	95% CIs		P value
			Lower	Upper	
Occupancy (Ψ_1)					
Normalized Difference Vegetation Index	1.00	-1.83 ± 0.66	-3.12	-0.54	0.0056
Quadratic Slope	1.00	-1.51 ± 0.62	-2.73	-0.29	0.0148
Human disturbance index	0.96	-1.06 ± 0.54	-2.12	-0.004	0.0484
Slope	0.88	0.94 ± 0.52	-0.08	1.96	0.0831
Colonization (γ)					
Normalized Difference Vegetation Index	0.62	-1.39 ± 1.00	-3.34	0.56	0.1652
Extinction (ε)					
Human disturbance index	0.15	0.50 ± 0.44	-0.36	1.35	0.2587
Normalized Difference Vegetation Index	0.10	0.86 ± 0.63	-0.38	2.10	0.1731
Detection (ρ)					
Season (pooled)	1.00	0.19 ± 0.27	-0.34	0.73	0.4914
Temperature	1.00	0.37 ± 0.13	0.12	0.63	0.0045
Normalized Difference Vegetation Index	0.38	-0.24 ± 0.16	-0.55	0.07	0.1338

As expected, temperature was significantly positively correlated with the detectability of Harwood's Francolins across stations and it was increased by 64% (β_{mean} ± SE = 0.37 ± 0.13; 95% CI: 0.12, 0.63) (Table 3.3, Figure 3.4). We found a positive association between season and detectability and there was also a negative association between vegetation greenness and detectability, albeit non-significant values among them (Table 3.3). The colonization probability was associated negatively with NDVI, but 95% CI overlapped zero (β_{mean} ± SE = -1.39 ± 1.00; 95% CI: -3.34, 0.56). The local extinction probability was positively correlated with human disturbance index and NDVI but found no statistical support (Table 3.3).

Our models also show that elevation and its quadratic effect had generally negligible influence on occupancy and related parameters. Similarly, precipitation and quadratic temperature had insignificant influence on the detectability of Harwood's Francolins during our study seasons. Quadratic slope did not seem to be an important covariate to affect the dynamic parameters. From a model averaged estimate perspective, we also showed occupancy and detection probability patterns as a function of significant covariates across stations (Figure S1).

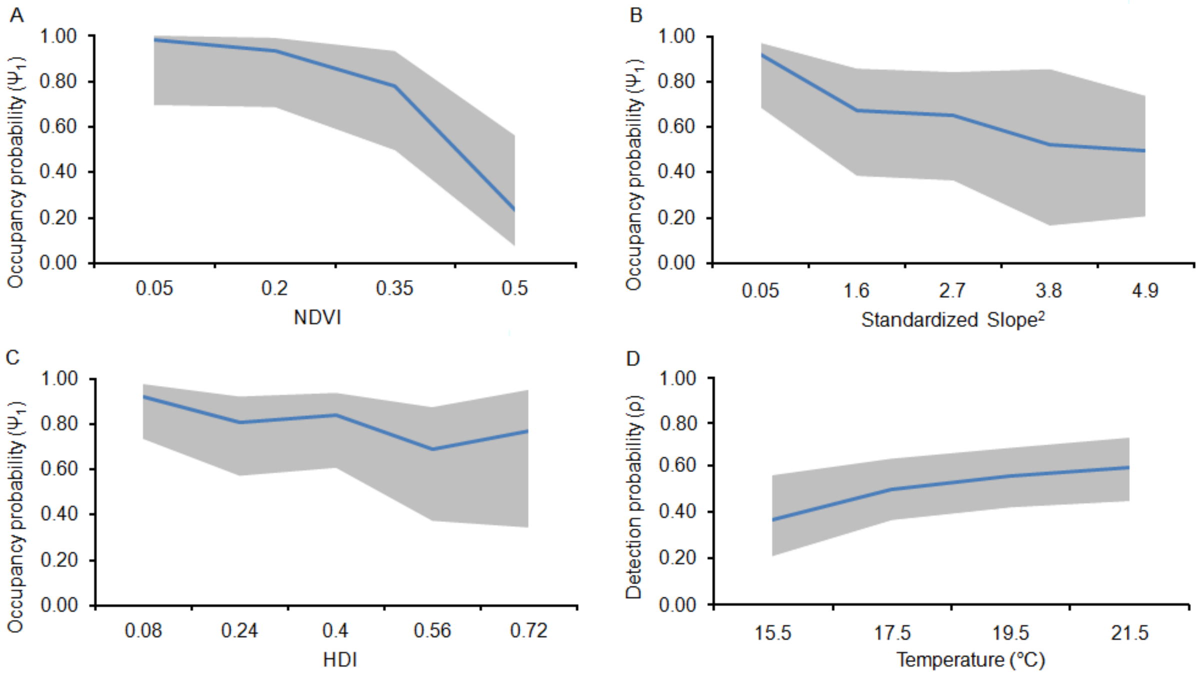

Figure 3.4. Model averaged estimates of initial occupancy (ψ_1) and detection (ρ) probabilities for Harwood's Francolins. The left column (A and C) and right column (B) indicate the influence of NDVI, quadratic term of standardized slope and HDI on initial occupancy probability (ψ_1), respectively. The bottom right (D) indicates the influence of temperature (°C) on detection probability (ρ) of the species in UBNB. Parameter estimates were derived from the top-ranked models and the shaded area in each graph indicates 95% confidence intervals.

3.5. Discussion

3.5.1. Dynamic occupancy patterns of Harwood's Francolins

The dynamic occupancy modeling is applied for the first time in Ethiopia (see also Devarajan et al., 2020) to study habitat use and distribution of Harwood's Francolins across a huge geographical scale in the Upper Blue Nile Basin (UBNB). In this study, we also incorporated previously poorly documented populations from west of the Mid-Abbay IBA dominated by *Combretum-Terminalia* woodland and wooded grasslands (CTW) in the Sudan-Guinea Savanna biome. The nearest and the only locality recorded (*c*.140 km) to our new stations was found at Kalo Ford by Cheesman and Sclater (1935) and recently confirmed by Ash and Atkins (2009), which is near to the junction between Muger and Abbay River. Our results show that the target species essentially uses a mosaic of habitats across several sub-basins, comprising a larger geographic scale than previously known (Ash and Gullick, 1989; Robertson et al., 1997; Abrha and Nigus, 2017; Abrha et al., 2017). Most of our localities for this species also supported the exhaustive field survey of Ash and Atkins (2009).

By pooling seasons, the averaged detection probability of Harwood's Francolins (0.55 ± 0.07 SE) was more than doubled in occupancy modeling than reported using conventional distance sampling (CDS) method from Jema valley in Afrotropical Highlands biome (Abrha and Nigus, 2017). This suggests that occupancy modeling delivers more reliable estimations for this restricted range species than another method which do not explicitly account for imperfect detection, in concordance with other reports across different taxa (Kéry et al., 2010; Thapa and Kelly, 2017; Taylor et al., 2021).

Dynamic occupancy modeling also demonstrated to model colonization and extinction probabilities of Harwood's Francolins with and without covariates. Even though colonization probability was greater than extinction probability (Figure 3.3B), the overall level of occupancy of Harwood's Francolins was decreasing between seasons. This is because the estimated net probability of extinction was larger than the estimated net probability of colonization depending on the inference of population trajectory (Mackenzie et al., 2018). The highest extinction probability at plantations was not surprising because this habitat is highly disturbed due to human activities (including hunting, cutting, burning, etc.) and livestock grazing (Abrha et al., 2017). Natural predation, which is a known threat for ground dwelling pheasants (Little and Crowe, 2004), could also be a possible cause for local extinction of Harwood's Francolins. Our models also revealed that extinction probability was positively associated with both HDI and NDVI (Table S1).

Drawing inference from a two-season dataset could yield erroneous parameter estimates, yet our preliminary study showed important findings for occupancy and the dynamic parameters of Harwood's Francolins. Interestingly, the employed field techniques enabled us to scrutinize about the mechanisms that drive the spatiotemporal occupancy patterns and dynamics of the target species across two contiguous biomes in UBNB. Similarly, it has been reported that using combined methods generates effective parameter estimates and facilitates appropriate bird conservation plans and recommendations for future studies (De Almeida-Rocha et al., 2019; Zamora-Marín et al., 2021; Zwerts et al., 2021).

3.5.2. Influence of covariates on habitat use of Harwood's Francolins

Bird species occupancy is influenced by finer-scale and landscape scale covariates (e.g., Harms et al., 2017; Smith et al., 2017; Green et al., 2019; Morante-Filho et al., 2021; Gumede et al., 2022), particularly galliform species (Ramesh and Downs, 2014; Maseko et al., 2017; Bitani et al., 2023). Our results showed that NDVI significantly negatively affected the occupancy of Harwood's Francolins (Figure 3.4A). NDVI shows seasonal phenological dynamics in UBNB (Muir et al., 2021; Moisa et al., 2022). The average NDVI derived from wet and dry season data ranged from 0.05 to 0.45 (mean = 0.22; SD = 0.1), implying that stations were dominated by herbaceous and sparse vegetation. The lowest occupancy probability was recorded in plantation habitats along the course of tributary rivers, which had the highest spectral reflectance of vegetation. Therefore, occupancy probability decreased with increasing NDVI, meaning that Harwood's Francolins preferred low vegetation or sparse trees, evergreen scrub vegetation and herbaceous-dominated habitats in CTW and its transformed habitat to farmland mosaics, in concordance with previous results on the ecology of the target species (Abrha and Nigus, 2017), the endangered Black-fronted Francolin (*Pternistis atrifrons*) (Töpfer et al., 2014; Gedeon et al., 2017) in south Ethiopia and other francolin species in Africa (van Niekerk, 2017; Lerm et al., 2019). The distribution of evergreen vegetation is identified on the lower edge of the DAF (Friis et al., 2010) and it is treated as DAF vegetation habitat in this study. Our results also show that forest habitat (DAF) had high NDVI and were shelters for Harwood's Francolins, particularly during dry season, yet the habitat was not highly preferred as human, livestock grazing and other stressors considerably existed as compared to other habitats.

Our results also emphasize that the quadratic term of slope significantly limits the occupancy probability, suggesting that Harwood's Francolins preferred flat, gentle and moderate slopes over steep and extremely steep slopes (Figure 3.4B), similar to the results of Li et al. (2009); Abrha and Nigus (2017) and Abrha et al. (2018). Across most stations, flat, gentle and moderate slopes were characterized by herbaceous, scattered trees and bushy vegetation important for food and nesting grounds (pers. obs.). Flat low and high-elevation habitats are highly disturbed areas, whereas steep and extremely steep slopes are less disturbed due to inaccessible to human encroachment (Abrha and Nigus, 2017). The flat terrain and plateau of UBNB are dominated by farming activities (Tekleab et al., 2013). The steep and extremely steep slopes featured by rocks and escarpments are home to raptors, primates and carnivores in the Western highlands of Ethiopia (Saavedra, 2009). Our results show that Harwood's Francolins mostly avoided these gradients possibly due to 1) the presence of potential predators and in such distinctive gradients, for instance, Leopards (*Panthera pardus*) are reported to prey upon francolins in the Abune Yosef massif (Saavedra et al., 2009) and Gelada monkeys (*Theropithecus gelada*) in the Guassa Community Conservation Area (Lin et al., 2020); 2) because steep slopes are grass free stripes and are rarely cultivated in the highlands of Ethiopia (Nyssen et al., 2004).

Globally, the mass extinction of vertebrate species is intensified by anthropogenic disturbances (Dirzo et al., 2014; Ceballos et al., 2015; Ceballos et al., 2020). For instance, most bird species are threatened by human disturbances (Hilton-Taylor et al., 2009), particularly Galliformes (Keane et al., 2005; McGowan et al., 2012; Ramesh and Downs, 2014; Tian et al., 2018). In Ethiopia, anthropogenic disturbances increasingly threatened birds (Asefa et al., 2017), particularly francolin species (Töpfer et al., 2014; Abrha and Nigus, 2017; Abrha et al., 2017; Gedeon et al., 2017). Not surprisingly, our results show that human-induced disturbances posed a significant threat to Harwood's Francolins occurrence at the fine scale level (Figure 3.4C), which supported the *a priori* hypothesis. In this study, we did not include the effect of mining on the species due to budget and time constraints. Similar to our target species, the multitude of threats the Critically Endangered Djibouti Francolin (*Pternistis ochropectus*) faces are overgrazing, forest fragmentation, hunting and death of *Juniperus procera* trees (Fisher et al., 2009; BirdLife International, 2023). Previously, it was also reported that Harwood's Francolins avoid various threat factors (Robertson et al., 1997), specifically owing to vegetation disturbances, livestock grazing, burning, and hunting in Jema and Jara valleys (Abrha et al., 2017).

Colonization probability was also inversely correlated with HDI; albeit non-significant association. To confirm these findings, our hypothesis also supports that colonization probability decreased with increasing human disturbances. Our results also show a non-significant negative association between NDVI and colonization of Harwood's Francolins. However, a relatively high 95% CIs, and beta coefficient for model-averaged estimate of NDVI shows that colonization probability was greater in lower vegetation reflectance characterized by shrubby, bush and herbaceous stations in the area. There were no significant determinant covariates for colonization and extinction, suggesting little variation in the dynamic processes governing changes in the species-habitat association in spatiotemporal patterns.

In terms of temperature, we found a significant positive association of detection probability (Figure 3.4D), suggesting that Harwood's Francolins detectability was higher at higher temperature, similar to the findings of Skagen and Adams (2012). We encountered the target species commonly in scrub vegetation and herbaceous covers intermingled with sparse trees in CTW and adjacent vegetation habitats. Such land use is commonly characterized by low NDVI and high temperature and this phenomenon strongly facilitates the habitat use of Harwood's Francolins. Like our findings, temperature and NDVI are inversely correlated in Ethiopia (Muir et al., 2021), particularly for UBNB (Merga et al., 2022; Moisa et al., 2022). Therefore, across our study area, detectability increased with increasing temperature, and it was lower at stations with higher NDVI.

3.5.3. Conservation implications and future directions

Even though we did not contrast various methods for the occurrence data as it was not our focus, the combination of multiple field methods collects reliable and comprehensive datasets, thereby drawing fundamental inferences for conservation purpose of this cryptic species. There were no false positive detections in our surveys and false negative detections were minimized by study design, essentially the application of playback technique. However, we cannot rule out entirely that, due to the topography of the study area, our playback sometimes may have disturbed the target species located at other stations. Future studies should consider potential disturbances if stations are placed too close to each other.

The persistence of Harwood’s Francolins at lower ecosystem greenness and lower slope gradients has important implications for in-situ conservation strategy. The detection probability of the target species was strongly influenced by temperature, suggesting that the target species favors lowland areas featured by high temperature in UBNB. Ultimately, this factor could have important contribution to the breeding phenology of the species.

Determination of minimum and maximum survey efforts (*K*) to increase species detectability (Pellet and Schmidt 2005; Sewell et al., 2010; McGrath et al., 2015) is a critical step for future research design. Accordingly, the appropriate survey effort for the target species needed at 0.60 target detection probability is a single effort and a maximum of six efforts is required at 0.99 detection probability to confirm true absence of the species in a station.

To conclude, our results highlight that Harwood’s Francolins exist across a large geographical scale in UBNB. The dynamic occupancy modeling informs effective conservation and management implications for the target species. Nonetheless, the target species could also be affected by other covariates, particularly at a finer scale (e.g., plant species richness, canopy cover, shrub height, etc.) which we did not incorporate in this study due to budget limitations and time constraints.

Most IBAs in Ethiopia, particularly for UBNB are not protected and have little contribution to globally important restricted range species, such as Harwood’s Francolins and other biodiversity. We urge special attention to the conservation and management of this threatened pheasant species in *Combretum-Terminalia* woodland and grassland, farmland mosaics, evergreen scrub and riparian vegetation habitats across several sub-basins. We also recommend further study to test the influence of fine-scaled, landscape-scaled and climatic covariates on occupancy dynamics of Harwood’s Francolin across spatiotemporally replicated surveys.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Research Ethics Clearance

This part of AMA's PhD work was permitted by the Ethiopian Wildlife Conservation Authority (EWCA) in Amhara (Ref. No: 31/74/12), Oromia (Ref. No: 31/79/12) and Benishangul-Gumuz (Ref. No: 31/70/12) regional states.

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3.6. References

Abrha, A.M., Nigus, H.K., 2017. The ecology of Harwood's Francolin *Pternistis harwoodi* (Aves: Galliformes: Phasianidae) at Merhabete District, central highlands of Ethiopia: implications for conservation. J. Threat. Taxa. 9 (9), 10633–10641. http://doi.org/10.11609/jott.3189.9.9.10633-10641.

Abrha, A.M., Nigus, H.K., Weldetnsae, B.G., Tilahun, M., Nigusse, A.G., Deribew, K.T., 2017. Effects of human disturbances on two sympatric francolin species in the Central Highlands of Ethiopia. Podoces 12 (1), 13−21. https://wesca.net/Podoces/podoces12.1.html.

Abrha, A.M., Zelelew, S.A., Nigus, H.K., Alelign, A., 2018. Diurnal activity patterns of Harwood's Spurfowl *Pternistis harwoodi* in relation to habitat types and climatic conditions in the Central Highlands of Ethiopia. Ostrich 89 (2), 1–7. https://doi.org/10.2989/00306525.2018.1429505.

Abrha, A.M., Gedeon, K., Podsiadlowski, L., Weldesilasie, D.M., Töpfer, T., 2023. Occupancy of the Ethiopian endemic Moorland Francolin in pristine and degraded. https://doi.org/10.1002/ece3.10551

Arnold, T. W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manage. 74(6), 1175–1178. https://doi.org/10.2193/2009-367.

Asefa, A., Davies, A.B., McKechnie, A.E., Kinahan, A.A., van Rensburg, B.J., 2017. Effects of anthropogenic disturbance on bird diversity in Ethiopian montane forests. The Condor 119(3), 416–430. https://doi.org/10.1650/CONDOR-16-81.1.

Ash, J. S. & Atkins, J. 2009. Birds of Ethiopia and Eritrea: an atlas of distribution. Christopher Helm, London.

Ash, J.S., Gullick, T.M., 1989. The present situation regarding the endemic breeding birds of Ethiopia. Scopus, 13(1), 90–96. https://biostor.org/reference/135205.

Bagaria, P., Thapa, A., Sharma, L.K., Joshi, B.D., Singh, H., Sharma, C.M., Sarma, J., Thakur, M., Chandra, K., 2021. Distribution modelling and climate change risk assessment strategy for rare Himalayan Galliformes species using archetypal data abundant cohorts for adaptation planning. Clim. Risk Manag. 31, p.100264. https://doi.org/10.1016/j.crm.2020.100264.

Bailey, L.L., MacKenzie, D.I., Nichols, J.D., 2014. Advances and applications of occupancy models. Methods Ecol. Evol. 5(12), 1269–1279. https://doi.org/10.1111/2041-210X.12100.

Barber-Meyer, S.M., Jnawali, S.R., Karki, J.B., Khanal, P., Lohani, S., Long, B., MacKenzie, D.I., Pandav, B., Pradhan, N.M.B., Shrestha, R., Subedi, N., 2013. Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J. Zool. 289(1), 10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x.

BirdLife International. 2018. *Pternistis harwoodi*. The IUCN Red List of Threatened Species 2018: e.T22678815A131514381. https://www.iucnredlist.org/fr/species/22678815/131514381. Accessed on 27 June 2023.

BirdLife International, 2023. Important Bird Area factsheet: Mid-Abbay (Blue Nile) river basin. Downloaded from http://datazone.birdlife.org/site/factsheet/6250. Accessed on 10 May 2023.

BirdLife International (2023) Species factsheet: *Pternistis ochropectus*. Downloaded from http://datazone.birdlife.org/species/factsheet/djibouti-francolin-pternistis-ochropectus. Accessed on 19 June 2023.

Bitani, N., Cordier, C.P., Smith, D.A.E., Smith, Y.C.E., Downs, C.T., 2023. Microhabitat requirements and occupancy of understorey bird forest specialists in Southern Mistbelt Forests of KwaZulu-Natal, South Africa. Ecol. Manag. 549, 121484 https://doi.org/10.1016/j.foreco.2023.121484.

Blanco, G., Cortés-Avizanda, A., Frías, Ó., Arrondo, E., Donázar, J.A., 2019. Livestock farming practices modulate vulture diet-disease interactions. Glob. Ecol. Conserv. 17, p.e00518. https://doi.org/10.1016/j.gecco.2018.e00518.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., & Thomas, L., 2004. Advanced distance sampling: estimating abundance of biological populations. OUP Oxford.

Burner, R.C., Styring, A.R., Rahman, M.A., Sheldon, F.H., 2019. Occupancy patterns and upper range limits of lowland Bornean birds along an elevational gradient. J. Biogeogr. 46(11), 2583–2596. https://doi.org/10.1111/jbi.13691.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. New York: Springer-Verlag.

Campos-Cerqueira, M., Robinson, W.D., Augusto Leite, G., Mitchell Aide, T., 2021. Bird Occupancy of a Neotropical forest fragment is mostly stable over 17 years but influenced by forest age. Diversity 13(2), 50. https://doi.org/10.3390/d13020050.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Sci. Adv. 1(5), p.e1400253. https://www.science.org/doi/full/10.1126/sciadv.1400253.

Ceballos, G., Ehrlich, P.R., Raven, P.H., 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. Proc. Natl. Acad. Sci. 117(24), 13596–13602. https://doi.org/10.1073/pnas.1922686117.

Chaudhary, V., Wisely, S.M., Hernández, F.A., Hines, J.E., Nichols, J.D., Oli, M.K., 2020. A multi-state occupancy modelling framework for robust estimation of disease prevalence in multi-tissue disease systems. J. App. Ecol. 57(12), 2463–2474. https://doi.org/10.1111/1365-2664.13744.

Cisneros-Araujo, P., Goicolea, T., Mateo-Sánchez, M.C., García-Viñás, J.I., Marchamalo, M., Mercier, A., Gastón, A., 2021. The role of remote sensing data in habitat suitability and connectivity modeling: Insights from the cantabrian brown bear. Remote Sens. 13(6), 1138. https://doi.org/10.3390/rs13061138.

De Almeida-Rocha, J.M., Monsalvo, J.A.B., Oliveira, L.D.C., 2019. Diet specialisation reduces the occupancy of cocoa agroforests by diurnal raptors. Bird Conserv. Int. 29(4), 558–574. https://doi.org/10.1017/s0959270919000017.

De Rosa, A., Castro, I., Marsland, S., 2022. The acoustic playback technique in avian fieldwork contexts: a systematic review and recommendations for best practice. Ibis, 164(2), 371–387. https://doi.org/10.1111/ibi.13033.

Debela, M.T., Wu, Q., Li, Z., Sun, X., Omeno, O., Li, Y., 2021. Habitat Suitability Assessment of Wintering Herbivorous Anseriformes in Poyang Lake, China. Diversity 13(4), 171. https://doi.org/10.3390/d13040171.

Devarajan, K., Morelli, T.L., Tenan, S., 2020. Multi-species occupancy models: Review, roadmap, and recommendations. Ecography 43(11), 1612–1624. https://doi.org/10.1111/ecog.04957.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J., Collen, B., 2014. Defaunation in the Anthropocene. Science, 345(6195), 401–406. https://www.science.org/doi/abs/10.1126/science.1251817.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., Yates, C. J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.

Fisher, Z.S., Cartwright, S., Bealey, C., Rayaleh, H.A., McGowan, P., Milner-Gulland, E.J., 2009. The Djibouti francolin and juniper forest in Djibouti: the need for both ecosystem and species-specific conservation. Oryx, 43(4), 542–551. https://doi.org/10.1017/S0030605309990214.

Fishpool, L.D.C., & Evans, M. I. (eds), 2001. Important Bird Areas of Africa and associated islands: priority sites for conservation. Newbury/Cambridge, UK: Pisces Publications/BirdLife International.

Friis, I., Demissew, S., Breugel, P.V., 2010. Atlas of the potential vegetation of Ethiopia. Biol. Skr. 58, 1–307.

Gedeon, K., Rödder, D., Zewdie, C., Töpfer, T., 2017. Evaluating the conservation status of the Black-fronted Francolin *Pternistis atrifrons.* Bird Conserv. Int. 27, 1–9. https://doi.org/10.1017/S0959270917000363.

Goldman, M.R., Shinderman, M., Jeffress, M.R., Rodhouse, T.J., Shoemaker, K.T., 2023. Integrating multiple sign types to improve occupancy estimation for inconspicuous species. Ecol. Evol. 13(5), p.e10019. https://doi.org/10.1002/ece3.10019.

Green, A.W., Pavlacky Jr, D.C., George, T.L., 2019. A dynamic multi-scale occupancy model to estimate temporal dynamics and hierarchical habitat use for nomadic species. Ecol. Evol. 9(2), 793–803. https://doi.org/10.1002/ece3.4822.

Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A., McCarthy, M.A., 2014. Ignoring imperfect detection in biological surveys is dangerous: A response to ‘fitting and interpreting occupancy models'. PloS one, 9(7), p.e99571. https://doi.org/10.1371/journal.pone.0099571.

Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. Ecography 40(2), 281–295. https://doi.org/10.1111/ecog.02445.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135(2-3), 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9.

Gumede, S.T., Smith, D.A.E., Smith, Y.C.E., Ngcobo, S.P., Sosibo, M.T., Maseko, M.S., Downs, C.T., 2022. Occupancy of two forest specialist birds in the Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa. Bird. Conserv. Int. 32 (1), 27–42. https://doi.org/10.1017/S0959270920000544.

Harms, T.M., Murphy, K.T., Lyu, X., Patterson, S.S., Kinkead, K.E., Dinsmore, S.J., Frese, P.W., 2017. Using landscape habitat associations to prioritize areas of conservation action for terrestrial birds. PLoS One 12(3), e0173041. https://doi.org/10.1371/journal.pone.0173041.

Hilton-Taylor, C., Pollock, C.M., Chanson, J.S., Butchart, S.H., Oldfield, T.E., Katariya, V., 2009. State of the world's species, in: Vié, J.C., Hilton-Taylor, C., & Stuart, S.N. (Eds.), Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species: IUCN, pp. 15–41.

Hines, J.E. (2006). PRESENCE-software to estimate patch occupancy and related parameters. USGS-PWRC. http://www.mbr-pwrc.usgs.gov/software/presence.html.

Huete, A.R., Liu, H.Q., Batchily, K.V., Van Leeuwen, W.J.D.A., 1997. A comparison of vegetation indices over a global set of TM images for EOS-MODIS. Remote Sens. Environ. 59(3), 440–451. https://doi.org/10.1016/S0034-4257(96)00112-5.

Jean-Pierre, A., Loranger-Merciris, G., Cézilly, F., 2022. Spatial Occupancy, Local Abundance and Activity Rhythm of Three Ground Dwelling Columbid Species in the Forests of Guadeloupe in Relation to Environmental Factors. Diversity 14(6), 480. https://doi.org/10.3390/d14060480.

Jameel, M.A., Nadeem, M.S., Aslam, S., Ullah, W., Ahmad, D., Awan, M.N., Masroor, W., Mahmood, T., Ullah, R., Anjum, M.Z., Ali, K., 2022. Impact of human imposed pressure on pheasants of western Himalayas, Pakistan: Implication for monitoring and conservation. Diversity, 14(9), 752. https://doi.org/10.3390/d14090752.

Jha, A., Praveen, J., Nameer, P.O., 2022. Contrasting occupancy models with presence-only models: Does accounting for detection lead to better predictions? Ecol. Model. 472, p.110105. https://doi.org/10.1016/j.ecolmodel.2022.110105.

Keane, A., Brooke, M.D.L., McGowan, P.J.K., 2005. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). Biol. Conserv. 126(2), 216–233. https://doi.org/10.1016/j.biocon.2005.05.011.

Kearney, M., 2006. Habitat, environment and niche: what are we modelling?. Oikos 115(1), 186–191. https://doi.org/10.1111/j.2006.0030-1299.14908.x.

Keesing, F., Ostfeld, R.S., 2021. Impacts of biodiversity and biodiversity loss on zoonotic diseases. Proc. Natl. Acad. Sci. 118(17), e2023540118. https://doi.org/10.1073/pnas.2023540118.

Kéry, M., Gardner, B., Monnerat, C., 2010. Predicting species distributions from checklist data using site-occupancy models. J. Biogeogr. 37(10), 1851–1862. https://doi.org/10.1111/j.1365-2699.2010.02345.x.

Khan, Z.Z., Sushma, H.S., Koli, K.M., Neema, A., Meera, M.R., Arasumani, M., Robin, V.V., Jayapal, R., Mukherjee, S., 2023. Habitat determinants of species occupancy and niche partitioning among sympatric owlets: the paradoxical role of agricultural lands for the endangered Forest Owlet, *Athene blewitti*. J. Field Ornithol. 94(2). https://journal.afonet.org/vol94/iss2/art1/.

Kriegler, F.J., Malila, W.A., Nalepka, R.F., Richardson, W., 1969. Preprocessing transformations and their effect on multispectral recognition. Remote Sens. Environ. VI, 97–132.

Lahoz-Monfort, J.J., Guillera-Arroita, G., Wintle, B.A., 2014. Imperfect detection impacts the performance of species distribution models. Glob. Ecol. Biogeogr. 23(4), 504–515. https://doi.org/10.1111/geb.12138.

Lerm, R.E., Jansen, R., Underhill, L.G., 2019. Bird distribution dynamics - Indigenous francolins in South Africa, Lesotho, and Swaziland. Biodivers. Observ. 10, 1–31. https://doi.org/10.15641/bo.v10i0.599.

Leroux, S. J., 2019. On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. PLoS One 14(2), e0206711. https://doi.org/10.1371/journal.pone.0206711.

Leveau, L. M., Isla, F. I., Bellocq, M. I., 2018. Predicting the seasonal dynamics of bird communities along an urban-rural gradient using NDVI. Landsc. Urban Plan. 177, 103–113. https://doi.org/10.1016/j.landurbplan.2018.04.007.

Li, H.Q., Lian, Z.M., Chen, C.G., 2009. Winter foraging habitat selection of brown-eared pheasant (*Crossoptilon mantchuricum*) and the common pheasant (*Phasianus colchicus*) in Huanglong Mountains, Shaanxi Province. Acta Ecol. Sin. 29(6), 335–340. https://doi.org/10.1016/j.chnaes.2009.09.013.

Lin, B., Foxfoot, I.R., Miller, C.M., Venkatamaran, V.V., Kerby, J.T., Bechtold, E.K., Kellogg, B.S., Nguyen, N., Fashing, P.J., 2020. Leopard predation on gelada monkeys at Guassa, Ethiopia. Am. J. Primatol. 82(2), p.e23098. https://doi.org/10.1002/ajp.23098.

Little, R.M., Crowe, T.M., 2004. Effects of a predator control experiment on Grey-winged Francolin (*Scleroptila africanus*) populations. Ostrich, 75(4), 285–287. https://doi.org/10.2989/00306520409485456.

Liu, Z., Tian, S., Lu, S., Zhu, Z., Peng, Y., Li, J., Xu, J., Wang, Y., 2023. Climate and land-use changes threaten the effectiveness of protected areas for protecting Galliformes in Southeast Asia. Front. Ecol. Evol. 11, p.1216769. https://doi.org/10.3389/fevo.2023.1216769.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C. A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology, 83(8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84(8), 2200–2207. https://doi.org/10.1890/02-3090.

Mackenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42, 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., & Hines, J.E., 2018. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence, second edition. Elsevier.

Maseko, M.S., Ramesh, T., Kalle, R., Downs, C.T., 2017. Response of Crested Guinea-fowl (*Guttera edouardi*), a forest specialist, to spatial variation in land use in iSimangaliso Wetland Park, South Africa. J. Ornithol. 158, 469–477. https://doi.org/10.1007/s10336-016-1406-7.

Mares, R., Doutrelant, C., Paquet, M., Spottiswoode, C. N., Covas, R., 2017. Breeding decisions and output are correlated with both temperature and rainfall in an arid-region passerine, the sociable weaver. R. Soc. Open Sci. 4(9), 170835. https://doi.org/10.1098/rsos.170835.

Matsushita, B., Yang, W., Chen, J., Onda, Y., Qiu, G., 2007. Sensitivity of the enhanced vegetation index (EVI) and normalized difference vegetation index (NDVI) to topographic effects: a case study in high-density cypress forest. Sensors 7(11), 2636–2651. https://doi.org/10.3390/s7112636.

Matthiopoulos, J., Fieberg, J.R., & Aarts, G., 2020. Species Habitat Associations: Spatial Data, Predictive Models, and Ecological Insights. 2nd edition. University of Minnesota Libraries Publishing.

McGowan, P.J.K., Owens, L.L., Grainger, M.J., 2012. Galliformes science and species extinctions: what we know and what we need to know. Anim. Biodivers. Conserv. 35 (2), 321–331. https://raco.cat/index.php/ABC/article/view/259218.

McGrath, T., Guillera-Arroita, G., Lahoz-Monfort, J.J., Osborne, W., Hunter, D., Sarre, S.D., 2015. Accounting for detectability when surveying for rare or declining reptiles: turning rocks to find the grassland earless dragon in Australia. Biodivers. Conserv. 182, 53–62. https://doi.org/10.1016/j.biocon.2014.11.028.

Merga, B.B., Moisa, M.B., Negash, D.A., Ahmed, Z., Gemeda, D.O., 2022. Land surface temperature variation in response to land-use and land-cover dynamics: a case of Didessa River sub-basin in Western Ethiopia. Earth Syst. Environ. 1–13. https://doi.org/10.1007/s41748-022-00303-3.

Mohammed, J.A., Gashaw, T., Tefera, G.W., Dile, Y.T., Worqlul, A.W., Addisu, S., 2022. Changes in observed rainfall and temperature extremes in the Upper Blue Nile Basin of Ethiopia. Weather Clim. Extrem. 37, 100468. https://doi.org/10.1016/j.wace.2022.100468.

Moisa, M.B., Gabissa, B.T., Hinkosa, L.B., Dejene, I.N., Gemeda, D.O., 2022. Analysis of land surface temperature using Geospatial technologies in Gida Kiremu, Limu, and Amuru District, Western Ethiopia. Artif. Intell. Agric. 6, 90–99. https://doi.org/10.1016/j.aiia.2022.06.002.

Morante-Filho, J.C., Benchimol, M., Faria, D., 2021. Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. Landscape Ecol. 36(1), 105–117. https://doi.org/10.1007/s10980-020-01121-6.

Morrison, M.L., Marcot, B., Mannan, W., 2012. Wildlife-habitat relationships: concepts and applications, third ed. Island Press.

Muir, C., Southworth, J., Khatami, R., Herrero, H., Akyapı, B., 2021. Vegetation dynamics and climatological drivers in Ethiopia at the turn of the century. Remote Sens. 13(16), 3267. https://doi.org/10.3390/rs13163267.

Nyssen, J., Poesen, J., Moeyersons, J., Deckers, J., Haile, M., Lang, A., 2004. Human impact on the environment in the Ethiopian and Eritrean highlands-a state of the art. Earth-Sci. Rev. 64(3–4), 273–320. https://doi.org/10.1016/S0012-8252(03)00078-3.

Pellet, J., Schmidt, B.R., 2005. Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. Biol. Conserv. 123(1), 27–35. https://doi.org/10.1016/j.biocon.2004.10.005.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190(3-4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Qiu, J., Yang, J., Wang, Y., Su, H., 2018. A comparison of NDVI and EVI in the DisTrad model for thermal sub-pixel mapping in densely vegetated areas: A case study in Southern China. Int. J. Remote Sens. 39(8), 2105–2118. https://doi.org/10.1080/01431161.2017.1420929.

Ramesh, T., Downs, C.T., 2014. Land use factors determining occurrence of Red-necked Spurfowl (Pternistis afer) in the Drakensberg Midlands. South Afr. J. Ornithol.

Richards, S.A., 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86(10), 2805–2814. https://doi.org/10.1890/05-0074.

Richards, S.A., Whittingham, M.J., Stephens, P.A., 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. Behav. Ecol. Sociobiol. 65(1), 77–89. https://doi.org/10.1007/s00265-010-1035-8.

Robertson, P.A., Dellelegn, Y., Dejene, S., Shimelis, A., Alemayehu, M., 1997. Harwood's Francolin Francolinus harwoodi: recent observations on its status, distribution, habitat requirements, behaviour and threats. Bird Conserv. Int. 7(3), 275–282. https://doi.org/10.1017/S095927090000157X.

Rodrigues, G.C., Braga, R.P., 2021. Evaluation of NASA POWER reanalysis products to estimate daily weather variables in a hot summer Mediterranean climate. Agronomy 11(6), 1207. https://doi.org/10.3390/agronomy11061207.

Saavedra, D., 2009. The Abune Yosef Massif: Birds and mammals of a hidden jewel of Ethiopia. Centre de Recursos de Biodiversitat Animal, Facultat de Biologia, Universitat de Barcelona: Barcelona. Volume 2, 131 pp. http://hdl.handle.net/2445/152578.

Saavedra, D., Such-Sanz, À., Díaz, G., Mariné, R., Regalado, Í., López, M., Dantart, L., 2009. The Mammals of the Abune Yosef, in: Saavedra, D. (Eds.), The Abune Yosef Massif: Birds and Mammals of a hidden jewel of Ethiopia. Publicacions del Centre de Recursos de Biodiversitat Animal. Universitat de Barcelona, pp.26–70. http://hdl.handle.net/2445/152578.

Sewell, D., Beebee, T.J., Griffiths, R.A., 2010. Optimising biodiversity assessments by volunteers: the application of occupancy modelling to large-scale amphibian surveys. Biodivers. Conserv. 143(9), 2102–2110. https://doi.org/10.1016/j.biocon.2010.05.019.

Skagen, S. K., Adams, A.A.Y., 2012. Weather effects on avian breeding performance and implications of climate change. Ecol. Appl. 22(4), 1131–1145. https://doi.org/10.1890/11-0291.1.

Smith, D.A.E., Smith, Y.C.E., Ramesh, T., Downs, C.T., 2017. Camera-trap data elucidate habitat requirements and conservation threats to an endangered forest specialist, the Spotted Ground Thrush (*Zoothera guttata*). Ecol. Manag 400, 523–530. https://doi.org/10.1016/j.foreco.2017.06.045.

Sutherland, W.J., 2006. Ecological census techniques: a handbook. Cambridge university press.

Symonds, M.R., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol 65(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6.

Taylor, S.S., Cecco, G.D., Hurlbert, A.H., 2021. Using temporal occupancy to predict avian species distributions. Divers. Distrib. 27 (8), 1477–1488. https://doi.org/10.1111/ddi.13296.

Tekleab, S., Mohamed, Y., Uhlenbrook, S., 2013. Hydro-climatic trends in the Abay/upper Blue Nile basin, Ethiopia. *Phys. Chem. Earth.* Parts A/B/C 61, 32–42. https://doi.org/10.1016/j.pce.2013.04.017.

Thapa, K., Kelly, M.J., 2017. Prey and tigers on the forgotten trail: high prey occupancy and tiger habitat use reveal the importance of the understudied Churia habitat of

Nepal. Biodivers. Conserv. 26, 593–616. https://doi.org/10.1007/s10531-016-1260-1.

Tian, S., Xu, J., Li, J., Zhang, Z., Wang, Y., 2018. Research advances of Galliformes since 1990 and future prospects. Avian Res. 9(1), 1–13. https://doi.org/10.1186/s40657-018-0124-7.

Tilahun, S., Edwards, S., & Gebregziabher, T., 1996. Important Bird Areas of Ethiopia: a first inventory. Addis Ababa: Ethiopian Wildlife & Natural History Society.

Töpfer, T., Podsiadlowski, L., Gedeon, K., 2014. Rediscovery of the Black-fronted Francolin *Pternistis (castaneicollis) atrifrons* (Conover, 1930) (Aves: Galliformes: Phasianidae) with notes on biology, taxonomy and conservation. Vertebr. Zool. 64, 261–271. https://doi.org/10.3897/vz.64.e31494.

Tuanmu, M.N., Jetz, W., 2015. A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr. 24(11), 1329–1339. https://doi.org/10.1111/geb.12365.

Urban, E.K., Fry, C.H., & Keith, S., 1986. The birds of Africa, Volume 2. London: Academic Press

van Niekerk, J.H., 2017. Orange River Francolins (Scleroptila levaillantoides) persist in fragmented Highveld farming landscapes, South Africa. Avian Res. 8(1), 1–8. https://doi.org/10.1186/s40657-017-0069-2.

Wang, B., Xu, Y., Price, M., Yang, N., Liu, W., Zhu, B., Zhong, X., Ran, J., 2021. Niche partitioning among three montane ground-dwelling pheasant species along multiple ecological dimensions. Ibis, 163(1), 171–182. https://doi.org/10.1111/ibi.12842.

Worku, E.A., Bro-Jørgensen, J., Evangelista, P.H., Bekele, A., Atickem, A., Stenseth, N.C., 2023. Group size dynamics of the endangered mountain nyala (*Tragelaphus buxtoni*) in protected areas of the Arsi and Ahmar Mountains, Ethiopia. Glob. Ecol. Conserv. 46, p.e02546. https://doi.org/10.1016/j.gecco.2023.e02546.

Wu, J., Li, H., Wan, H., Wang, Y., Sun, C., Zhou, H., 2021. Analyzing the Relationship between Animal Diversity and the Remote Sensing Vegetation Parameters: The Case of Xinjiang, China. Sustainability 13(17), 9897. https://doi.org/10.3390/su13179897.

Zahoor, B., Liu, X., Songer, M., 2022. The impact of climate change on three indicator Galliformes species in the northern highlands of Pakistan. Environ. Sci. Pollut. Res. 29(36), 54330–54347. https://doi.org/10.1007/s11356-022-19631-y.

Zamora-Marín, J.M., Zamora-López, A., Calvo, J.F., Oliva-Paterna, F.J., 2021. Comparing detectability patterns of bird species using multi-method occupancy modelling. Sci. Rep. 11(1), 2558. https://doi.org/10.1038/s41598-021-81605-w.

Zwerts, J.A., Stephenson, P.J., Maisels, F., Rowcliffe, M., Astaras, C., Jansen, P.A., van Der Waarde, J., Sterck, L.E., Verweij, P.A., Bruce, T., Brittain, S., 2021. Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps, and passive acoustic sensors. Conserv. Sci. Pract. 3(12), p.e568. https://doi.org/10.1111/csp2.568.

3.7. Supplementary information

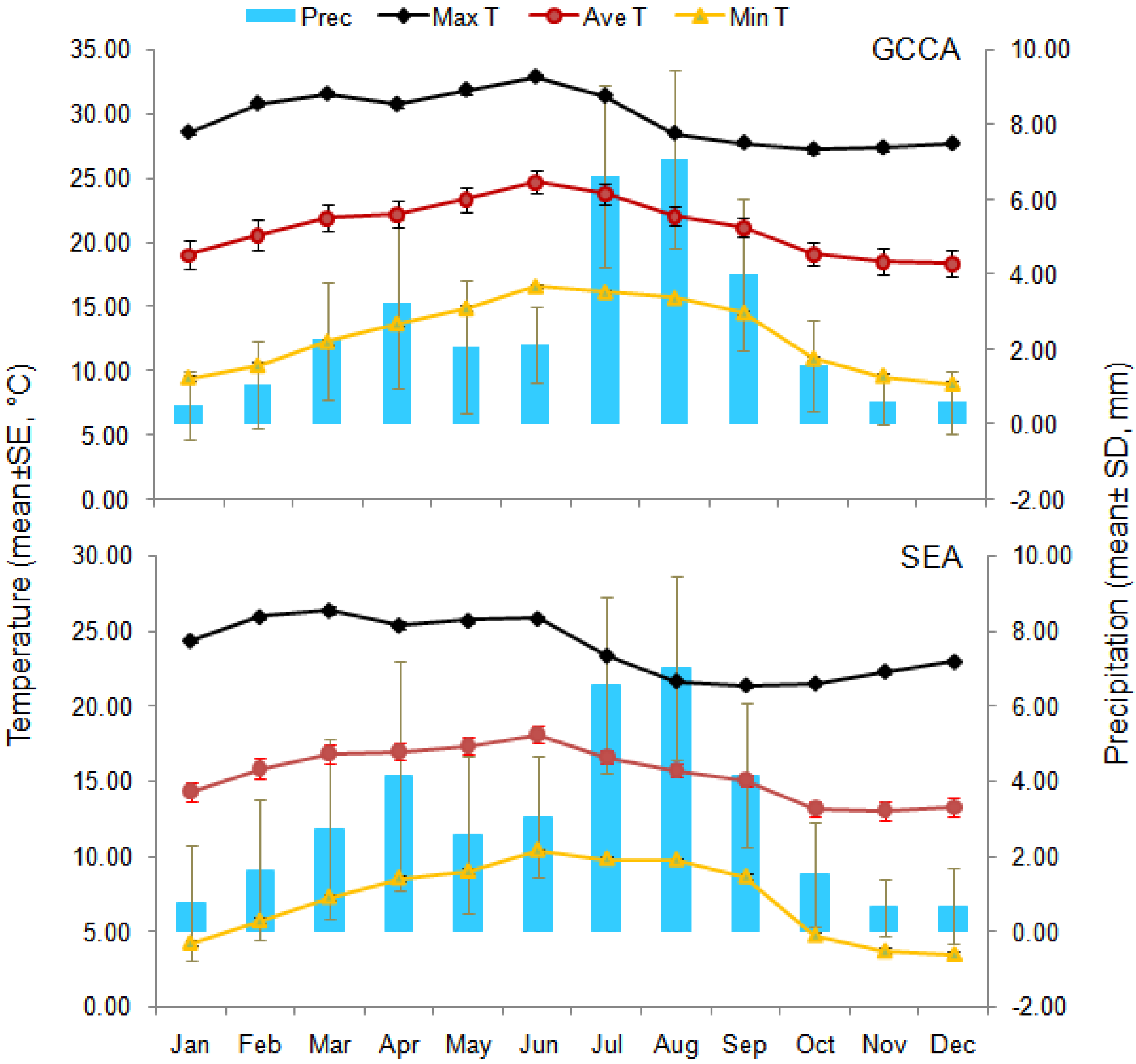

Figure S1. Climatic conditions of GCCA and SEA from 1981-2020 (https://power.larc.nasa.gov/data-access-viewer). Temperature (°C) and precipitation (mm) values are based on mean monthly data for each year (mean maximum, average and mean minimum temperatures).

Table S1. The Pearson correlation coefficient (r) of the predictor covariates.

Covariate	Elev	Elev^2	SL	SL^2	NDVI	HDI	T	T^2	P
Elev	1								
Elev^2	0.259^{**}	1							
SL	0.628^{**}	0.170^{*}	1						
SL^2	0.238^{**}	0.268^{**}	0.363^{**}	1					
NDVI	0.094	-0.218^{**}	-0.131	0.026	1				
HDI	0.166^{*}	-0.053	0.054	-0.029	0.039	1			
T	-0.273^{**}	-0.217^{**}	-0.239^{**}	-0.079	-0.101	0.053	1		
T2	0.133	-0.029	0.084	-0.070	0.280^{**}	0.004	-0.429^{**}	1	
P	0.079	0.082	0.179^{*}	0.036	0.029	-0.058	-0.079	0.056	1

Abbreviations: Elev = elevation, Elev^2 = quadratic term of elevation, SL= slope, SL^2 = quadratic term of slope, NDVI = Normalized Difference Vegetation Index, HDI = human disturbance index, T = temperature, T^2 = quadratic term of temperature, and P = precipitation. ** Correlation is significant at the 0.01 level (2-tailed), and * correlation is significant at the 0.05 level (2-tailed).

Table S2. Description of occupancy and dynamic parameters for null models.

Method	Parameter estimates (95% conf. interval)				
	Naïve Ψ for season 1 and season 2	Initial occupancy probability (ψ_1)	Detection probability (ρ)	Colonization probability (γ)	Extinction probability (ε)
DO	0.38 ; 0.60	0.57 (0.46-0.68)	0.61 (0.54-0.67)	0.42 (0.26-0.59)	0.03 (0.001-0.49)
DO+PB	0.49 ; 0.65	0.76 (0.64-0.86)	0.58 (0.52-0.63)	0.50 (0.25-0.75)	0.12 (0.04-0.28)

Abbreviations: DO = direct observation, and DO+PB = direct observation plus playback.

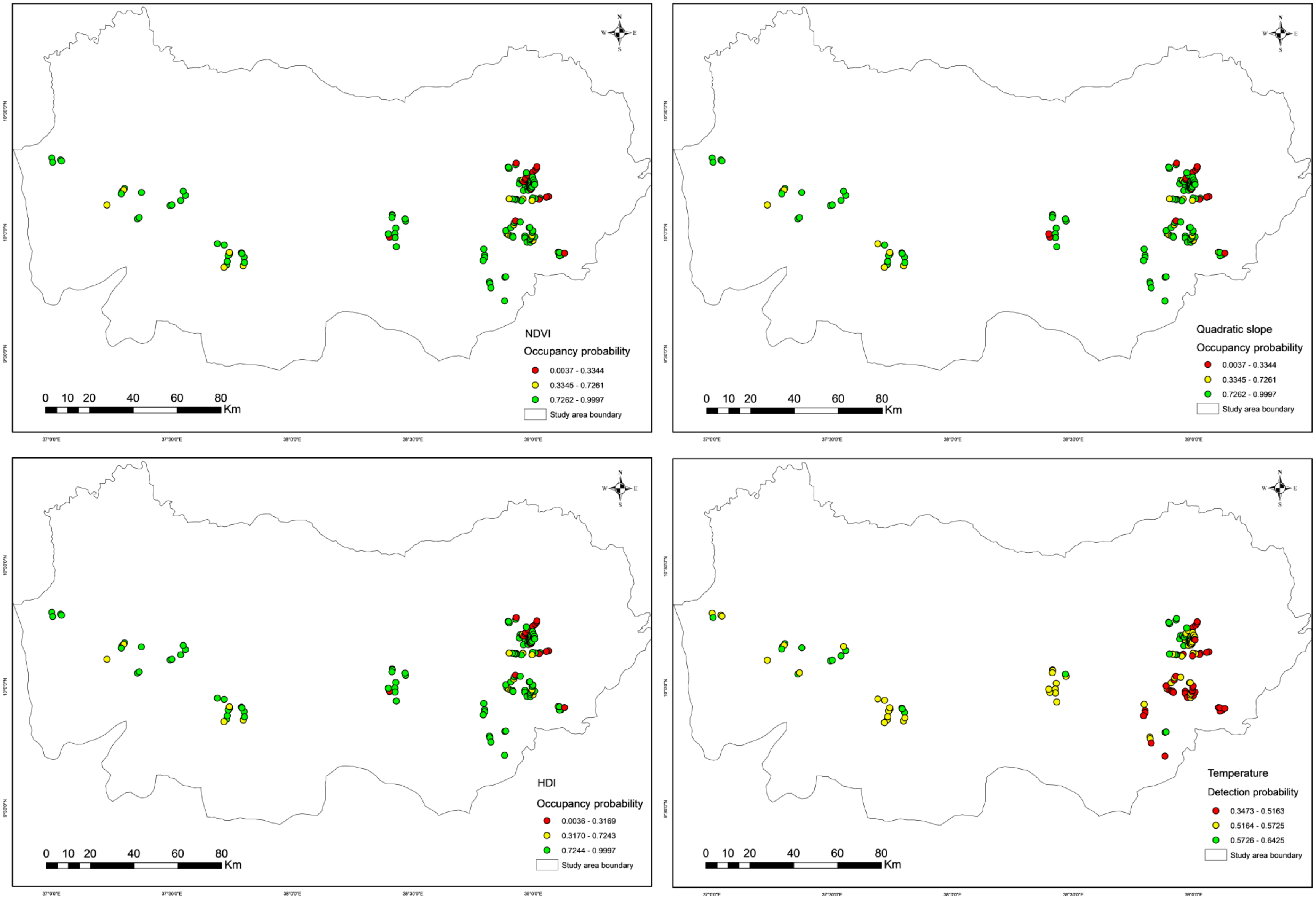

Figure S2. The estimates of occupancy and detection probabilities of Harwood's Francolins at each sampling station as functions of significant covariates.

Chapter 4

Nesting behavior, egg morphology, and breeding biology of Harwood’s Spurfowl (*Pternistis harwoodi*) in the Upper Blue Nile Basin, Ethiopia (Accepted)

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4.1. Abstract

This study aims to understand the life history of the endemic Harwood's Spurfowl (*Pternistis harwoodi*) including reproductive, behavioral and spatio-temporal variability of traits for the first time in the Upper Blue Nile Basin, Ethiopia. We used field observations and camera traps to collect data from August to December 2020. We observed a non-lekking polygyny mating system with females selecting the nesting sites. Most nests were designed to thwart predators through background matching, nest orientation and positioning, and reducing depositional odor trails. We found that the peak egg-laying period occurred in the first two weeks of October. There were significant differences of clutch-size variation spatiotemporally, as well as variation of the geometrical parameters of eggs spatially, excluding for shape index. The average hatching success was 4.12 chicks/nest (± 0.91 SD). The daily nest survival rates (DSR) was estimated at 98.82% ± 0.003 (95% CI: 98.31%–99.32%) and the total survival probability of the nests was 70.48% ± 0.01 (95% CI: 60.66%–81.82%). We document a uniparental care strategy with eggs being exclusively incubated by females and chicks being predominantly attended by their mothers, although males may support rearing the chicks during post-hatching period.

Keywords: background matching, breeding biology, daily nest survival rates, egg morphology, nesting behavior, parental care

4.2. Introduction

The breeding biology of most tropical bird species is poorly known (Xiao et al. 2017, Fierro-Calderón et al. 2021), yet the knowledge of it is an indispensable tool to carry out successful conservation measures (Green 2004, Kesler et al. 2018). For example, knowing the details of the breeding biology of landfowl (Galliformes) can help to mitigate negative influences on the populations (e.g., hunting, habitat loss, and human population growth) when taken into consideration during the development of appropriate management plans (Clark et al. 1999, Jiménez and Conover 2001, Tian et al. 2018). Nest site selection and nest design are among the most important determinants of reproductive success in birds (Mainwaring et al. 2014, Guillette and Healy 2015), and this is reflected in ground nesters such as galliforms through the interplay of resource availability, thermoregulation, crypticity, and risk-avoidance behaviors (Mayer et al. 2009, Carroll et al. 2015, Gómez et al. 2019).

Galliformes mostly select nest sites on the ground to build scrape nests (Madge and McGowan 2002). Scrape nests are structurally weak, but require less effort to build (Suárez et al. 2005, Mainwaring et al. 2014) than the burrow and mound nests of megapodes (Harris et al. 2014), yet great parental attention is invested during egg laying, incubation, and hatching (Persson and Göransson 1999, Suárez et al. 2005). However, there is a paucity of information on how such a nest confers reproductive success in many galliform species.

Globally, there are 54 genera in the family Phasianidae, seven of which (*Xenoperdix*, *Afropavo*, *Peliperdix*, *Campocolinus*, *Scleroptila*, *Margaroperdix,* and *Pternistis*) are confined to Africa (Gill et al. 2024). There is limited information on the breeding biology of most species, including francolins and spurfowls, from Sub-Saharan Africa (del Hoyo et al. 1994, Madge and McGowan 2002), with some studies only reported from South Africa (e.g., Little and Crowe 1993, Jansen 2001, van Niekerk 2001, 2017, 2018). In Ethiopia, Harwood's Spurfowl (*Pternistis harwoodi*) is an endemic sedentary species of the Sudan-Guinea Savanna biome and of the Afrotropical Highlands biome, excluding the Afroalpine and Sub-Afroalpine ecosystems (Abrha et al. 2023). The main threats to these biomes are agricultural expansion, livestock grazing, firewood collection, and settlement (Asefa et al. 2020), while the main menacing factors for francolins and spurfowls in Ethiopia are habitat loss and hunting pressure (Töpfer et al. 2014, Abrha et al. 2017, Gedeon et al. 2017, Abrha et al. 2023).

Some aspects of the ecology of Harwood's Spurfowl have hitherto been studied in the Jema and Jara valley sub-basins of the Upper Blue Nile Basin (Robertson et al. 1997, Abrha and Nigus 2017, Abrha et al. 2017, Abrha et al. 2018). From a life history standpoint, only a single egg-laying date and a polygamous mating system have previously been reported (Ash 1978, Robertson et al. 1997, Ash and Atkins 2009), and so its breeding biology remains essentially elusive. This study investigates the behavior and breeding biology of Harwood's Spurfowl for the first time. Specifically, it aims to understand life-history traits, such as reproductive (clutch size, egg geometrics, incubation, brood size, daily nest survival rates, breeding success, hatching failure and related traits) and behavioural traits (nest-site selection and design, social behavior, mating system, and parental care), as well as spatiotemporal variation among traits.

4.3. Methods

4.3.1. Study area

The study area lies in the Upper Blue Nile Basin (UBNB; Figure 4.1) and the area consists of two main study sites separated by a distance of approximately 100 km. The main vegetation types are Dry evergreen Afromontane forest and grassland complex (DAF) and *Combretum-Terminalia* woodland and wooded grasslands (CTW) (Friis et al. 2010). The common native tree species are *Combretum* spp, *Terminalia* spp, *Acacia* spp and *Juniperus* spp. The CTW also harbors socio-economically important plants such as Frankincense (*Boswellia papyrifera*) and Lowland bamboo (*Oxytenanthera abyssinica*) (Friis et al. 2010). According to Fishpool and Evans (2001), the lower elevations (mean = 1322 m, range = 840–1941 m, N = 27 nests) of the study area belong to the Sudan-Guinea Savanna biome (SG), whereas the higher elevations (mean = 1712, range = 1245–2192 m, N = 65 nests) are part of the Afrotropical Highlands biome (AH) (Figures. 4.1 and 4.2). The study areas do not contain Afroalpine and Sub-Afroalpine ecosystems as defined by Töpfer and Gedeon (2020). The major soil types of the area are Vertisols ("black cotton soils") and Leptosols ("grey-brown or brown soils") (Last 2009).

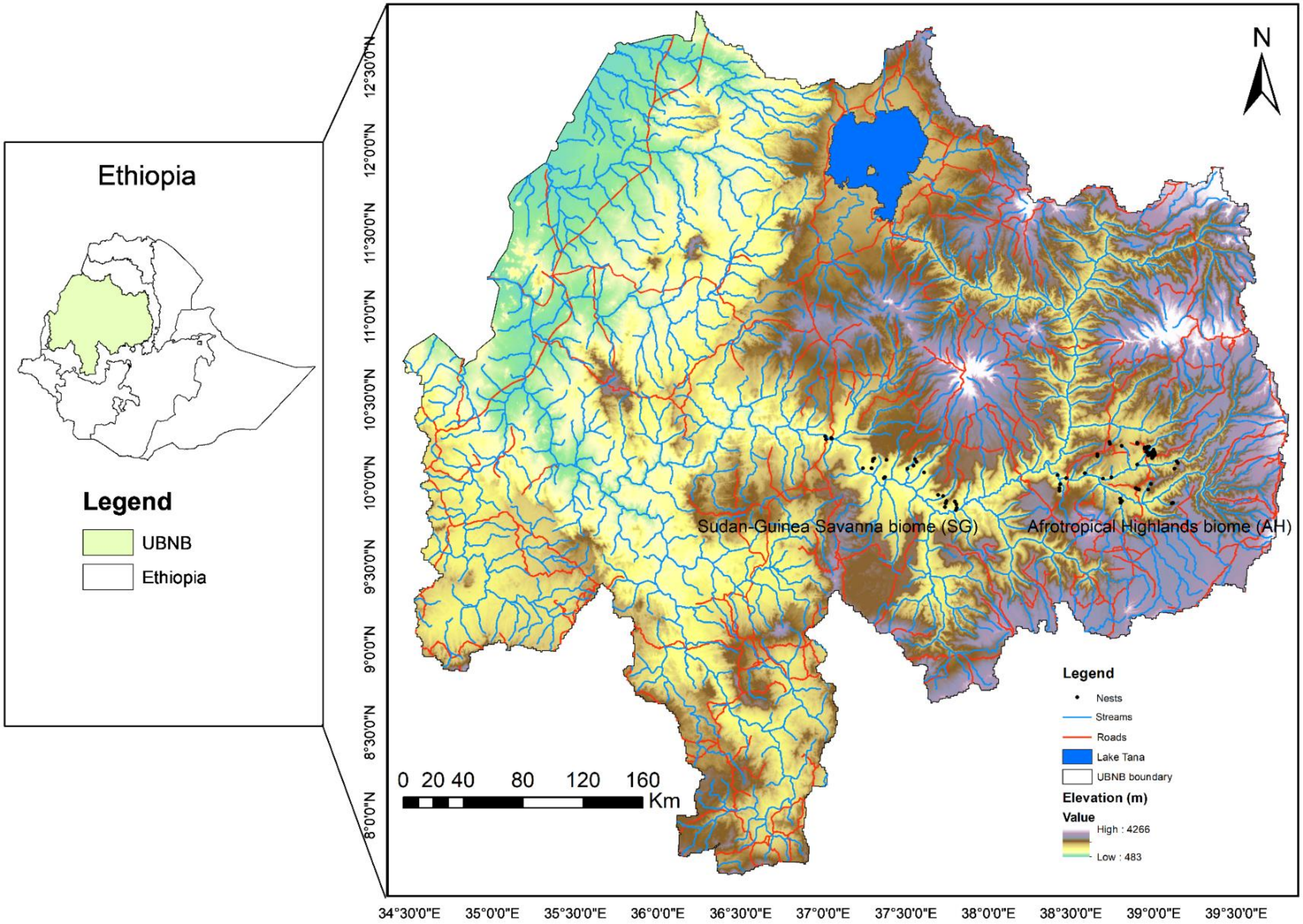

Figure 4.1. Study area and the two main study sites of Harwood’s Spurfowls in the Upper Blue Nile Basin (UBNB): Western nests belong to the Sudan-Guinea Savanna biome (SG) and eastern nests to the Afrotropical Highlands biome (AH).

Figure 4.2. Habitat types in the Afrotropical Highlands biome (top) and the Sudan-Guinea Savanna biome (bottom) in the Upper Blue Nile Basin.

4.3.2. Field Methods

We searched for nesting sites from mid-August to the last week of December in 2020 along predetermined line transects in farmland, CTW and DAF habitats (Abrha et al. 2023). We intensively searched in the morning and evening, when the species exhibits peak feeding and calling activity (Abrha et al. 2018). In particular, the distinctive vocalizations of territorial males were important signals as were courtship displays. Incubating birds were detected by random searches in habitats where the species was known to breed (Figure 4.3). An active scrape was considered as a permanent nesting site when it contained at least one egg during that breeding season. Females squatting on freshly scraped ground were also considered as signs for a potential nest.

In total, we found 119 nests in the two biomes (27 in SG; 92 in AH). We collected complete data from 92 nests (referred to as “measured nests”). For the remaining 27 nests (“unmeasured nests”), we only documented clutch size, nesting period (backdated), nest fate (successful and failed) and nest dimensions in order to understand the effect of nest visits on the breeding success of the species. A nesting period is defined as the time from

Figure 4.3. Nesting sites of Harwood’s Spurfowls on relatively flat terrain in farmland (A-C) and on a steep slope in DAF (D). Nest locations proper are highlighted by white-dashed circles. Nests are effectively covered by vegetation (partly placed aside for photography) and are positioned and oriented to avoid excessive exposure to weather conditions and disturbances. Images also show effective camouflaging against the background substrate.

the first egg laying until hatching and a nest was considered successful when at least one egg hatched (Klett et al. 1986, Steenhof and Newton 2007). We checked 79% of measured nests in a 2–3 day intervals and 21% of the nests in intervals of 4–5 days. We applied camera traps to investigate breeding activity in 40 nests in the eastern study site in AH biome (Figure S1). Camera traps were situated at a 2–3 m radius from the nests after clutch initiation in order to avoid nest desertion. All cameras were mounted on short trees or wooden stakes approximately 40–60 cm above the ground. Cameras were programmed to operate during incubation and hatching. We set cameras to take photos and enabled video mode for three consecutive days; finally each day was pooled into a single survey following Kross and Nelson (2011). Using these methods, we were able to observe the frequency of egg laying during morning and evening, egg-laying intervals (number of egg/day), trips to and from the nest, nest attendance during feeding activity (time/day), hatching (time) and vocalizing males and potential predators.

4.3.3. Nest site characterization

During our fieldwork, we collected four traits to characterize the nest microhabitat as follows:

1) Background matching: we captured digital photographs to assess the contrast between the birds' plumage color and the background. By minimizing disturbance, a minimum distance of 1 m between the observer and the female was assumed during photographing.

2) Nest orientation and positioning: exposure to extreme weather conditions (e.g., solar radiation, rainfall, and wind conditions) and slope gradient (gentle to steep slope) was determined as “oriented” or “non-oriented”. Furthermore, the presence or absence of vegetation cover and nesting in association with other bird species was visually assessed.

3) Nest dimensions: we measured internal diameter, external diameter and depth of both measured and unmeasured nests and we identified the different nesting materials after hatching.

4) Nest spacing: We applied GPS to assess the minimum nest spacing between two nests and distance between a territorial male and the nearest nest.

4.3.4. Geometrical parameters and coloration of eggs

Egg dimensions and mass of fresh eggs were gauged in the field using digital calipers (to the nearest 0.01 mm) and digital balances (to the nearest 0.01 g), respectively. Egg measurements were conducted when females had left the nests for foraging or after antipredator responses. We wore gloves during measurements to reduce our scent on the eggs in order to avoid the attraction of mammalian predators common in the study area. We calculated the egg shape index, surface area and volume from two egg parameters: maximum length (L) and maximum breadth (B). The egg shape index (SI) was computed as a percent ratio of egg breadth and egg length (B/L*100) (Preston 1968). Egg volume was calculated using the equation $V = Kv \times L \times B^2$ (Hoyt 1979). Based on the modified Hügelschäffer's model with two parameters (Narushin et al. 2022), the formula for *Kv* coefficient for an ovoidal egg shape is: $Kv = -0.0012(B/L)^2 + 0.0035B/L + 0.5115$, where *Kv* = specific mass coefficient of egg. The detailed formulae for both egg surface area and egg volume are given in Narushin et al. (2022).

We dichotomized dominant phenotypic egg traits for egg color as being white or dusty white with tiny white spots and egg texture as being smooth and partly smooth (hence rough) (Figure S2).

4.3.5. Data analysis

We checked the normality assumptions of our data using a Shapiro-Wilk test and homoscedasticity to apply appropriate statistical tests. Adhering to these assumptions: (1) we applied paired and unpaired sample t-tests to contrast the mean differences of fresh eggs-laid per nest between morning and evening time blocks and nest measurements between successful and failed nests, respectively; (2) we used Pearson’s correlation test to check the linear relation between egg geometrical parameters; (3) the ordinary least squares (OLS) regression method was used to analyze the relationship between clutch size and egg-laying dates; (4) we also used nonparametric tests such as Chi-Square (χ^2) Goodness of Fit test, Mann–Whitney test *U* and Kruskal–Wallis test *H*. The Chi-Square test was used to contrast the observed and expected distribution of nest orientation, egg color and texture of eggs. The Mann–Whitney and the Kruskal–Wallis tests were used to analyze spatiotemporal variation of egg biometrics and hatching success between measured and unmeasured nests. A post-hoc Dunn's test with Bonferroni error adjustment method was used for pairwise comparisons of each parameter between habitats. Data was analyzed with IBM SPSS Statistics v20.0. Data of life-history traits was presented as mean ± SD, and a two-tailed hypothesis test with an alpha value of 5%.

Because not all nests were encountered simultaneously, nest fate (i.e., successful = 0 and failed = 1) of Harwood's Spurfowls was derived from daily nest survival rates (DSR) in program MARK (White and Burnham 1999, Dinsmore et al. 2002). Accordingly, we calculated 95% CI of DSR and total nest survival probability (or breeding success) using a maximum likelihood estimation. Mayfield's (1975) formula for DSR is:

$$\mathrm{DSR} = 1 - \frac{\text{Number of failed nests}}{\text{Number of exposure days}}$$

The 'exposure days' are defined as the duration from the first nest observation until the final fate of nests. The overall probability of a nest survival rate of d days is DSR^{d}. Where, d refers to the summation of egg-laying and incubation periods (Mayfield 1975, Rotella et al. 2004) in our model species.

4.4. Results

4.4.1. Social behavior and mating system

Harwood's Spurfowl is sympatric with Erckel's Spurfowl (*Pternistis erckelii*) at higher elevations in AH and with Helmeted Guineafowl (*Numida m. meleagris*) at lower elevations in CTW and farmlands. Male Harwood's Spurfowls were territorial and interacted with domestic and wild animals (Figure 4.4A–C). Constant territorial calls of individual males were noticed throughout the breeding season. We observed males producing territorial calls during the mornings (6:00 – 11:00) and afternoons (15:00 – 12:30). In a continuous habitat, four to eight males were calling in a distance of approximately 90 m from each other. Within each of these individual territories, we found at least two nests. On average, males were recorded at a distance of 23.6 m away from incubating females (14.5 – 45.0 m, *N* = 23 nests). Average distances between nests were

30.1 m in farmland (14.5 – 52.0 m, *N* = 22 nests), 39.1 m in CTW (19.0 – 70.0 m, *N* = 8 nests), and 48.7 m in DAF (32.0 – 66.0 m, *N* = 3 nests). There was no significant difference of nest spacing between habitat types (Kruskal–Wallis test *H* = 4.30, df = 2, *P* = 0.07). Most nests were constructed in and around farmlands (60.87%, *N* = 56), followed by CTW (31.52%, *N* = 29 nests) and DAF (7.61%, *N* = 7 nests). According to our observations of five sites, the mating system of Harwood's Spurfowl is polygynous. During the season, individual males chased down several females and initiated courtship behavior before nest building mainly after mid-August in 2020.

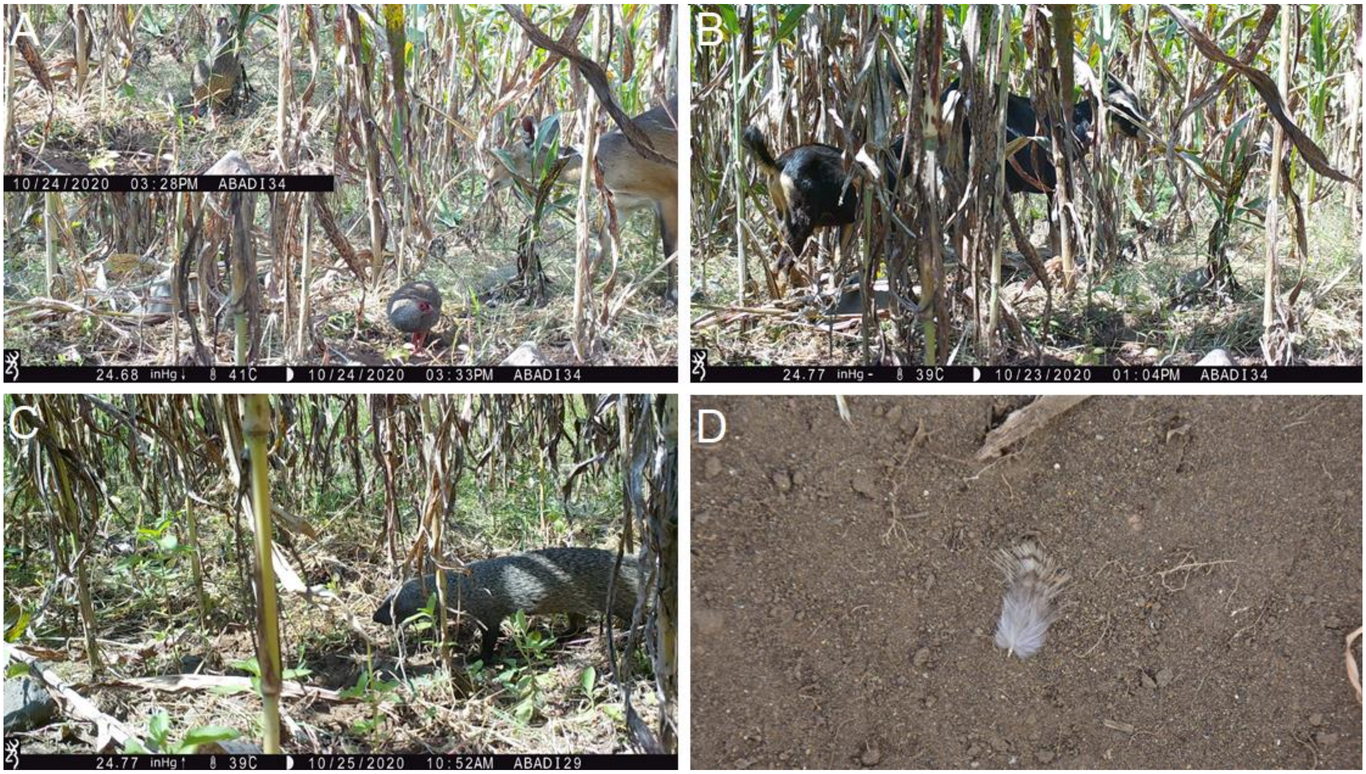

Figure 4.4. A territorial male feeding in association with Common Duiker *Sylvicapra grimmia* (A) and domestic goats *Capra* sp. (B), but fled from the feeding ground and gave off warning calls when approached by predators like White-tailed Mongoose *Ichneumia albicauda* (C). Males scratch the ground to feed, dust-bathe and preen their bodies during quiescence, as indicated by remaining feathers (D).

4.4.2. Nest-site selection and nest-building behavior

Nests were inconspicuous and usually well-hidden in herbaceous vegetation with some short trees and often surrounded by rocks and stones. Most nests were found on black cotton soil adjacent to stones (60.86%, *N* = 56), as well as underneath overhanging rocks (18.48%, *N* = 17 nests) and under thorny and bushy vegetation (11.96%, *N* = 11 nests)

(Figure 4.5). The grey-brown to dark-brown vermiculated patterns and colors of the breeding females' plumage matched the background very well. Only eight nests (8.70%) were built in heaps of *Sorghum* stalks, where females were less camouflaged. Females usually remained motionless during photography (Figures 4.3 and 4.5). Many nests were oriented away from excessive exposure to weather conditions like sunlight, rainfall and strong wind (63.04%, $N = 58$ nests), being sheltered by an extensive vegetation cover and by the selection of slopes and rocks on microhabitat levels (Figure 4.3). There was a statistically significant difference between the observed and expected distribution of nest orientation in the study area ($\chi^2 = 31.34$, df = 1, $P < 0.001$).

The nest itself is placed in a flat scrape and consists of a structurally weak arrangement of dried grasses and thin twigs, lined with the females' down or other soft body feathers (Figure 4.5). Green plant material was not observed in any nest and our videos confirmed that females selectively plucked and incorporated dried twigs and grasses to the construction while crouched low on the nest. The average external and internal diameters of the nests were 19.94 ± 1.76 cm and 16.85 ± 1.81 cm ($N = 40$ nests), respectively. The average depth of nests was 6.20 ± 1.43 cm. There was no significant difference in external diameter between successful and failed nests (unpaired-$t = 1.565$, df = 38, $P = 0.126$). Similarly, there was no significant difference in depth of successful and failed nests (unpaired-$t = 0.370$, df = 38, $P = 0.714$). In contrast, successful nests were significantly wider in internal diameter (1.4 cm) than failed nests (unpaired-$t = 2.529$, df = 38, $P = 0.016$).

Figure 4.5. Examples of nest structure and composition in different habitat types. The color and patterns of the incubating females provides camouflage against the background of rocks, stones and soil. Typical nest sites are shown on black (A) and brown to grey brown soils (B) and underneath rocks (C and D). Egg colors ranged from white (A, C, and D) to dusty white with tiny white spots (B). Nests with eggs close to hatching were usually filled with soft down feathers (C).

4.4.3. Egg laying and egg description

On average, in each nest a single egg was laid per day (mean = 1 d, range = 0–2 d, *N* = 23 nests) and the average egg-laying span was 8.34 days (± 2.87, range = 3–13 d, *N* = 41 nests). Our results showed that there was a statistically significant difference in eggs laid between morning and evening (paired-*t* = 5.21, df = 30, $P < 0.001$). The earliest clutch initiation was recorded on 9 September 2020, while the latest was recorded on 29 December 2020, with 52.20% of the clutches initiated in October (peaking in the first two weeks of October). There was a linear relationship indicating that clutch size declines significantly from the start of the laying season to the end ($R^2 = 0.11$; F = 6.786, df = 1,57, $P = 0.012$) (Figure 4.6). The color of 67.39% of the eggs was white and 32.61% were dusty white. Egg texture was either rough (73.91%) or smooth (26.09%) (Figure 4.5; Figure S2). There were significant differences in egg color ($\chi^2 = 11.13$, df = 1, $P = 0.001$), as well as in egg texture ($\chi^2 = 21.04$, df = 1, $P < 0.001$) across nests.

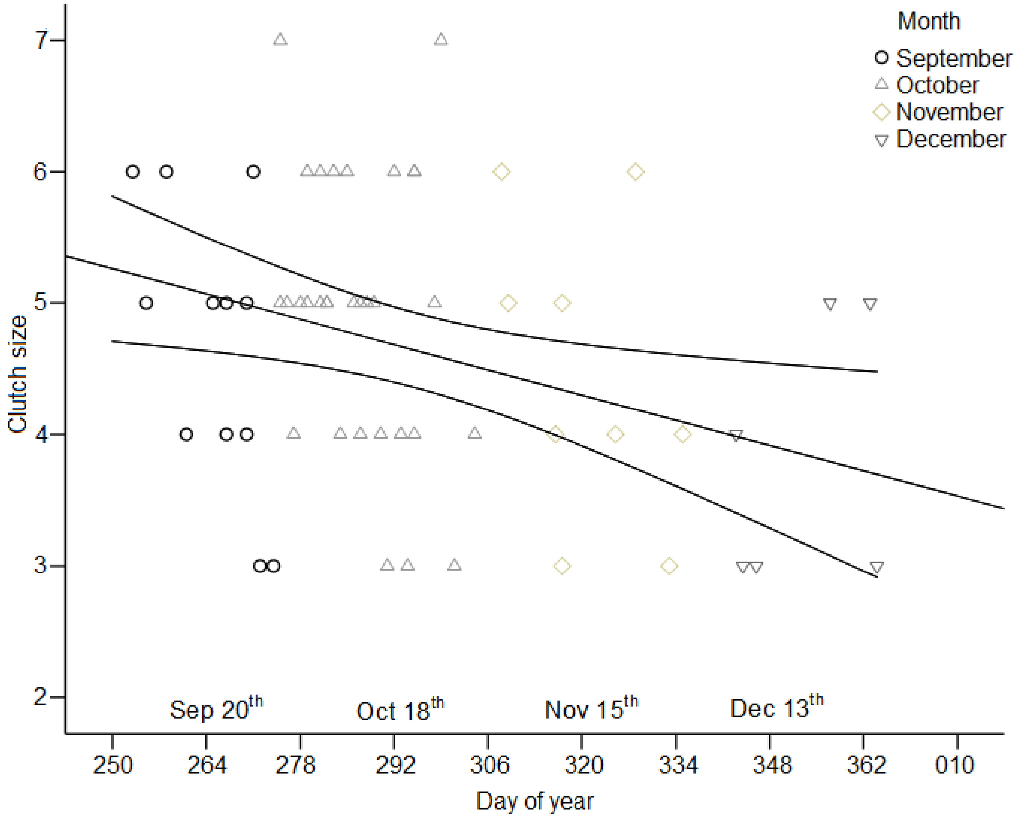

Figure 4.6. Linear relationship between clutch size and egg-laying dates of Harwood's Spurfowls (*N* = 59), indicating clutch size to decline significantly with laying date. The line fit is mean with 95% CI. $y = -0.33x + 5.35$: y = clutch size and x = days passed after the first egg laid.

4.4.4. Geometrical parameters of eggs and spatiotemporal variation of clutch size

Egg measurements were conducted on 224 fresh eggs (54.63%) from 66 nests. Fresh eggs weighed on average 25.20 g. The average egg length and breadth were 42.13 mm and 32.95 mm, respectively. The average egg volume and surface area were 23.35 cm^3 and 34.12 cm^2, respectively. The average shape index was 78.25%. Across habitat types, most egg parameters showed significant differences, except for egg shape index (Kruskal–Wallis test H = 0.78, P = 0.677) (Table 4.1). The average clutch size was 4.46 eggs/nest (± 1.09, range = 2–7, N = 410 eggs from 87 nests), with a modal clutch size of four eggs. Pearson correlation showed a significant positive association between most parameters. Only egg length showed a significant negative association with shape index and mass and surface area did not show significant associations with egg shape index (Table S1). Clutch size showed significant differences across habitats (Kruskal–Wallis test H = 13.95, P = 0.001), biomes (Mann–Whitney test U = 443.5, P < 0.001) and months (Kruskal–Wallis test H = 12.99, P = 0.003) (Table 4.2).

Table 4.1. Geometrical egg parameters in three habitat types in UBNB (N = 224 eggs). Values are given as Mean ± SD for the whole data set (habitats combined) and separately per habitat. The same superscript letter within a row indicates a non-significant difference. Abbreviations: CTW = *Combretum-Terminalia* woodland and wooded grasslands and DAF = Dry evergreen Afromontane forest and grassland complex.

Geometric parameter	Habitats combined	Habitat			*H*	*P*
		CTW = 55	DAF = 25	Farmland = 144		
Length (mm)	42.13 (± 0.86; 40.02–43.70)	41.63 ± 0.88^{b}	42.44 ± 0.71^{a}	42.26 ± 0.81^{a}	23.38	<0.001
Breadth (mm)	32.95 (± 0.73; 30.98–34.85)	32.62 ± 0.73^{b}	32.95 ± 1.00^{ab}	33.08 ± 0.63^{a}	12.74	0.002
Mass (g)	25.20 (± 1.74; 21.29–28.76)	23.94 ± 1.56^{b}	25.95 ± 1.18^{a}	25.55 ± 1.66^{a}	40.85	<0.001
Volume (cm^3)	23.51 (± 1.31; 20.12–26.65)	22.76 ± 1.23^{b}	23.69 ± 1.63^{a}	23.77 ± 1.17^{a}	21.87	<0.001
Surface area (cm^2)	34.12 (± 1.23; 31.04–36.88)	33.37 ± 1.16^{b}	34.36 ± 1.39^{a}	34.36 ± 1.11^{a}	24.43	<0.001
Shape index (%)	78.25 (± 1.79; 73.41–82.74)	78.37 ± 2.06^{a}	77.64 ± 2.23^{a}	78.31 ± 1.57^{a}	0.78	0.677

Table 4.2. Spatiotemporal variation of clutch size. Abbreviations: AH-Afrotropical Highlands biome and SG-Sudan-Guinea Savanna biome. * Mann–Whitney test *U* = 443.5 and *P* < 0.001.

Category	Subcategory	Clutch size						N	Total	Mean ± SD	*H*	*P*
		2	3	4	5	6	7					
Habitat	CTW	0	14	8	5	2	0	29	111	3.83 ± 0.97^{b}	13.95	0.001
	DAF	0	1	1	3	2	0	7	34	4.86 ± 1.07^{ab}		
	Farmland	1	4	19	19	11	2	56	265	4.73 ± 1.04^{a}		
Biome*	AH	0	9	17	23	14	2	65	308	5.14 ± 0.90^{a}	NA	NA
	SG	1	10	11	4	1	0	27	102	3.78 ± 0.89^{b}		
Month	September	0	3	5	4	4	0	16	73	4.56 ± 1.09^{ab}		
	October	0	5	12	16	10	2	45	216	4.80 ± 1.04^{a}	12.99	0.003
	November	1	6	9	3	2	0	21	83	3.95 ± 1.02^{b}		
	December	0	5	3	3	0	0	11	38	3.82 ± 0.87^{b}		

4.4.5. Incubation, hatching and parental care

Based on our three days of continuous video recordings, only females incubated the eggs. The average incubation lasted for 20.81 days (± 1.09, 19–23 d, *N* = 36) and 66.67% of the eggs were incubated for 20 and 21 days. Additionally, the videos documented that females were never provisioned with food by males, but left their nests unattended, likely in search of food (mean 74.71 ± 38.90 min/day, 11–188 min, *N* = 108 observations), which corresponded to 5.19% of their daily time budget (± 0.02%, range = 0.76–13.06%). Videos from farmland nest sites showed that females sometimes foraged directly from seeds of grasses covering the nests. Females left the nests for feeding frequently in the morning and in the evening, with higher activity observed in the morning (Mann–Whitney test *U* = 213, P < 0.001). The average nesting period for measured and unmeasured nests were 29.36 days (± 3.51, 22–35 d, *N* = 36) and 31.53 days (± 1.81, 26–33 d, *N* = 19 nests), respectively. Hatching was synchronous and lasted on average for 137.27 min (± 79.44, 68–298 min, *N* = 11 nests). Usually only females were present during hatching, while in four nests (5.3%) both sexes fed chicks in the nest during the post-hatching period.

4.4.6. Breeding success and hatching failure

Out of 92 nests, we evaluated the fate of most measured nests (*N* = 78 nests, 84.78%). Accordingly, 73.08% (*N* = 57 nests) were successful and 26.92% (*N* = 21 nests) failed.

Only 14 nests (15.22%) were censored due to extreme weather conditions, logistical constraints and accessibility. Among the successful nests, all eggs (100%) hatched in 23 nests. Altogether 235 chicks hatched, of which seven chicks (2.99%) were found dead in and around seven nests during our last nest visit, possibly due to adverse weather conditions. The average hatching success was 4.12 chicks/nest (± 0.91, 2–6 chicks), which was equivalent to 86.94% (± 11.60) chicks/nest in measured nests. In these nests, the daily nest survival rates (DSR) was estimated at 98.82% ± 0.003 (95% CI: 98.31%–99.32%) and total nest survival probability (DSR^d) was 70.48% ± 0.01 (95% CI: 60.66%–81.82%) (Table 4.3). The average hatching success for the unmeasured nests was 5.22 (± 0.80, 4–7 chicks) or 95.47% (± 7.88) chicks/nest. DSR and nest survival probability were 99.45% ± 0.003 (95% CI: 98.92%–99.99%) and 84.14% ± 0.01 (95% CI: 71.00%–99.61%), respectively (Table 4.3). Our results showed that unmeasured nests had higher hatching success than measured nests (Mann–Whitney test $U = 380$, $P = 0.002$).

Table 4.3. Breeding parameters for measured and unmeasured nests of Harwood's Spurfowls.

Parameter	Measured nests			Unmeasured nests		
	Mean	SD	N	mean	SD	N
Clutch size	4.46	1.09	92	5.48	0.80	27
Hatching success	4.12	0.91	57	5.22	0.80	23
Daily nest survival rates (DSR) (%)	98.82	0.003	78	99.45	0.003	27
Total nest survival probability ($\hat{S}$) (%)	70.48	0.01	36	84.14	0.01	23

The status of 38 eggs from 34 nests was categorized as unhatched (47.37%), collected (23.68%), disappeared (21.05%), and rolled out of nest (7.89%) (Table 4.4). Human footprints, photographs and noise recorded by camera traps in the nest environment documented that herdsmen and farmers collected eggs. Rainfall coupled with strong winds also rolled eggs out of the nest and broke some of them. The main factors for nest failure were predation (52.39%, including hunting) followed by farming operations (19.05%), and desertion (9.52%) (Table 4.4). Potential predators commonly observed on the study sites were White-tailed Mongoose (Figure 4.4C), Common Genets *Genetta genetta* and Fan-tailed Ravens *Corvus rhipidurus*.

Table 4.4. Causes of breeding failure in Harwood's Spurfowls.

Successful nests (*N* = 57 nests)		Failed nests (*N* = 21 nests)			
Factor	Egg	Factor	Nest level	Laying parent	Total
Unhatched	18 (47.37%)	Predation	3 (14.29%)	1 (4.76%)	4 (19.05%)
Disappeared eggs	8 (21.05%)	Desertion	2 (9.52%)	-	2 (9.52%)
Egg collecting	9 (23.68%)	Hunting	8 (38.10%)	3 (14.29%)	11 (52.38%)
Sprawl/rolled eggs	3 (7.89%)	Farming	4 (19.05%)	0	4 (19.05%)
Total	38 (100%)	Total	17 (80.95%)	4 (19.05%)	21 (100%)

4.5. Discussion

4.5.1. Mating system, nest-site selection and nest-building behavior

We confirmed a polygamous, non-lekking mating system in Harwood's Spurfowl as previously reported (Robertson et al. 1997, Abrha et al. 2018). This is a resource-defense polygyny strategy (Emlen and Oring 1977, Gill 2007) typical of many gallifom species (Lislevand et al. 2009). Nest-site selection and nest-building behavior are critical for the breeding success of ground-nesting birds (Mainwaring et al. 2014, Mayer et al. 2009, Gómez et al. 2019). According to our results, only female Harwood's Spurfowls select nest sites. Their specific nest-site selection and nest-building behavior predominantly aims at reducing the risk of predation by the following mechanisms:

1) Plumage color and patterns of females often matched the background of the nest microhabitat (e.g., black soil, stones, rocks and bushy thorns: Figure 4.5, Figure S1). Such crypsis through background matching is a fundamental tactic of predator avoidance (Merilaita and Stevens 2011, Michalis et al. 2017, Ruxton et al. 2019, Terrill et al. 2023) and is very common in ground nesting birds (Lovell et al. 2013, Troscianko et al. 2016). In Ethiopia, some larks and other ground-breeding songbirds have evolved plumage traits to match different soil types (Last 2009). Based on our observations, incubating females remained motionless until being approached up to 1 meter, suggesting that plumage crypsis plays the most important role for the survival of clutches because the lightly colored eggs are relatively conspicuous when unattended, even though the nests may be covered by vegetation. In support of this, motionlessness is known to reinforce anti-predator coloration in many animal species

(Stevens and Merilaita 2011, Stevens and Ruxton 2019), particularly among ground nesting birds (Troscianko et al. 2016).

2) The location of most nests in terms of orientation, positioning, substrate, and slope gradient (accessibility) was apparently chosen to thwart unfavorable exposure to weather and to minimize the risk of predation. Consistent with this findings, ground nesters are known to employ such mechanisms to maintain a favorable thermal environment (Deeming and Mainwaring 2015, Mainwaring et al. 2015, Duursma et al. 2018) thereby optimizing nest safety (Gill 2007). Most Harwood's Spurflows' nests were effectively hidden in vegetation and some were located under single short thorny trees (up to 5 m) on steep slopes. This strategy minimized nest predation as suggested by Conover (2007) and Mainwaring et al. (2014).

3) Female Harwood's Spurfowls possibly also reduced the risk of depositional odor trails during feeding. Our camera trap recordings showed that incubating females never flew off directly from their nests and mainly left the nest in the morning. Instead, they typically walked away from the nests in different directions. Besides, we did not see individuals leaving the nest during rain and intensive solar radiation. Such behavior could, together with reducing visual encounters with predators, suggest that females minimize the risk of depositional odor trails in concordance with other reports on ground-dwelling birds (Conover 2007, Winkler 2016). For example, we had two failed nests due to olfactory-orientated predators, White-tailed Mongoose and Common Genet, who likely followed contact odor trails created by repeated visits, suggesting that breeding spurfowl females may be olfactory inconspicuous.

4.5.2. Egg laying, geometrical parameters of eggs, and clutch size

The onset of breeding was from the end of August, right after big rainfalls ceased, to December (in Ethiopia, this season is also known as "harvesting season" or "spring"). We found that Harwood's Spurfowl has a single breeding season instead of a prolonged or non-synchronous breeding as mentioned in Robertson et al. (1997). Such a difference in breeding phenology could be attributed to temporally changes of favorable habitats and climatic conditions, as well as differences in disturbances level. For example, the rainfall in the Upper Blue Nile Basin (UBNB) is highly variable but has trended towards significant decrease since 1980 (Mohammed et al. 2022). This could possibly influence the timing of breeding of the species. Indeed, the breeding season of Harwood's Spurfowl is associated with the rainy season (Robertson et al. 1997, Abrha et al. 2018) as in related species, such as Swainson's Spurfowl (*Pternistis swainsonii*) (Jansen and Crowe 2005) and most galliformes species (McGowan 1994), probably due to food peaks after heavy and consecutive rainfall ceases.

Our results demonstrated that the earliest clutches were initiated in September and peak egg laying occurred in October when the conditions were wet with occasional rainfall (Figure S4). Conversely, earlier studies reported the earliest egg-laying dates during the driest conditions in December and January (Ash 1978, Ash and Gullick 1986, Ash and Atkins 2009). However, these reports lacked systematic and detailed breeding observation of the target species in the area. According to our camera trap data (77.50%), many eggs were laid in the morning, which is consistent with other birds (Winkler 2016). The females laid on average a single egg per day, similar to other pheasants (Khalil et al. 2016) and other precocial species (Hepp and Kennamer 2018). Significant variation in the geometrical parameters of eggs across habitats could be explained by climatic conditions and food availability for females. The clutch size (4.66) for Harwood's Spurfowls was similar to that of Swainson's Spurfowl (Jansen and Crowe 2005). We found clutch size of Harwood's Spurfowl to decrease significantly as the breeding season progresses, possibly as a result of a gradual decline in food resources and nest cover, as well as an increase in threats (predominantly predation). This phenomenon is common in ground nesting birds (Lu and Zheng 2003, Suárez et al. 2005, Balasubramaniam and Rotenberry 2016) because breeding females progressively face food scarcity (Winkler 2016).

While linear egg dimensions of Harwood's Spurfowl were similar to its sister species, Clapperton's Spurfowl (*Pternistis clappertoni*) (Schönwetter 1961), we rely on the derived parameter (i.e. egg shape), as this parameter has an adaptive value for life-history traits in birds (Stoddard et al. 2017, Montgomerie et al. 2021). Moreover, egg shapes could be determined by clutch size (Barta and Székely 1997, Montgomerie et al. 2021). Following the classification of egg shape index (Sarica and Erensayin 2004, de Oliveira-Boreli et al. 2023), Harwood's Spurfowl has more spherical and whiter eggs, regardless of some phenotypic variation in shape, spottiness and color across habitats (Figures S2 and S3).

Because spherical egg shapes are featured by a uniform shell thickness (Stoddard et al. 2017) and resistance to breakage (Bain 1991, Montgomerie et al. 2021), such traits (including egg color) in our study species could also represent an adaptation to excessive sunlight and erratic weather conditions in UBNB. For example, in Australian songbirds, the most spherical eggs were found among those species who bred in open nests under the hottest conditions, which exposed them to the highest amount of solar radiation (Duursma et al. 2018). We consider it possible that the spherical shape of Harwood's Spurfowls' eggs is a similar adaption to the harsh sunlight conditions in UBNB, which could also explain the spherical eggs shape of other tropical galliform species (Stoddard et al. 2017, Montgomerie et al. 2021). To which extent the colors and patterns of Harwood's Spurfowls' eggs actually contribute to temperature regulation, which ultimately may account for enhanced breeding success, remains to be tested.

4.5.3. Incubation, hatching and parental care

We found incubation to last for approximately 21 days, which matches the known incubation period of 21-23 days in other spurfowl species from South Africa (Little and Crowe 1993, Jansen et al. 2001). Although females sit on the nest after laying the first egg, incubation is delayed until the clutch is completed to guarantee hatching synchronicity. This is consistent with reports for many precocial birds, particularly ground nesters (e.g., Persson and Göransson 1999, Gill 2007, Mayer et al. 2009, Balasubramaniam and Rotenberry 2016, Winkler 2016). The average daily nest attendance of nearly 95% indicates that females actively reduce the risk of predation and egg hypothermia by leaving the nest only briefly for feeding. Our data thus documented that Harwood's Spurfowl has an almost uniparental care strategy with females exclusively incubating the eggs and guiding their freshly hatched chicks to the nearby vegetation. The role of territorial males was mainly to escort the nesting females. Only in rare cases males were observed tossing foods towards chicks. This indicates that males predominantly control the resources for the breeding females and by doing so, participate at least indirectly in raising their chicks. This is in accordance with the hitherto reported uniparental strategy in the congeneric Swainson's Spurfowl *Pternistis swainsonii* from South Africa (van Niekerk 2017).

4.5.4. Breeding success and failure

The average hatching success (86.94% at measured and 95.47% at unmeasured nests) of Harwood's Spurfowl is similar to some African (Grey-winged Francolin *Scleroptila afra*: Little and Crowe 1993, Red-winged Francolin *Scleroptila l. levaillantii*: Jansen et al. 2001) and Asian francolin species (Black Francolin *Francolinus francolinus asiae*: Kumar et al. 2020), but higher than reported for the other Grey Francolin (*Ortygornis pondicerianus interpositus*: Khalil et al. 2016). Even though we cautiously removed the vegetation cover and fenced trails leading to nests, we suspected that disturbances during repeated visits (e.g. camera placement, nest measurements, egg handling) could have exacerbated the failure of measured nests indirectly. Indeed, breeding success of measured nests was lower than of unmeasured (random) nests, mainly due to predation and farming activities (Table 4.4). The relatively high percentage (47.37%) of unhatched eggs in successful nests could be due to infertility and embryo mortality. Touching eggs and catching laying parents in particular (Radnezhad et al. 2011, Zhao et al. 2020), as well as nest visits in general were reported as factors for hatching failure in other birds (Green 2004, Zhao et al. 2020). Because Harwood's Spurfowl is a ground nester mainly in and around farmlands, it is pronouncedly hunted for food (Robertson et al. 1997, Ash and Atkins 2009, Abrha and Nigus 2017, Abrha et al. 2017, Abrha et al. 2023). Farming operations also exacerbated hatching failure of the species, consistent with studies in other pheasant species (Coates et al. 2017). Globally, predation is a major important threat for several galliform species (e.g. Little and Crowe 1993, Clark et al. 1999, Persson and Göransson 1999, Lu and Zheng 2003, Balasubramaniam and Rotenberry 2016, Zhao et al. 2020).

To conclude, since predation was the main reason for the nesting failure, we recommend limiting mowing grasses and cutting trees during the breeding season in and around farmlands and other habitats (including woodlands, scrub and bush vegetation) where Harwood's Spurfowls are dwelling in order to avoid disturbance, sun exposure and access to nesting sites. Hunting (including egg collecting) should be prohibited throughout the year, and conservation education and awareness creation should be delivered to the local communities.

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Ethics statement

This study did not require any ethical approval; hitherto we followed and respected the authority guideline.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

Data will be made available on request.

CRediT authorship contribution statement

Abadi Mehari Abrha: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. Kai Gedeon: Conceptualization, Funding acquisition, Supervision, Validation, Writing – review & editing. Lars Podsiadlowski: Conceptualization, Funding acquisition, Supervision, Validation, Writing – review & editing. Till Töpfer: Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing.

4.6. References

Abrha. A. M., K. Gedeon, L. Podsiadlowski, and T. Töpfer. 2023. Dynamic occupancy modeling of a cryptic ground-dwelling pheasant species in the Upper Blue Nile Basin in Ethiopia. Global Ecology and Conservation 48:e02710. https://doi.org/10.1016/j.gecco.2023.e02710

Abrha, A. M., and N. K. Nigus. 2017. The ecology of Harwood's Francolin *Pternistis harwoodi* (Aves: Galliformes: Phasianidae) at Merhabete District, central highlands of Ethiopia: implications for conservation. Journal of Threatened Taxa 9(9):10633-10641. https://doi.org/10.11609/jott.3189.9.9.10633-10641

Abrha, A. M., H. K. Nigus, B. G. Weldetnsae, M. Tilahun, A. G. Nigusse, and K. T. Deribew. 2017. Effects of human disturbances on two sympatric francolin species in the Central Highlands of Ethiopia. Podoces 12(1):13-21. https://wesca.net/Podoces/podoces12.1.html

Abrha, A. M., S. A. Zelelew, H. K. Nigus, and A. Alelign. 2018. Diurnal activity patterns of Harwood's Spurfowl *Pternistis harwoodi* in relation to habitat types and climatic conditions in the Central Highlands of Ethiopia. Ostrich 89(2):1-7. https://doi.org/10.2989/00306525.2018.1429505

Asefa, M., M. Cao, Y. He, E. Mekonnen, X. Song, and J. Yang. 2020. Ethiopian vegetation types, climate and topography. Plant Diversity 42(4):302-311. https://doi.org/10.1016/j.pld.2020.04.004

Ash, J. S. 1978. The undescribed female of Harwood's Francolin *Francolinus harwoodi* and other observations on the species. Bulletin of the British Ornithologists' Club 98(2):1-15. https://www.biodiversitylibrary.org/item/126876#page/7/mode/1up

Ash, J. S., and T. M. Gullick. 1989. The present situation regarding the endemic breeding birds of Ethiopia. Scopus 13:90-99. https://biostor.org/reference/135205

Ash, J., and J. Atkins, editors. 2009. Birds of Ethiopia and Eritrea: an atlas of distribution. Christopher Helm, London.

Balasubramaniam, P., and J. T. Rotenberry, 2016. Elevation and latitude interact to drive life-history variation in precocial birds: a comparative analysis using galliformes. Journal of Animal Ecology 85(6):1528-1539. https://doi.org/10.1111/1365-2656.12570

Bain, M. M. 1991. A reinterpretation of eggshell strength. Pages 131-145 in S.E. Solomon, editor. Egg and Eggshell Quality. Wolfe, London.

Barta, Z., and Székely, T. 1997. The optimal shape of avian eggs. Functional Ecology 11(5): 656-662. https://doi.org/10.1046/j.1365-2435.1997.00136.x

Carroll, J. M., C. A. Davis, R. D. Elmore, and S. D. Fuhlendorf. 2015. A ground-nesting galliform's response to thermal heterogeneity: implications for ground-dwelling birds. PLoS One 10(11):1-20. https://doi.org/10.1371/journal.pone.0143676

Clark, W. R., R. A. Schmitz, and T. R. Bogenschutz. 1999. Site selection and nest success of ring-necked pheasants as a function of location in Iowa landscapes. Journal of Wildlife Management 63(3):976-989. https://doi.org/10.2307/3802812

Coates, P. S., B. E. Brussee, K. B. Howe, J. P. Fleskes, I. A. Dwight, D. P. Connelly, and et al. 2017. Long-term and widespread changes in agricultural practices influence ring-necked pheasant abundance in California. Ecology and Evolution 7(8): 2546-2559. https://doi.org/10.1002/ece3.2675

Conover, M. R. 2007. Predator-prey dynamics: role of olfaction. Taylor & Francis Group, LLC.

Deeming, D. C., and M. C. Mainwaring. 2015. Functional properties of nests. Pages 29-49 in D. C. Deeming and S. J. Reynolds, editors. Nests, eggs and incubation: new ideas about avian reproduction. Oxford University Press.

de Oliveira-Boreli, F. P., D. F. Pereira, J. A. Gonçalves, V. Z. da Silva, and I. de A. Nääs. 2023. Non-destructive assessment of hens' eggs quality using image analysis and machine learning. Smart Agricultural Technology 4:100161. https://doi.org/10.1016/j.atech.2022.100161

del Hoyo, J., A. Elliott, and J. Sargatal, editors. 1994. Handbook of the Birds of the World, Vol. 2. New Word Vultures to Guineafowl. Lynx Edicions, Barcelona.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83(12):3476-3488. https://doi.org/10.1890/0012-9658(2002)083[3476:ATFMAN]2.0.CO;2

Duursma, D. E., R. V. Gallagher, J. J. Price, and S. C. Griffith. 2018. Variation in avian egg shape and nest structure is explained by climatic conditions. Scientific Reports 8(4141):4141. https://doi.org/10.1038/s41598-018-22436-0

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197(4300):215-223. https://www.science.org/doi/10.1126/science.327542

Fierro-Calderón, K., M. Loaiza-Muñoz, M. A. Sánchez-Martínez, D. Ocampo, S. David, H. F. Greeney, and G. A. Londono. 2021. Methods for collecting data about the breeding biology of Neotropical birds. Journal of Field Ornithology 92(4):315-341. https://doi.org/10.1111/jofo.12383

Fishpool, L. D., and M. I. Evans. 2001. Important Bird Areas in Africa and associated islands: Priority sites for conservation. Cambridge: BirdLife International.

Friis, I., S. Demissew, and P. van Breugel. 2010. Atlas of the Potential Vegetation of Ethiopia. Biologiske Skrifter 58:1-307. https://doi.org/10.1093/aob/mcq242

Gill, F. B. 2007. Ornithology, third edition. W. H. Freeman, New York, NY, USA.

Gill, F., D. Donsker, and P. Rasmussen, editors. 2023. IOC World Bird List (v 13.2). Doi 10.14344/IOC.ML.13.2. http://www.worldbirdnames.org/ (accessed 8 February 2024).

Gómez, J., G. Liñán-Cembrano, C. Ramo, M. Castro, A. Pérez-Hurtado, and J. A. Amat, 2019. Does the use of nest materials in a ground-nesting bird result from a compromise between the risk of egg overheating and camouflage? Biology Open 8(12):1-8. https://doi.org/10.1242/bio.042648

Gedeon, K., D. Rödder, C. Zewdie, and T. Töpfer. 2017. Evaluating the conservation status of the black-fronted francolin *Pternistis atrifrons*. Bird Conservation International 28(4):653-661. https://doi.org/10.1017/S0959270917000363

Green, R. E, 2004. Breeding biology. Pages 57-83 in W. J. Sutherland, I. Newton and R.E. Green, editors. Bird Ecology and Conservation: A handbook of Techniques. Oxford University Press Inc., New York.

Guillette, L. M., and S. D. Healy. 2015. Nest building, the forgotten behaviour. Current Opinion in Behavioral Sciences 6:90-96. https://doi.org/10.1016/j.cobeha.2015.10.009

Harris, R. B., S. M. Birks, and A. D. Leaché. 2014. Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). Journal of Biogeography 41(11): 2045-2056. https://doi.org/10.1111/jbi.12357

Hepp, G. R., and R. A. Kennamer. 2018. Laying sequence interacts with incubation temperature to influence rate of embryonic development and hatching synchrony in a precocial bird. PloS One 13(1):e0191832. https://doi.org/10.1371/journal.pone.0191832

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weights of bird eggs. The Auk 96(1):73-77. https://academic.oup.com/auk/article/96/1/73/5184694

Jansen, R. 2001. Population biology, behavioural ecology and management of the Redwing Francolin *Francolinus levaillantii* and Swainson’s Spurfowl *Pternistis swainsonii*. Ph.D. thesis, Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7701, South Africa. http://hdl.handle.net/11427/6276

Jansen, R., and T. M. Crowe. 2005. Relationship between breeding activity and rainfall for Swainson's Spurfowl, *Pternistis swainsonii*, within southern Africa, with specific reference to the Springbok Flats, Limpopo Province, South Africa. Ostrich-Journal of African Ornithology 76(3-4):190-194. https://doi.org/10.2989/00306520509485492

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29(1):62-69.

Kesler, D. C., E. B. Webb, and J. R. Walters. 2018. Conservation Tools and Strategies. Pages 830-852 in M.L. Morrison, A.D. Rodewald, G. Voelker, M.R. Colón and J.F. Prather, editors. Ornithology: Foundation, Analysis, and Application. Johns Hopkins University Press.

Khalil, S., M. Anwar, and I. Hussain. 2016. Breeding Biology of Grey Francolin (*Francolinus pondicerianus*) in Salt Range, Pakistan. Pakistan Journal of Zoology 48:115-123.

Klett, A. R., H. F. Duebbert, C. A. Faanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Fish and Wildlife Service Resource Publication Number 158.

Kross, S. M., and X. J. Nelson. 2011. A portable low-cost remote videography system for monitoring wildlife. Methods in Ecology and Evolution 2(2):191-196. https://doi.org/10.1111/j.2041-210X.2010.00064.x

Kumar, A., D. K. Sharma, R. Lochan, S. Dewan, and S. Negi. 2020. Relative abundance, habitat preference, and breeding ecology of Asian Black francolin, *Francolinus*

francolinus asiae (Bonaparte, 1856) (Galliformes: Phasianidae) from North-Western Himalaya. Journal of Asia-Pacific Biodiversity 13(2):162-168. https://doi.org/10.1016/j.japb.2020.02.001

Last, G. 2009. The Geology and Soils of Ethiopia and Eritrea. Pages 25-26 in J. Ash and J. Atkins, editors. Birds of Ethiopia and Eritrea: an atlas of distribution. Christopher Helm, London.

Lislevand, T., J. Figuerola, and T. Szekely. 2009. Evolution of sexual size dimorphism in grouse and allies (Aves: Phasianidae) in relation to mating competition, fecundity demands and resource division. Journal of Evolutionary Biology 22(9):1895-1905. https://doi.org/10.1111/j.1420-9101.2009.01802.x

Little, R. M., and T. M. Crowe. 1993. The breeding biology of the Greywing Francolin *Francolinus africanus* and its implications for hunting and management. South African Journal of Zoology 28(1):6-12. https://doi.org/10.1080/02541858.1993.11448291

Lovell, P. G., G. D. Ruxton, K. V. Langridge, and K. A. Spencer. 2013. Egg-laying substrate selection for optimal camouflage by quail. Current Biology 23(3):260-264. https://doi.org/10.1016/j.cub.2012.12.031

Lu, X., and G. Zheng. 2003. Reproductive ecology of Tibetan Eared Pheasant *Crossoptilon harmani* in scrub environment, with special reference to the effect of food. Ibis 145(4):657-666. https://doi.org/10.1046/j.1474-919X.2003.00204.x

Madge, S., and P. McGowan. 2002. Pheasants, Partridges and Grouse. Christopher Helm, London.

Mainwaring, M. C., I. R. Hartley, M. M. Lambrechts, and D. C. Deeming. 2014. The design and function of birds' nests. Ecology and Evolution 4(20):3909-3928. https://doi.org/10.1002/ece3.1054

Mainwaring, M. C., S. J. Reynolds, K. Weidinger. 2015. The influence of predation on the location and design of nests. Pages 50-64 in D.C. Deeming and S.J. Reynolds, editors. Nests, eggs and incubation: new ideas about avian reproduction. Oxford University Press.

Matysioková, B., and V. Remeš. 2024. Nest predation decreases with increasing nest height in forest songbirds: A comparative study. Journal of Ornithology 165(1):257-261. https://doi.org/10.1007/s10336-023-02108-1

Mayer, P. M., L. M. Smith, R. G. Ford, D. C. Watterson, M. D. McCutchen, and M. R. Ryan. 2009. Nest construction by a ground-nesting bird represents a potential trade-off between egg crypticity and thermoregulation. Oecologia 159:893-901. https://doi.org/10.1007/s00442-008-1266-9

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

McGowan, P. J. K. 1994. Family Phasianidae (pheasants and partridges). Pages 434-552 in J. del Hoyo, A. Elliott and J. Sargatal, editors. Handbook of the Birds of the World, Vol. 2. New Word Vultures to Guineafowl. Lynx Edicions, Barcelona.

Merilaita, S., and M. Stevens. 2011. Crypsis through background matching. Pages 17-33 in M. Stevens and S. Merilaita, editors. Animal Camouflage: Mechanisms and Function. Cambridge University Press.

Michalis, C., N. E. Scott-Samuel, D. P. Gibson, and I. C. Cuthill. 2017. Optimal background matching camouflage. Proceedings of the Royal Society B: Biological Sciences 284:20170709. https://doi.org/10.1098/rspb.2017.0709

Mohammed, J. A., T. Gashaw, G. W. Tefera, Y. T. Dile, A. W. Worqlul, and S. Addisu. 2022. Changes in observed rainfall and temperature extremes in the Upper Blue Nile Basin of Ethiopia. Weather and Climate Extremes 37:10046. https://doi.org/10.1016/j.wace.2022.100468

Montgomerie, R., N. Hemmings, J. E. Thompson, and T. R. Birkhead. 2021. The shapes of birds' eggs: Evolutionary constraints and adaptations. The American Naturalist 198(6):E215-31. https://doi.org/10.1086/716928

Narushin, V. G., M. N., Romanov, and D. K. Griffin. 2022. Delineating an ovoidal egg shape by length and breadth: A novel two-parametric mathematical model. Biosystems Engineering 224:336-345. https://doi.org/10.1016/j.biosystemseng.2022.11.003

Persson, I., and G. Göransson. 1999. Nest attendance during egg laying in pheasants. Animal Behaviour 58(1):159-164. https://doi.org/10.1006/anbe.1999.1107

Preston, F. W. 1968. The shapes of birds' eggs: Mathematical aspects. The Auk 85(3):454-463. https://doi.org/10.2307/4083294

Radnezhad, H., N. Satei, M. Kaboli, M. Karami, N. Khorasani, R. Prodon, M. Foroughi, M. Abari, and S. Cheraghi. 2011. Breeding ecology of the Iranian ground jay (*Podoces* *pleskei*). African Journal of Biotechnology 10(21):4494-4500. https://www.ajol.info/index.php/ajb/article/view/93655

Robertson, P. A., D. Yilma, D. Sileshi, S. Anteneh, W. Tadesse, and A. Million. 1997. Harwood's Francolin *Francolinus harwoodi*: recent observations on its status, distribution, habitat requirements, behaviour and threats. Bird Conservation International 7:275-282. https://doi.org/10.1017/S095927090000157X

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27(1):187-205.

Ruxton, G. D., W. L. Allen, T. N. Sherratt, and M. P. Speed. 2019. Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry. Oxford University Press.

Sarica, M., and C. Erensayin. 2004. Poultry products. Pages 100-160 in M. Turkoglu and M. Sarica, editors. Poultry Science. Bey-Ofset, Ankara, Turkey.

Schönwetter, M. 1961. Galliformes. Pages 196-293 in W. Meise, editor. Handbuch der Oologie. Band I. Berlin: Akademie-Verlag.

Steenhof, K., and I. Newton. 2007. Assessing nesting success and productivity. Raptor research and management techniques 181-192.

Stevens, M., and S. Merilaita. 2011. Animal Camouflage: Mechanisms and Function. Cambridge University Press.

Stevens, M., G. D. Ruxton. 2019. The key role of behaviour in animal camouflage. Biological Reviews 94(1):116-134. https://doi.org/10.1111/brv.12438

Stoddard, M. C., E. H. Yong, D. Akkaynak, C. Sheard, J. A. Tobias, and L. Mahadevan. 2017. Avian egg shape: Form, function, and evolution. Science 356(6344):1249-1254. https://doi.org/10.1126/science.aaj1945

Suárez, F., M. B. Morales, I. Mínguez, and J. Herranz. 2005. Seasonal variation in nest mass and dimensions in an open-cup ground-nesting shrub-steppe passerine: the Tawny Pipit *Anthus campestris*. Ardeola 52(1):43-51. https://www.ardeola.org/en/volumes/521/articles/43-51/?stc=ko

Terrill, R. S., and A. J. Shultz. 2023. Feather function and the evolution of birds. Biological Reviews 98(2):540-566. https://doi.org/10.1111/brv.12918

Tian, S., J. Xu, J. Li, Z. Zhang, and Y. Wang. 2018. Research advances of Galliformes since 1990 and future prospects. Avian Research 9(32):1-13. https://doi.org/10.1186/s40657-018-0124-7

Töpfer, T., L. Podsiadlowski, and K. Gedeon. 2014. Rediscovery of the black-fronted francolin *Pternistis* (*castaneicollis*) *atrifrons* (Conover, 1930) (Aves: Galliformes: Phasianidae) with notes on biology, taxonomy and conservation. Vertebrate Zoology 64(2):261-271. https://doi.org/10.3897/vz.64.e31494

Töpfer, T., and K. Gedeon. 2020. Alpine birds of Africa. Pages 505-517 in M.I. Goldstein and D.A. DellaSala, editors. Encyclopedia of the World's Biomes, Volume 1. Elsevier.

Troscianko, J., J. Wilson-Aggarwal, M. Stevens, and C. N. Spottiswoode. 2016. Camouflage predicts survival in ground-nesting birds. Scientific Reports 6 (19966):19966. https://doi.org/10.1038/srep19966

van Niekerk, J. H. 2001. Social and breeding behaviour of the crested francolin in the Rustenburg district, South Africa. South African Journal of Wildlife Research 31(1):35-42. https://hdl.handle.net/10520/EJC117117

van Niekerk, J. H. 2017. Female-only care of Swainson's Spurfowl *Pternistis swainsonii* chicks frees males for territorial maintenance. Ostrich 88(3):207-216. https://doi.org/10.2989/00306525.2017.1283366

van Niekerk, J. H. 2018. Coalition formation, mate selection and pairing behaviour of the Crested Francolin. Ostrich 89(1):71-78. https://doi.org/10.2989/00306525.2017.1409289

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46 (1):120-139. https://doi.org/10.1080/00063659909477239

Winkler, D. W. 2016. Breeding Biology of Birds. Pages 407-450 in I. J. Lovette and J. W. Fitzpatrick, editor. Handbook of bird biology. John Wiley and Sons.

Xiao, H., Y. Hu, Z. Lang, B. Fang, W. Guo, Q. Zhang, X. Pan, and X. Lu. 2017. How much do we know about the breeding biology of bird species in the world? Journal of Avian Biology 48(4):513-518. https://doi.org/10.1111/jav.00934

Zhao, J. M., C. Yang, Y. Q. Lou, M. Shi, Y. Fang, and Y. H. Sun. 2020. Nesting season, nest age, and disturbance, but not habitat characteristics, affect nest survival of Chinese grouse. Current Zoology 66(1):29-37. https://doi.org/10.1093/cz/zoz024

4.7. Supplementary information

Figure S1. Camera placement adjacent to nest location (A). A typical rock-dependent nest (B) and a nest under a short *Vachellia tortilis* tree (C and D) show background matching (plumage color and patterns of females and nesting sites) in Upper Blue Nile Basin (UBNB).

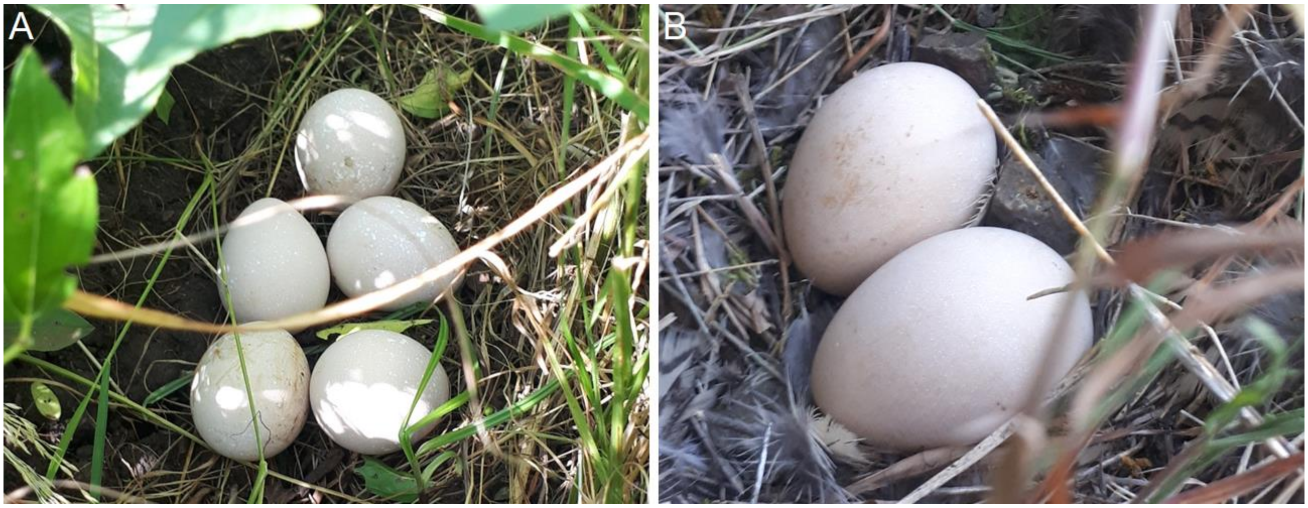

Figure S2. Variability in Harwood's Spurfowl egg colors and texture. Egg colors were white (A) and dusty white (B) with tiny spots in both nests. The clutch for (A) was taken out of the nest for handling and photography.

Figure S3. Variability in Harwood’s Spurfowl egg shapes. Egg shapes ranged from oval to more spherical. The photographs depict both intra- and inter-clutch variation (A-D).

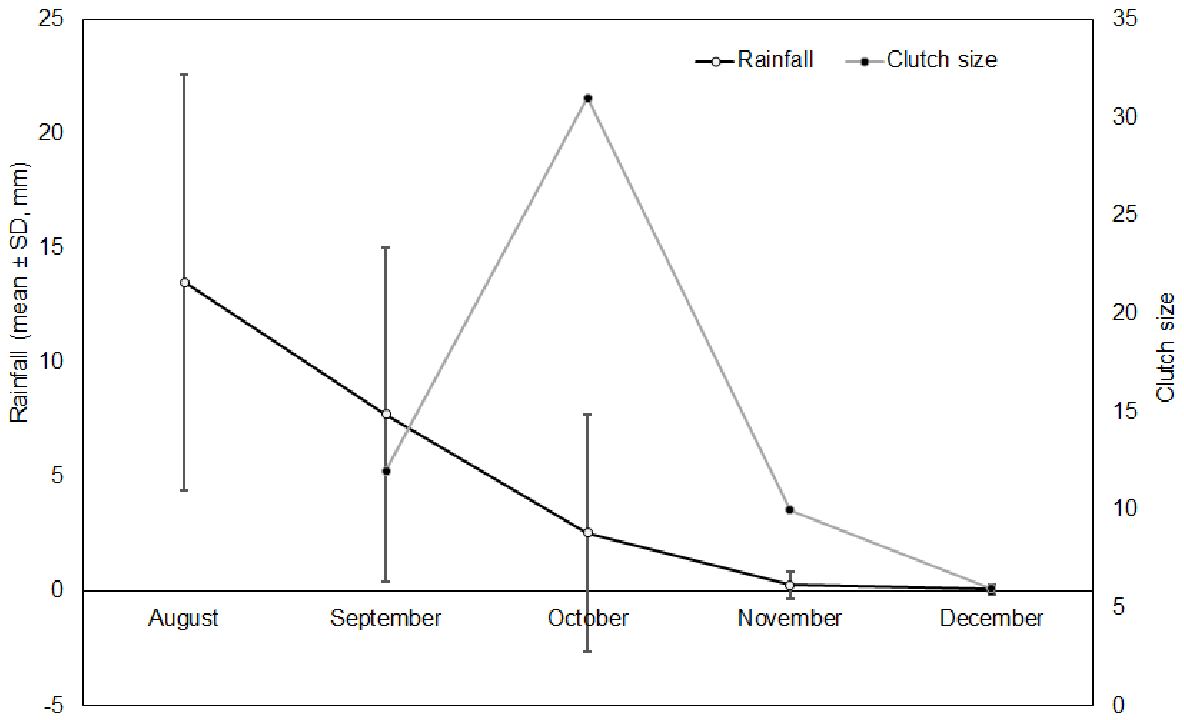

Figure S4. Average rainfall distribution and clutch size initiation in each month during the study period. Rainfall data was extracted from NASA/POWER satellite-based weather system (https://power.larc.nasa.gov/data-access-viewer/).

Table S1. Pearson correlation coefficients for the geometrical egg parameters of Harwood's Spurfowl. ** Implies very significant correlation between parameters (P < 0.001).

Parameters	Length	Breadth	Weight	Volume	Surface area	Shape index
Length	1					
Breadth	.431**	1				
Weight	.434**	.277**	1			
Volume	.704**	.944**	.376**	1		
Surface area	.821**	.869**	.413**	.983**	1	
Shape index	-.488**	.577**	-.124	.276**	.097	1

Chapter 5

Impact of climate change on mountaintop endemic birds in the Ethiopian highlands: A case study of Moorland Francolin (*Scleroptila psilolaema*) (Submitted)

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5.1. Abstract

Mountaintop endemic bird species are highly vulnerable to climate change and habitat loss in the tropics. However, there is a lack of knowledge on most alpine birds of the Eastern Afromontane Biodiversity Hotspot. In this study, we used ensemble species distribution modeling to assess the current and future habitat suitability for Moorland Francolin endemic to the Ethiopian highlands, the largest alpine habitat in Africa. Our results demonstrated that the average predictive accuracy of six algorithms had high discrimination ability (AUC = 0.99; TSS = 0.95). Temperature variables were the main determinants of habitat suitability for Moorland Francolin, with BIO1 (annual mean temperature) making the largest contribution, and to a lesser extent, BIO2 (mean diurnal range), BIO4 (temperature seasonality) and BIO7 (temperature annual range). Accordingly, the results showed that the extent of the current suitable habitat for Moorland Francolin in the alpine habitats of the Ethiopian highlands is 6861.99 km^2. However, the range will be contracted to 389.48 km^2 when projecting our ensemble on climate change scenarios, i.e., assuming the intermediate shared socio-economic pathways (SSP 126) between 2041-2060, and no suitable habitat will be available assuming the highest shared socio-economic pathways (SSP 370 and SSP 585). We also evaluated which areas exceed the training conditions of the models in projections using Multivariate Environmental Similarity Surface (MESS) to understand potential future niche dynamics of the species. Current climate change and habitat loss on the mountaintops of the Ethiopian highlands may pose a serious threat to Moorland Francolin, as major parts of its currently realized niche may be reduced. Our results also suggest that the species could be classified as Vulnerable (VU). Species-specific conservation measures are needed to mitigate the effects of climate change on alpine habitats.

Keywords: mountaintop extinction, endemic, climate change, ensemble species distribution modeling, Moorland Francolin, conservation

5.2. Introduction

Anthropogenic climate change is a substantial threat to global biodiversity and assumed to be a major driver of future species extinction (e.g., Thomas et al. 2004; Bellard et al. 2012; Cahill et al. 2013; Urban 2015; Habel et al. 2019). Global biodiversity hotspots, which support high species richness and endemism (Myers et al. 2000), are particularly prone to climate change (Malcolm et al. 2006; Trew and Maclean 2021). Thus, climate change affects species distribution across several taxa and regions (Gitay et al. 2002; Colwell et al. 2008). For instance, global warming as part of climate change causes upslope shifts in the distribution and abundance of montane butterflies (Rödder et al. 2021) and tropical bird species (Freeman et al. 2018; Bender et al. 2019; Neate-Clegg et al. 2021). Specifically, mountaintop endemic bird species are the most sensitive groups to climate change due to their limited geographical ranges (e.g., Gitay et al. 2002; Harris et al. 2014; Freeman et al. 2018; Neate-Clegg et al. 2021). However, for most mountaintop endemic tropical birds, there is insufficient evidence of their vulnerability to current and future climate change. Accordingly, urgent assessment and conservation action has been recommended for endemic birds at higher elevations in the tropics where they are experiencing range contractions due to climate change (Harris et al. 2014; Freeman et al. 2018; Neate-Clegg et al. 2021).

The Ethiopian highlands contribute high levels of endemism to the Eastern Afromontane biodiversity hotspot (De Klerk et al. 2002). They cover the largest plateau above 3000 m in the Afrotropics (Chignell et al. 2019; Groos et al. 2021), and are sometimes referred to as the Afroalpine "sky islands", because they consist of isolated mountains surrounded by different ecosystems at lower elevations. Specifically, the total surface area of Afroalpine habitats above 3500 m is approximately 5000 km^2 (Groos et al. 2021), of which nearly 27% are represented by the Bale Mountains alone (Kidane et al. 2019). Ethiopia has two extensive highland blocks namely the western and eastern highlands, divided by the Ethiopian sector of the East African Rift Valley (Friis et al. 2010). These highlands host high bird species richness and endemism next to the Albert Rift and East African Montane in Africa (De Klerk et al. 2002). The mountaintops of Ethiopia are part of the Afroalpine and Sub-Afroalpine vegetation (Ash and Atkins 2009; Friis et al. 2010) featured by a distinct endemic flora (Friis et al. 2010; Kandziora et al. 2022) and avifauna (De Klerk et al. 2002; Ash and Atkins 2009; Gedeon et al. 2017a; Töpfer and Gedeon 2020). The habitats are affected by human population growth (Chignell et al. 2019; Fashing et al. 2022), and are experiencing a rapid fragmentation due to erratic climatic conditions and other anthropogenic factors (Asefa et al. 2017; Razgour et al. 2020). More recently, ongoing climate change has also been predicted to affect the Ethiopian highlands (Kidane et al. 2019; Kidane et al. 2022) and African sky islands as the whole (Kandziora et al. 2022). This global impact may overwhelmingly affect species with restricted ranges, particularly mammals and birds in Ethiopia. To address the ongoing multiple stressors, especially on the mountaintops, the Alliance for Zero Extinction (AZE) (https://zeroextinction.org/) has initiated conservation actions to prevent the extinction of some critical species at four sites in the country. Notwithstanding, scarce information is available to attest the effects of climate change on mountaintop bird species.

To understand the potential impact of climate change on species, several algorithms for species distribution modeling have been proposed, including regression-based and machine-learning algorithms (e.g., Thuiller et al. 2009; Thuiller et al. 2016; Guisan et al. 2017; Gobeyn et al. 2019; Urbina-Cardona et al. 2019). Species distribution models (SDMs) are useful tools for assessing the conservation status of species (de Castro Pena et al. 2014; Breiner et al. 2017) and prioritize conservation plan of species under climate change scenarios (Guisan and Thuiller 2005; Elith et al. 2006; Urbina-Cardona et al. 2019). There is a plethora of studies on the usefulness of the models across several taxa (Guisan and Thuiller 2005; Urbina-Cardona et al. 2019), including cryptic (Tôrres et al. 2012), rare (Breiner et al. 2015), and poorly known species (Urbina-Cardona et al. 2019). Most importantly, the models allow discovery of potentially suitable (or isolated) areas for species (Raxworthy et al. 2007). However, these models also have caveats regarding sample size, temporal dynamics, encountering of species during migration, and detectability (Lissovsky et al. 2021).

Although most of Ethiopian’s endemic birds are concentrated in the mountainous landscapes (De Klerk et al. 2002; Ash and Atkins 2009; Gedeon et al. 2017a; Gedeon et al. 2023), there is paucity of information on the effect of climate change and related anthropogenic disturbances on these taxa (Fashing et al. 2022). However, there is evidence of three endemic bird species, but only from the lowlands (Gedeon et al. 2017b;

Bladon et al. 2021). Moorland Francolin (*Scleroptila psilolaema*) is an endemic mountaintop and near-threatened galliform species of Afroalpine and Sub-Afroalpine habitats in Ethiopia, making it an ideal species to test the effect of climate change on endemic high-elevation bird species. Most galliform species (megapodes, guans, guineafowls, New World quails, pheasants and allies) (Winkler et al. 2015; Kimball et al. 2021) are weak fliers, but rather excellent runners (Heers 2018). This phenomenon is linked to their heavy body and short wings, resulting in a low hand-wing index (HWI) (Hosner et al. 2017; Sheard et al. 2020). Therefore, their inability to disperse over long distances and the natural elevational limit of the mountains may exacerbate the situation for ground-dwelling mountaintop endemics such as the Moorland Francolin.

Moorland Francolin subsists in pristine and disturbed Afroalpine and Sub-Afroalpine habitats of the Ethiopian highlands (Tilahun et al. 1996; Ash and Atkins 2009; Gedeon et al. 2017a; Töpfer and Gedeon 2020; Abrha et al. 2023). Its occupancy (i.e., habitat use) is determined by factors related to vegetation traits, landscape connectivity metrics, climatic conditions, and sampling occasion in the central highlands of Ethiopia (Abrha et al. 2023). However, the habitat suitability and determinants of the spatial distribution for the species across the Ethiopian highlands remain elusive and show a decreasing trend due to anthropogenic disturbances (BirdLife International 2024). Therefore, our objectives were: (1) to identify the main determinants of environmental factors on the distribution of the species, (2) to predict the current and future suitable geographical distribution of the species.

5.3. Methods

5.3.1. Study Area

The study area was located in two of the Ethiopian highlands (Figure 5.1). It stretched from Bale Mountains National Park (BMNP) and Arsi Mountains National Park in the eastern highlands to Entoto Natural Park and escarpment, Sululta Plain, Ankober-Debresina escarpment, Guassa Community Conservation Area (GCCA), Borena Sayint National Park, Guguftu, Dessie highlands, and Abune Yosef in the western highlands. The study sites comprised one community-based conservation area, three national parks, four Important Bird Areas (IBAs), and other human-shaped landscapes (Tilahun et al. 1996).

Furthermore, it included other areas between these sites in both highland blocks (Figures 5.1 and 5.4). The main habitat consisted of moorland with an elevation range of 2400 to 4228 m.

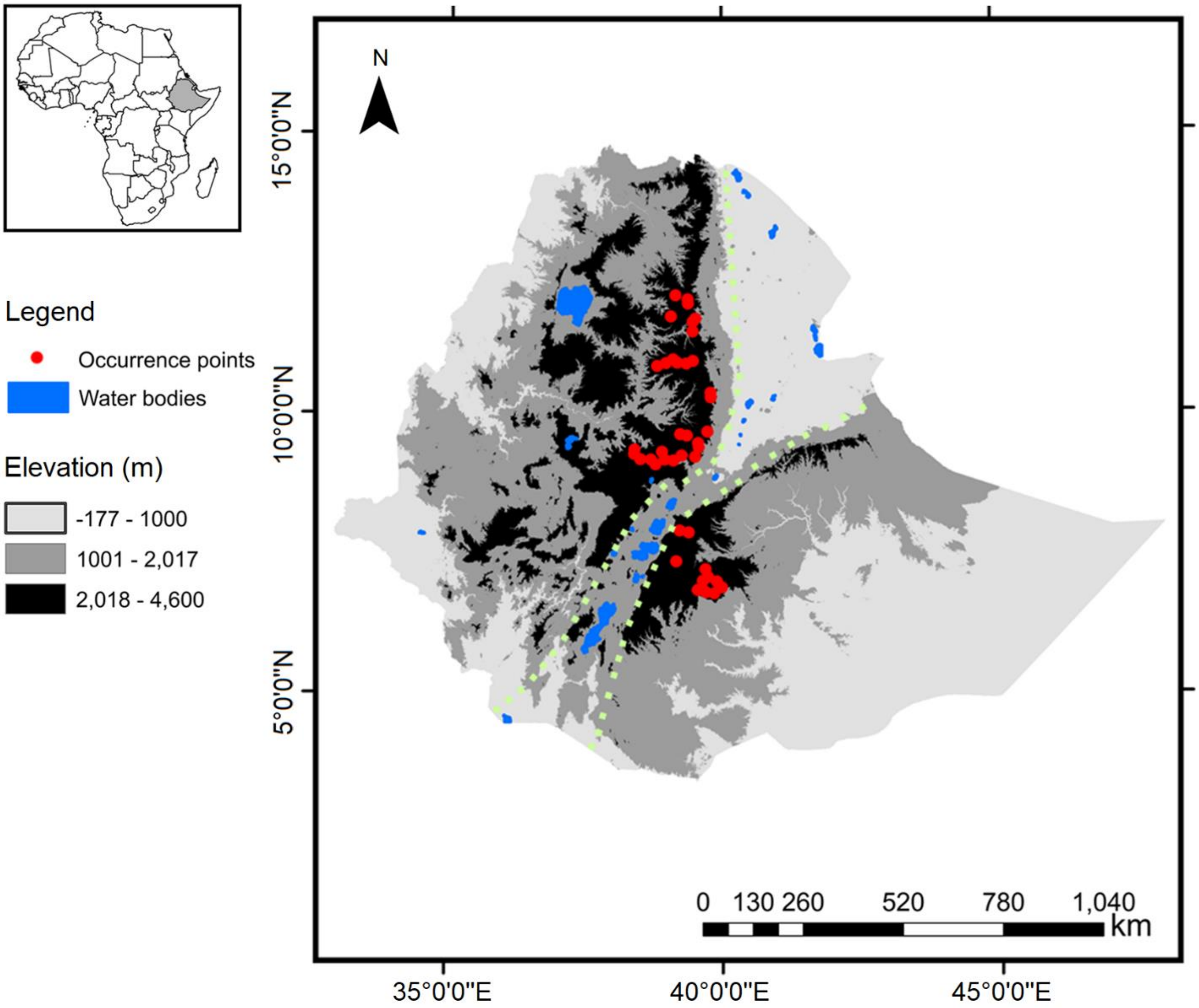

Figure 5.1. Study area and occurrence points of Moorland Francolin in the highlands of Ethiopia. The Rift Valley, indicated by the two dotted lines, separates the western highlands and the eastern highlands.

Most of the study sites comprised two major high montane vegetation zones, the Ericaceous belt (also called the Sub-Afroalpine belt featured by elevation ranging from 3000 to 3200 m) and the Afroalpine belt (above 3200 m) (Ash and Atkins 2009; Friis et al. 2010). The habitats of other sites below 3000 m included *Eucalyptus* plantations mixed with *Juniperus procera*, and anthropized meadows. Typically, this ecoregion is characterized by erratic climatic conditions, a very short dry season (about two months), and an average annual temperature of 8 °C. The highlands are top mountain massifs and volcanic cones and encompass bimodal rainfall patterns with intensified rainfall in summer in July and August and with predominantly short dry season during the early summer (Friis et al. 2010).

5.3.2. Species occurrence data

Most occurrence (i.e., presence-only) data were collected in 2019-2020 from two of the large, geographically separated highlands of Ethiopia. In our fieldwork protocol, we used multiple techniques to confirm the occurrence of the study species, i.e., direct observation, playback survey, and feather collection (Abrha et al. 2023). Furthermore, we crosschecked and evaluated previous occurrence data from published articles, books and citizen science data. Ground truthing data were collected to an accuracy of 3-5 m using a handheld Garmin etrax 30 GPS. Geographic data were originally collected in terms of Universal Transverse Mercator (UTM) coordinates. The overall dataset considered 506 occurrence records of Moorland Francolin from several locations, and each GPS location was verified prior to analysis. Approximately 34% of the data were collected from the eastern highlands, while 66% of the records belonged to the western highlands. Finally, a subset of 231 occurrence data were selected in a two-step selection procedure to model the ecological niche of the species in the study region after removing duplicates and selecting only one record per 1 x 1 km grid resolution for model training. We then computed a semivariogram using the relevant functions of the ecospat package for R (Broennimann et al. 2023) and selected 42 records with a minimum distance of 0.075° to remove potential negative effects of spatial autocorrelation.

5.3.3. Environmental data and variable selections

We downloaded 19 bioclimatic variables from CHELSA (http://chelsa-climate.org; Karger et al. 2017), with a spatial resolution of approximately 30 arcsec (ca. 1 km) for projections. The current climate represented the past 30 years (average of 1970–2000), while the future climate scenarios included three shared socio-economic pathways (SSP 126, SSP 370 and SSP 585) for the periods 2021-2040, 2061-2080, and 2081-2100, respectively. We conducted variable selection to improve model performance and accuracy for habitat suitability modeling (Hirzel and Lay 2008). We assessed for multicollinearity among variables using pairwise Spearman's rank correlation (r_s) to meet the requirement of statistical assumptions. Among pairs of predictor variables with critical value of $r_s \geq |0.70|$, only one variable that was hypothesized to biologically influence the francolin species was used for further analyses (Dormann et al. 2013) (Tables S1 and S2). Finally, only nine predictor variables were selected to generate species distribution models of Moorland Francolin under the current and future scenarios. The variables were as follows: BIO1 (annual mean temperature), BIO2 (mean diurnal range), BIO4 (temperature seasonality), BIO7 (temperature annual range), BIO12 (annual precipitation), BIO14 (precipitation of driest month), BIO15 (precipitation seasonality), BIO18 (precipitation of warmest quarter), and BIO19 (precipitation of coldest quarter). All the predictor variables had equal spatial resolution of 1 km × 1 km grid to match the species occurrence data.

5.3.4. Algorithms for Species Distribution Models

For our ensemble SDM approach, we selected six algorithms (two statistical regression and four machine learning) from the 10 algorithms in the biomod2 package based on their performance (AUC > 0.7) (Thuiller et al. 2009; Thuiller et al. 2016) in estimating habitat suitability for the target species (Table S3). The set of algorithms used to assess the potential distribution of the species were: (1) Artificial Neural Networks (ANN: Ripley 2007); (2) Classification Tree Analysis (CTA: Breiman et al. 1984); (3) Generalized Additive Models (GAM: Hastie and Tibshirani 1995; Hastie 2017); (4) Generalized Boosted Model (GBM: Friedman 2001; Elith et al. 2008), also known as Gradient Boosting Machine or Boosted Regression Trees; (5) Generalized Linear Models (GLM: Nelder and Wedderburn 1972; Guisan et al. 2002; Zuur et al. 2010); and (6) Maximum Entropy (MaxEnt: Phillips et al. 2006; Elith et al. 2011; Hijmans et al. 2013). Here, we used presence-background data for all algorithms because our data lacks species absence (Hao et al. 2019). Therefore, instead of missing data (true absence), we generated background data (i.e., pseudo-absence) (Barbet-Massin et al. 2012). To do this, we randomly generated 10,000 pseudo-absence locations using the relevant functions in the biomod2 (Wisz and Guisan 2009), i.e., the disk strategy with a minimum distance from the species records of 0.1 km and a maximum distance of 100 km.

5.3.5. Modeling procedure and validation

For model evaluation and calibration, our occurrence datasets were split into 80% used for training and 20% for testing using a bootstrap approach with 10 replications for each algorithm. We used area under the curve (AUC) of the receiver operating characteristics (ROC) and true skill statistics (TSS) metrics to evaluate model performance and accuracy (Fielding and Bell 1997; Manel et al. 2001; Thuiller et al. 2005). TSS considers sensitivity and specificity (Allouche et al. 2006), and its value ranges from -1 to +1, with values close to +1 indicating the best performance of the model, while values close to zero or below zero indicate poor performance (Landis and Koch 1977; Allouche et al. 2006), or sometimes below 0.4 is generally reported as poor model performance (Beaumont et al. 2016). The AUC values can range between 0 and 1 (0.5-0.7 = poor performance, 0.7-0.9 = good performance and > 0.9 = high performance of the model) (Swets 1988). The contribution of each bioclimatic variable was determined using the permutation producer in the biomod2 package.

To assess potential areas requiring extrapolation of the models beyond their training range due to non-analogous bioclimatic conditions, the Multivariate Environmental Similarity Surface (MESS) (Elith et al. 2010) were computed using the dismo R package based on the training data of the models. MESS maps were binarized into a similar (positive values) and dissimilar (negative values) index to visualize and distinguish between intra- and potential extrapolation areas (Elith et al. 2010).

5.3.6. Combining model predictions

All selected algorithms were run using the default settings for prior validation process (Hao et al. 2019; Thuiller et al. 2009; Thuiller et al. 2021). Then we computed model averaging by combining them into an ‘ensemble model’ (e.g., Araújo and New 2007; Seni and Elder 2010; Grenouillet et al. 2011) using a weighted mean (Hao et al. 2019; Thuiller et al. 2021) and decay factor of 0.7. The biomod2 package V.3.5.1 (Thuiller et al. 2021) was used to carry out the analysis. Finally, we chose the weighted mean method over other methods (i.e., mean, median and committee averaging) for the ensemble model due to its best predictive performance (Marmion et al. 2009; Hao et al. 2019). SDMs maps were then binarized to calculate changes in size of suitable habitats using the minimum training presence threshold.

5.3.7. IUCN RED List assessment

Moorland Francolin is currently classified as Near Threatened (BirdLife International 2024). Based on our extensive dataset, we re-assessed the conservation status based on the established IUCN criteria. For this, we used GeoCAT (Bachman et al. 2011) to determine the extent of occurrence (EOO) and area of occurrence (AOO) from the total number of occurrence records (n = 506). We used the IUCN recommended grid size of 2 km to calculate AOO. We used the IUCN recommended grid size of 2 km × 2 km to calculate AOO (IUCN Standards and Petitions Committee 2024).

5.4. Results

5.4.1. Model evaluation

The average predictive accuracy of each algorithm suggested a high discrimination ability of the models, with most having AUC > 0.90 and TSS > 0.91. The metrics of each algorithm, in descending order, were as follows: GBM (AUC = 1.00; TSS = 0.98), GLM (AUC = 0.98; TSS = 0.93), ANN (AUC = 0.97; TSS = 0.93), GAM (AUC = 0.94; TSS = 0.91), MaxEnt (AUC = 0.98; TSS = 0.88), and CTA (AUC = 0.92; TSS = 0.83) (Figure 5.2). Compared to the individual models, the binary ensemble model showed the highest performance, but it was closely behind GBM (AUC = 0.99; TSS = 0.95). Therefore, we retained the ensemble model (i.e., weighted mean by AUC) to predict the distribution of Moorland Francolin under climate change because the first four competing algorithms showed similar and high performance based on the two evaluation metrics.

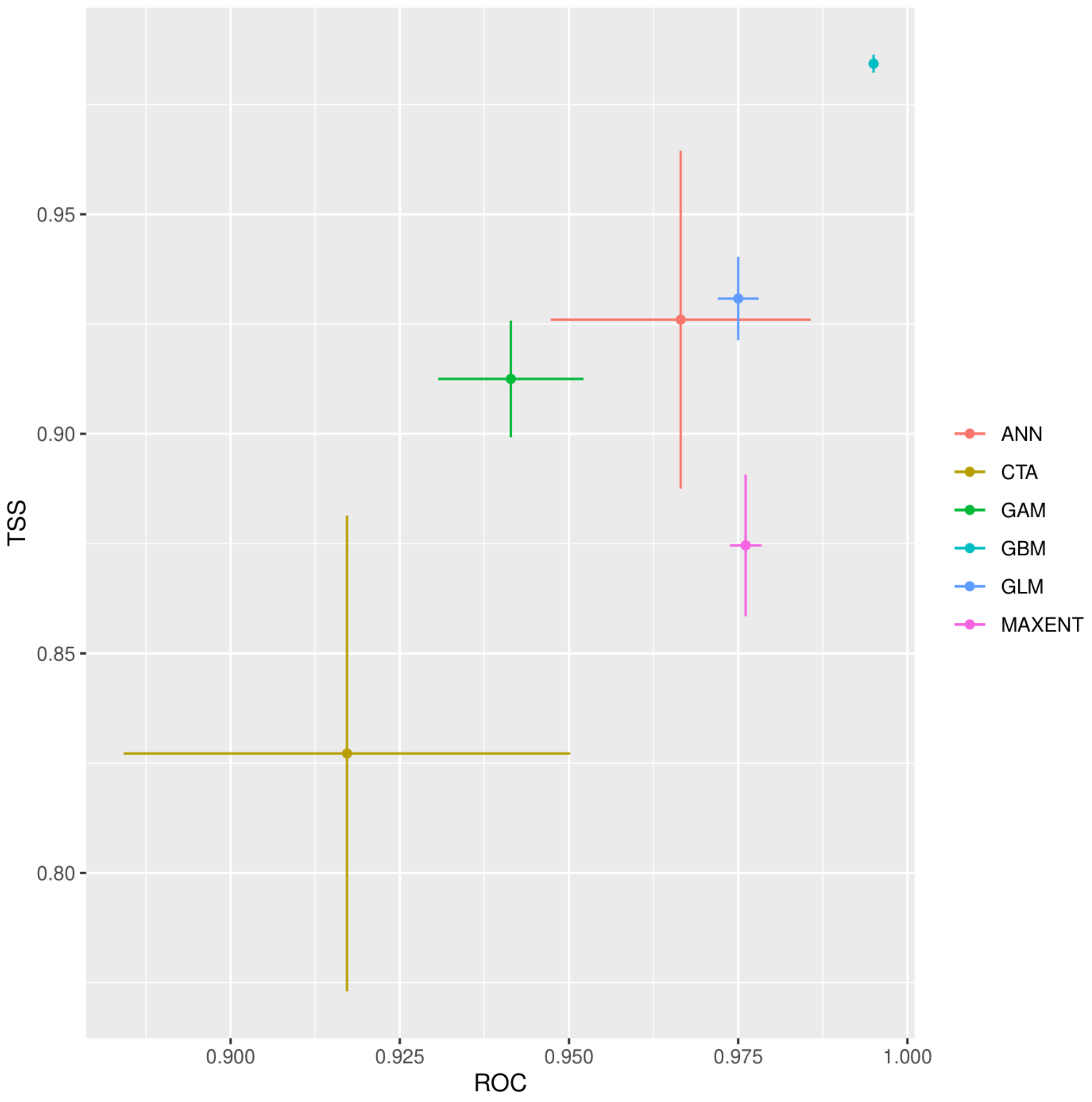

Figure 5.2. Average and range scores of TSS and ROC (AUC) to evaluate predictive performance of each selected algorithm.

5.4.2. Variable importance

All variables showed significant variation across algorithms. In our analysis, BIO1 (Annual Mean Temperature) revealed the highest influence, with variable importance scores ranging from 0.73 (GAM) to 0.99 (CTA), on the habitat suitability of Moorland Francolin in the Afroalpine and Sub-Afroalpine habitats of Ethiopia. Other variables, including BIO2 (Mean Diurnal Range), BIO4 (Temperature Seasonality) and BIO7 (Temperature Annual Range) showed slight contributions to the distribution of the species (Table 5.1).

Table 5.1. Individual and averaged variables importance for different models for habitat suitability modeling of Moorland Francolin.

Variable	ANN	CTA	GAM	GBM	GLM	MaxEnt	Mean
BIO1	0.91	0.99	0.73	0.93	0.96	0.97	0.92
BIO2	0.53	0.00	0.61	0.01	0.49	0.05	0.28
BIO4	0.48	0.00	0.37	0.02	0.57	0.01	0.24
BIO7	0.48	0.00	0.39	0.01	0.37	0.00	0.21
BIO12	0.33	0.00	0.16	0.08	0.04	0.10	0.12
BIO14	0.18	0.11	0.11	0.04	0.06	0.21	0.12
BIO15	0.33	0.00	0.19	0.09	0.14	0.10	0.14
BIO18	0.26	0.00	0.11	0.07	0.05	0.02	0.09
BIO19	0.21	0.00	0.31	0.05	0.05	0.01	0.11

5.4.3. Current and future habitat suitability of Moorland Francolin

The estimated potential distribution as derived from the species realized niche under current climatic conditions is 6861.99 km^2 based on ensemble modeling. The modeling also suggested other potential suitable habitats beyond the known occurrences, notably the Choke Mountains (also locally known as Arat Mekerakirt), the Guna Mountain, and the Simien Mountains National Park. Nevertheless, ground truthing data and literature did not confirm the occurrence of the species in these Afroalpine and Sub-Afroalpine habitats of the Ethiopian highlands (Figures 5.3 and 5.4).

Based on the intermediate SSP 126 climate change scenario, an estimated area of 389.48 km^2 was predicted to be a suitable habitat for the species. Here, the Choke Mountains, Borena Sayint Mountain, Arsi Mountains, Bale Mountains (very small areas of Harenna Forest), and other highlands adjacent to the Rift Valley were also predicted potentially suitable habitats for the species. However, no suitable habitat was predicted to be available under future climate change scenarios in the 2061–2080 (SSP 370) and 2081–2100 (SSP 585) projection periods (Figure 5.5).

Due to model uncertainty of future predictions, the Multivariate Environmental Similarity Surface (MESS) analysis showed extensive areas exceeding current conditions requiring model extrapolation, signifying that the predicted sites were beyond the model training range (calibration range), hence highly dissimilar. In contrast, some localities, mainly the central highlands of Ethiopia, showed no extrapolation suggesting the predicted sites were similar to the model training range (i.e., analogous climatic conditions) (Figure 5.6). Therefore, all future predicted ranges require careful interpretation. Our results showed that the predicted suitable areas were novel compared to the currently realized niche, suggesting that model uncertainty associated with extrapolation showed overpredictions, e.g. the occurrence of the species below 1500 m.

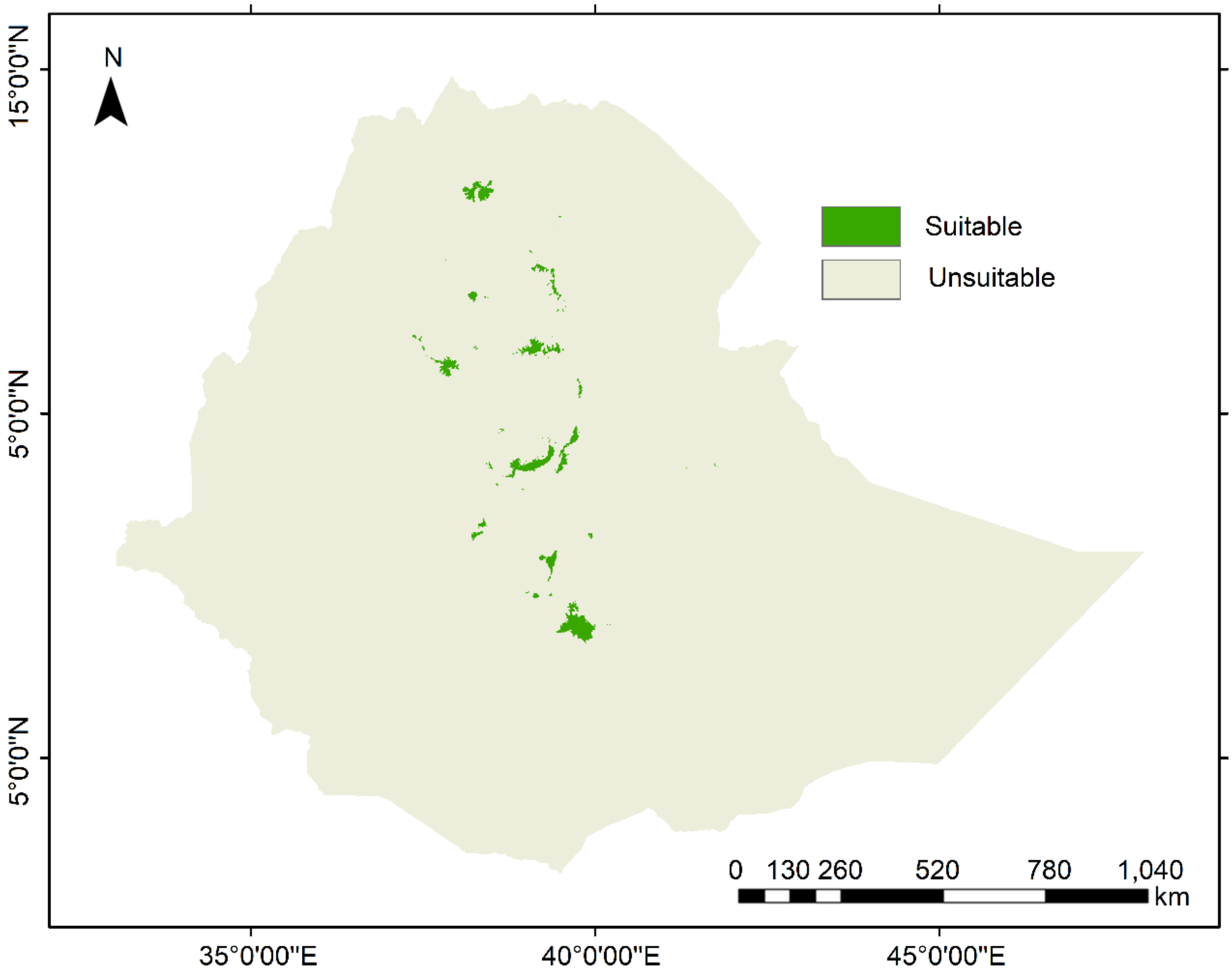

Figure 5.3. Habitat suitability modeling of Moorland Francolin projection using weighted mean ensemble model in the context of current climatic conditions (1970-2000).

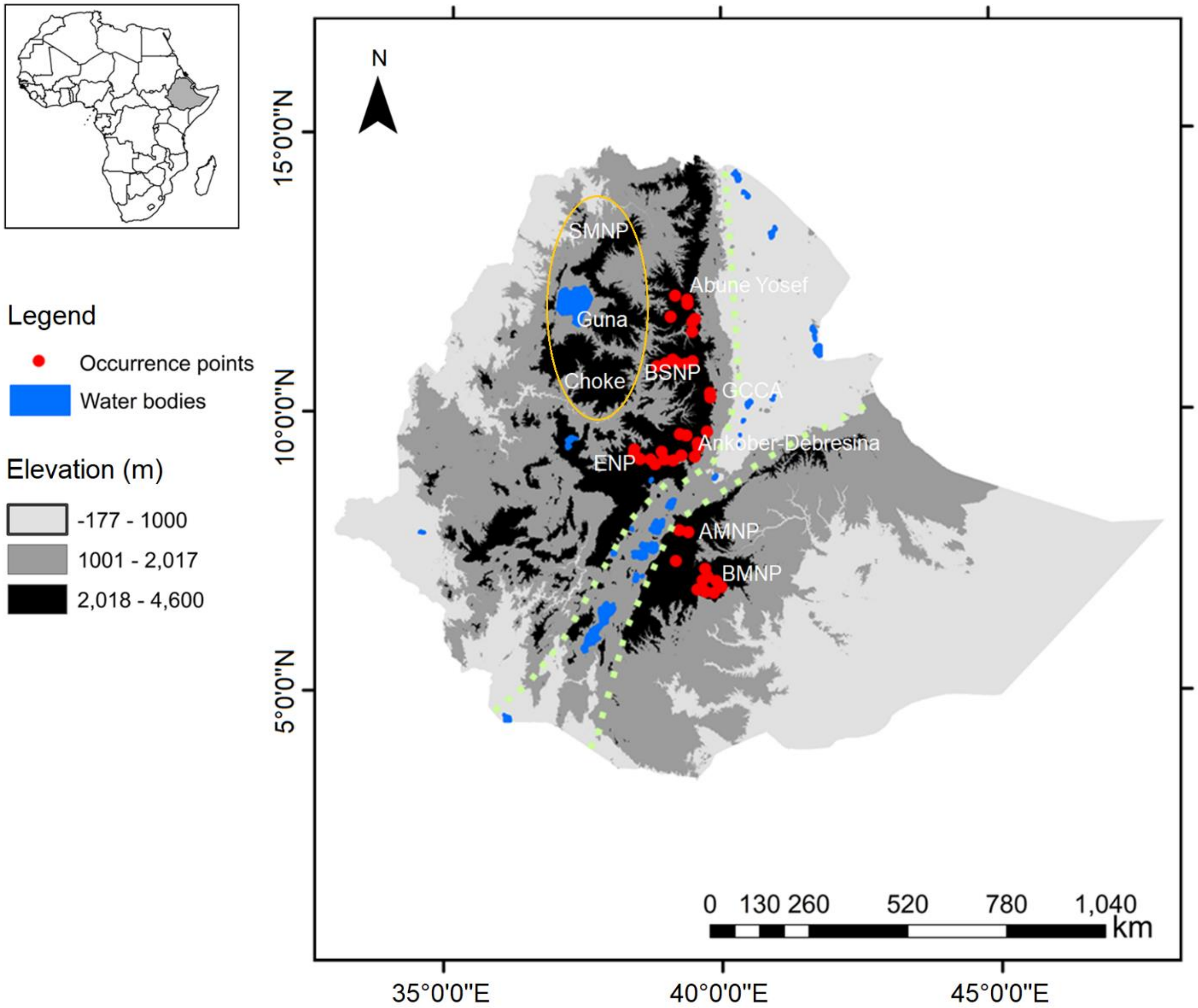

Figure 5.4. Current locations of Moorland Francolin in the Ethiopian highlands (BMNP = Bale Mountains National Park, AMNP = Arsi Mountains National Park, ENP = Entoto Natural Park and its surroundings, Ankober-Debresina escarpments, GCCA = Guassa Community Conservation Area, BSNP = Borena Sayint National Park and Guguftu highland, Dessie highlands and Abune Yosef). The species was not detected in other predicted suitable habitats in north-west mountaintops (highlighted with an oval circle) (Choke Mountains, Guna Mountain and SMNP = Semien Mountains National Park).

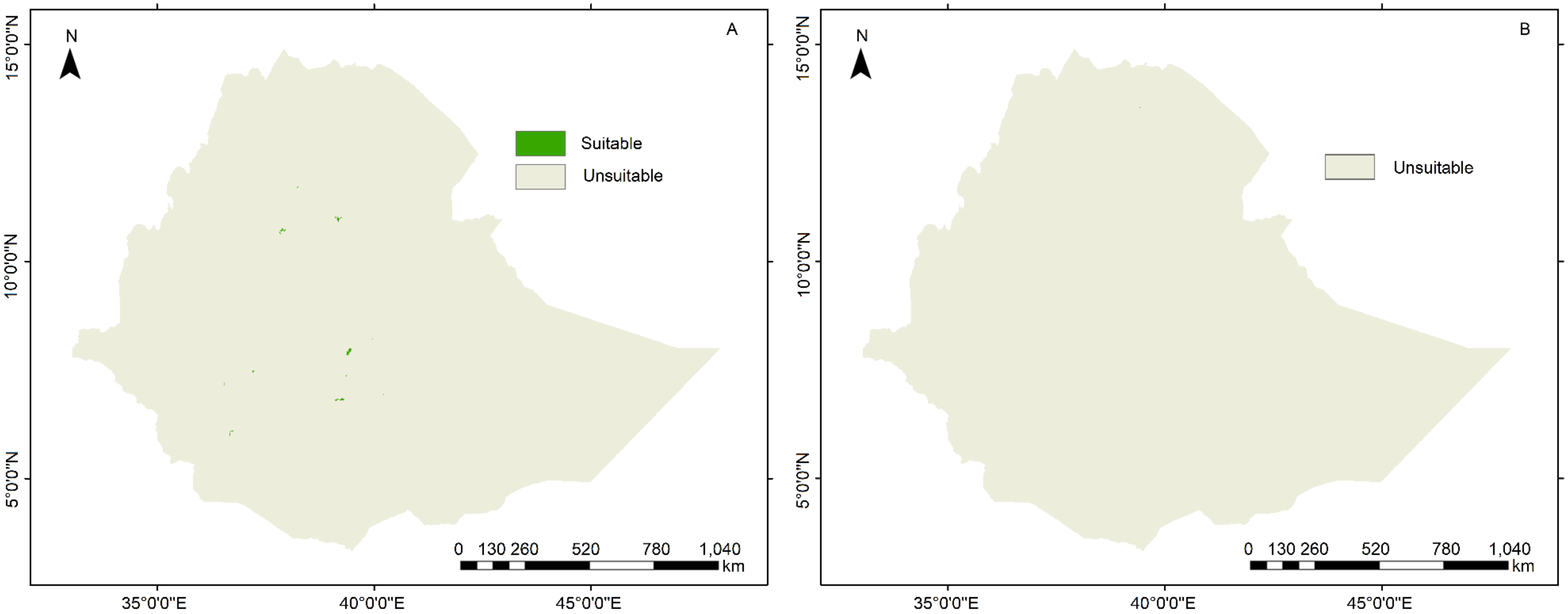

Figure 5.5. Habitat suitability modeling of Moorland Francolin using weighted mean ensemble model projected for 2021–2040 (SSP 126) (A), and 2061–2080 (SSP 370) and 2081–2100 (SSP 585) (both in B).

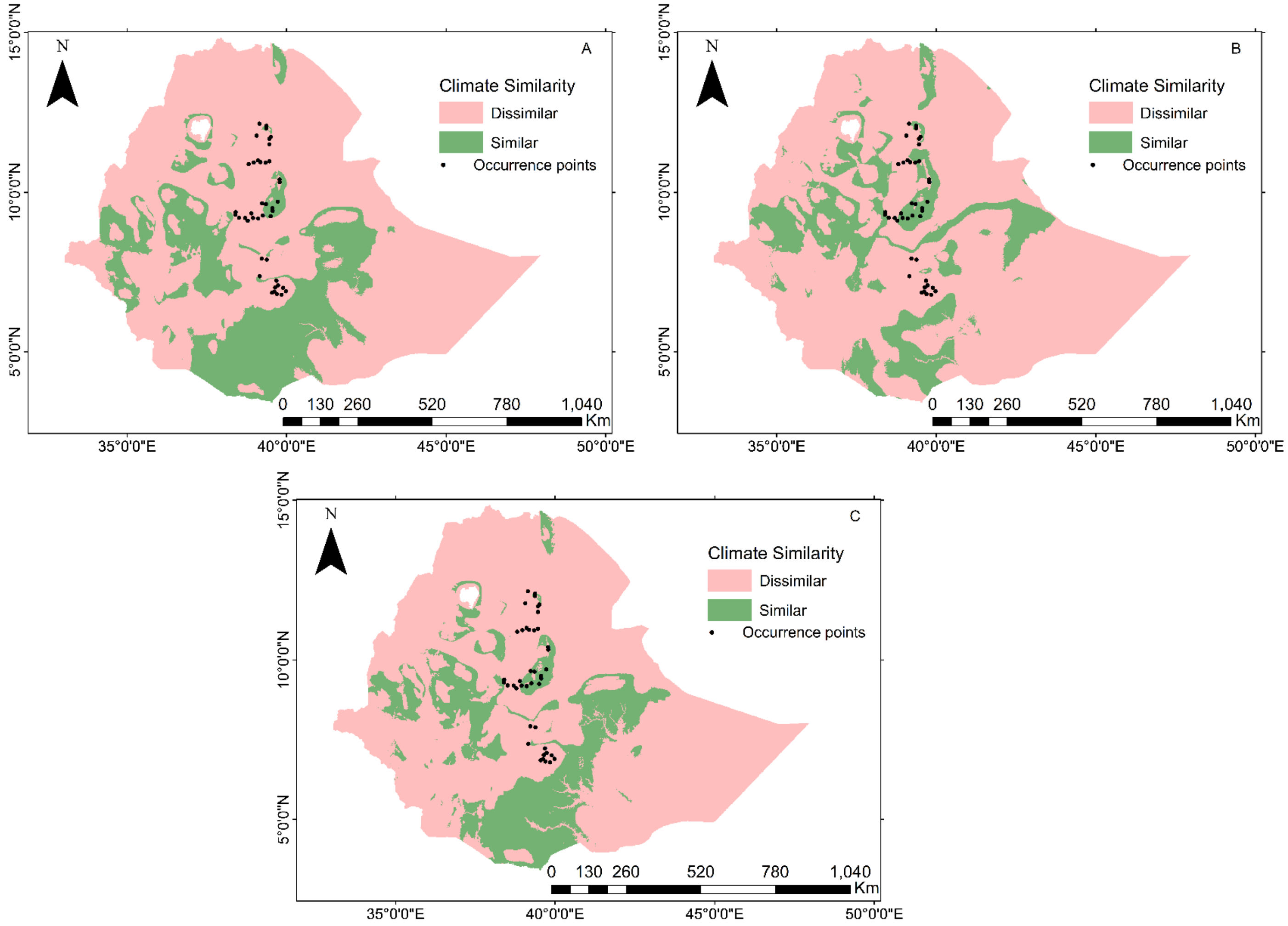

Figure 5.6. Maps showing areas requiring model extrapolation based on the Multivariate Environmental Similarity Surfaces (MESS) approach. Dissimilar maps (negative values) represent habitats that are novel climate relative to the training range and similar maps (positive values) represent habitats analogous to the training range. The future climate change scenarios are SSP 126 (A), SSP 370 (B), and SSP 585 (C).

5.4.4. IUCN Red List assessment

Based on the GeoCAT analysis, the total occurrence records (n = 506) of Moorland Francolin revealed an extent of occurrence (EOO) and area of occupancy (AOO) of 64,175.5 km^2 and 912.0 km^2, respectively. The result from AOO showed that the species is classified as Vulnerable.

5.5. Discussion

In this study, we investigated the consequences of climate change on Moorland Francolin distribution using algorithms in the biomod2 package (Thuiller et al. 2009; Thuiller et al. 2016). Because the predictive performance of models varies considerably, we used the biomod2-based ensemble model, which combines competing algorithms to reduce the noise of individual models (Araújo and New 2007; Thuiller et al. 2009; Thuiller et al. 2016). Although there is evidence in favor of individual models such as MaxEnt (Kaky et al. 2020), our results showed that the ensemble model (i.e., modeling averaging) outperformed most competing models, in line with many previous reports (e.g., Araújo and New 2007; Seni and Elder 2010; Grenouillet et al. 2011), especially for modified parameters in the package (Valavi et al. 2022).

In this study, AUC and TSS metrics were used for evaluation and validation of individual algorithms, while the weighted mean consensus method was used to generate the ensemble. Individual algorithms and the ensemble showed good predictive performance in terms of both metrics (AUC > 0.90; TSS > 0.80), suggesting that SDMs adequately discriminate the presence and background samples of Moorland Francolins. Although the ensemble model was slightly outperformed by the Generalized Boosted Model (GBM), we retained it for our habitat suitability modeling. This is because weighted mean is essential in ecology to reduce the prediction error of each contributing model (Dormann et al. 2018).

Our ensemble model suggests that the current potential distribution area of Moorland Francolin is 6,861.99 km^2. With respect to the model estimation, it is assumed that the current projected suitable area may slightly overestimate the actual distribution area of the species, as it extends over most of the geographically separated highlands, except the Tigray highlands (Figures 5.3 and 5.4). The results depicted that the north-west mountaintops of the country, namely the Simien Mountains National Park (412 km^2; Craig et al. 2020), Choke Mountains (299 km^2: Teferi et al. 2010) and Guna Mountain (197.1 km^2; Belay et al. 2022) are projected as suitable habitats for the species, while the actual presence of the species on these mountaintops has not been confirmed for almost three decades (Tilahun et al. 1996; Ash and Atkins 2009; Gedeon et al. 2023). This suggests that the ensemble model overpredicts the occurrence of the species where it was not actually detected in our field surveys (i.e., false positives). This phenomenon, popularly known as commission error, is a typical feature of species distribution models (SDMs), where species are predicted to occur in suitable locations without actually occurring (Allouche et al. 2006; Pearson 2007, Lissovsky and Dudov 2021).

Based on our exhaustive field surveys and model averaging, we expected that the range of Moorland Francolin could be less than 6000 km^2. This is partly because the Ethiopian highlands are increasingly affected by land-use change (Belay et al. 2022). The Bale Mountains National Park currently represents the most extensive suitable habitat. The park is relatively intact and contiguous compared to most mountain ranges in Ethiopia, and covers a large area of the country's alpine habitat (Chignell et al. 2019; Groos et al. 2021), making it a favorable habitat for diverse plant and animal species. Due to its high species richness and endemism, the park is registered as world heritage site (UNESCO 2023) and confirmed as Alliance for Zero Extinction (AZE) site. This global importance, along with other local and international conservation initiatives, could provide long-term support to mitigate effects of climate change and to counter habitat loss, ultimately benefiting the park's ecological integrity and human well-being.

Based on the ensemble model, temperature variables were the key determinants of the distribution of Moorland Francolin. Specifically, BIO1 (annual mean temperature) constituted the highest contribution for the habitat suitability of the species, suggesting that the current cooler temperature of the summit region is the most influential predictor for the occurrence of the species. In line with this, Gedeon et al. (2017b) found that annual mean temperature was the highest contributor to the habitat suitability of Black-fronted Francolin (*Pternistis atrifrons)* in the eastern highlands of Ethiopia.

In general, several recent empirical studies have similarly reported that rising temperatures are a threatening factor for endemic mountain bird species in the tropics (Freeman et al. 2018). In the context of future climate change, only 6% of the current suitable habitat will remain under SSP126. Surprisingly, the largest alpine habitat (i.e., the Sanetti Plateau) in the Bale Mountains was predicted to be unsuitable for the species, yet only a tiny site in the Harenna Forest was predicted to maintain the species in this scenario, which actually did not occur in the current habitat suitability modeling (Figure

5.2). Indeed, Moorland Francolins are averse to using montane forests and dense Ericaceous vegetation where predators abound (Abrha et al. 2023). A recent report shows that the Ericaceous vegetation of the Bale Mountains is expanding upwards due to the ongoing climate change (Kidane et al. 2022), with many endemic mountaintop plants are predicted to become locally extinct (Kidane et al. 2019). The consequences are expected to disrupt the distinctive ecological zonation across elevational gradients, and thus for several birds and other wildlife with specific habitat requirements. The greater phenotypic plasticity of Ericaceous, and possibly other vegetation types, is replacing moorland and grassland habitats (Kidane et al. 2022) suitable for Moorland Francolins (Abrha et al. 2023).

The currently realized niche will gradually contract under SSP 126, and Moorland Francolin will be absent in the context of the extreme future climate change scenarios SSP 370 and SSP 585 (Figure 5.5). The extrapolation based on the Multivariate Environmental Similarity Surface (MESS) approach demonstrated that the species is predicted to be displaced from its currently realized niche, which showed potentially unsuitable habitats (Figure 5.6). Since the species is endemic, diet-specialized and limited to the cold climate of the Ethiopian mountaintops, it is expected to be maladapted to the novel climatic conditions. In such a stochastic event, as reported by Ihlow et al. (2012), we are uncertain whether non-analogous bioclimatic variables are acting or whether future climatic conditions actually threaten the species.

In general, the current and future distribution of Moorland Francolin is consistent with the observed effects of anthropogenic climate change on mountaintop extinction in the tropics (e.g., Harris et al. 2014; Freeman et al. 2018; Neate-Clegg et al. 2021). The high vulnerability of birds to climate change may be exacerbated by: (1) species traits (e.g., low dispersal ability) (Sheard et al. 2020); (2) habitat traits, including limited habitat requirements and elevational range limits (Gitay et al. 2002; Harris et al. 2014; Freeman et al. 2018; Neate-Clegg et al. 2021), (3) the effects of upslope shifts (Freeman et al. 2018; Neate-Clegg et al. 2021), and (4) human activities, including deforestation, habitat loss and associated threats (Harris et al. 2014; Freeman et al. 2018; Neate-Clegg et al. 2021). As a result, Moorland Francolin is predicted to be at high risk of extinction under future climate change, unless novel phenotypic plasticity evolves against multiple environmental stressors.

We did not use ensemble model to estimate extent of occurrence (EOO) and area of occupancy (AOO) due to model uncertainty (IUCN Standards and Petitions Committee 2024). Our geographic range estimate showed that EOO was 43% lower than that calculated by IUCN Red List of Threatened Species (BirdLife International 2024). This discrepancy is likely due to differences in the data sources. We found that populations of Moorland Francolins exhibit high fragmentation caused by human activities and are notably isolated by geographical barriers, such as the Rift Valley and substantial distances between mountain summits. Therefore, based on our estimates of the AOO and the assumption of increasing multiple stressors, the species could be classified as Vulnerable (VU).

5.6. Conclusions

We conducted a baseline study to predict the habitat suitability of the endemic Moorland Francolin in the mountaintop of the Ethiopian highlands under climate change scenarios. With respect to the current suitable area of Moorland Francolin, almost 94% of the habitat will be gradually lost assuming the intermediate shared socio-economic pathway (SSP 126), and no suitable habitat is predicted to remain under worst-case scenarios. Annual mean temperature and other temperature-related variables contributed to the distribution of the species. The ensemble-based habitat suitability modeling for our target species supported the existing empirical knowledge on mountaintop extinction of tropical birds. Based on our assessment, the species could be classified as Vulnerable (VU). To mitigate the effects of climate change and habitat loss on irreplaceable alpine habitats, species-specific conservation measures (habitat management, increasing habitat connectivity, creating nature reserves) are needed.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

Data will be made available on request

Competing interests

The authors declare that they have no conflict of interest.

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Authors' contributions

Abadi Mehari Abrha: Conceptualization, Formal analysis, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. Dennis Rödder: Formal analysis, Methodology, Software, Visualization, Writing – review & editing. Kai Gedeon: Conceptualization, Writing – review & editing. Lars Podsiadlowski: Writing – review & editing. Till Töpfer: Conceptualization, Methodology, Writing – review & editing.

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5.7. References

Abrha AM, Nigus HK, Weldetnsae BG, Tilahun M, Nigusse AG, Deribew KT (2017) Effects of human disturbances on two sympatric francolin species in the Central Highlands of Ethiopia. Podoces 12:13–21

Abrha AM, Gedeon K, Podsiadlowski L, Weldesilasie DM, Töpfer T (2023) Occupancy of the Ethiopian endemic Moorland Francolin in pristine and degraded Afroalpine biome using a camera trap approach. Ecol Evol 13:e10551

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Applied Ecol 43:1223–1232

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–47

Asefa A, Davies AB, McKechnie AE, Kinahan AA, van Rensburg BJ (2017) Effects of anthropogenic disturbance on bird diversity in Ethiopian montane forests. Condor: Ornithol Appl 119:416–430

Ash J, Atkins J (ed) (2009) Birds of Ethiopia and Eritrea: an atlas of distribution. Christopher Helm, London

Bachman S, Moat J, Hill AW, De La Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. ZooKeys 150:117–126

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol Evol 3:327–338

Beaumont LJ, Graham E, Duursma DE, Wilson PD, Cabrelli A, Baumgartner JB, ... VanDerWal, J. (2016). Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges? Ecol Model 342:135–146

Belay T, Melese T, Senamaw A (2022) Impacts of land use and land cover change on ecosystem service values in the Afroalpine area of Guna Mountain, Northwest Ethiopia. Heliyon 8:e12246

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377

Bender IM, Kissling WD, Böhning-Gaese K, Hensen I, Kühn I, Nowak L, Töpfer T, Wiegand T, Dehling DM, Schleuning M (2019) Projected impacts of climate change on functional diversity of frugivorous birds along a tropical elevational gradient. Sci Rep 9(1):17708

BirdLife International (2024) Species factsheet: *Scleroptila psilolaema*. Downloaded from https://datazone.birdlife.org/species/factsheet/moorland-francolin-scleroptila-psilolaema on 12/05/2024

Bladon AJ, Donald PF, Collar NJ, Denge J, Dadacha G, Wondafrash M, Green RE (2021) Climatic change and extinction risk of two globally threatened Ethiopian endemic bird species. PloS One 16:e0249633

Breiman L, Friedman JH, Olshen RA, Stone CJ (1984) Classification and regression trees. Brooks. Wadsworth and Brooks, Monterey, CA.

Breiner FT, Guisan A, Nobis MP, Bergamini A (2017) Including environmental niche information to improve IUCN Red List assessments. Divers Distrib 23:484–495

Breiner FT, Guisan A, Bergamini A, Nobis MP (2015) Overcoming limitations of modelling rare species by using ensembles of small models. Methods Ecol Evol 6:1210–1218

Broennimann O, Di Cola V, Guisan A (2023) Package ‘ecospat’: Spatial Ecology Miscellaneous Methods. R package version 3.5.1, https://CRAN.R-project.org/package=ecospat

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X, Karanewsky CJ, Yeong Ryu H, Sbeglia GC, Spagnolo F, Waldron JB, Warsi O, Wiens JJ (2013) How does climate change cause extinction? Proc R Soc B 280: 20121890

Chignell SM, Laituri MJ, Young NE, Evangelista PH (2019) Afroalpine wetlands of the Bale Mountains, Ethiopia: Distribution, dynamics, and conceptual flow model. Ann Am Assoc 109:791–811

Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261

Craig EW, Stanley WT, Kerbis Peterhans JC, Bryja J, Meheretu Y (2020). Small terrestrial mammal distributions in Simien Mountains National Park, Ethiopia: a reassessment after 88 years. J Mammal 101:634–647

de Castro Pena JC, Kamino LHY, Rodrigues M, Mariano-Neto E, de Siqueira MF (2014) Assessing the conservation status of species with limited available data and disjunct distribution. Biol Conserv 170:130–136

De Klerk, HM, Crowe TM, Fjeldså J, Burgess ND (2002) Biogeographical patterns of endemic terrestrial Afrotropical birds. Divers Distrib 8:147–162

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Dormann CF, Calabrese JM, Guillera-Arroita G, Matechou E, Bahn V, Bartoń K, Beale CM, Ciuti S, Elith J, Gerstner K, Guelat, J (2018) Model averaging in ecology: A review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecol Monogr 88:485–504

Elith J, Graham CH, Anderson RP, Dudík, M., Ferrier S, Guisan A et al (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57

Fashing PJ, Nguyen N, Demissew S, Gizaw A, Atickem A, Mekonnen A, Nurmi NO, Kerby JT, Stenseth NC (2022) Ecology, evolution, and conservation of Ethiopia's biodiversity. Proc Nat Acad Sci 119:e2206635119

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW (2018) Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. Proc Nat Acad Sci 115:11982–11987

Friedman JH (2001) Greedy function approximation: a gradient boosting machine. Ann Stat 29: 1189–1232

Friis I, Demissew S, Breugel PV (2010) Atlas of the potential vegetation of Ethiopia. Biologiske Skrifter 58:1–307

Gedeon K, Rödder D, Zewdie C, Töpfer T (2017b) Evaluating the conservation status of the Black-fronted Francolin *Pternistis atrifrons*. Bird Conserv Int 28:653–661

Gedeon K, Seyring M, Abrha AM, Ejeta CZ, Abate NT, Töpfer T (2023) Birds of Ethiopia: Checklist and Range Maps. Bonn zool Bull, Suppl 66:1–636

Gedeon K, Zewdie C, Töpfer T (2017a) The birds (Aves) of Oromia, Ethiopia – an annotated checklist. Eur J Taxon 306:1–69

Gitay H, Suárez A, Watson, RT, Dokken DJ (eds.) (2002) Climate change and biodiversity. IPCC Technical Paper V. Intergovernmental Panel on Climate Change, Geneva

Gobeyn S, Mouton AM, Cord AF, Kaim A, Volk M, Goethals P L (2019) Evolutionary algorithms for species distribution modelling: A review in the context of machine learning. Ecol Model 392:179–195

Grenouillet G, Buisson L, Casajus N, Lek S (2011) Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography 34:9–17

Groos AR, Akçar N, Yesilyurt S, Miehe G, Vockenhuber C, Veit H (2021) Nonuniform late Pleistocene glacier fluctuations in tropical eastern Africa. Sci Adv 7:eabb6826

Guisan A, Thuiller W, (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993e1009

Guisan, A, Edwards Jr TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: Setting the scene. Ecol Model 157: 89–100

Guisan A Thuiller W, Zimmermann NE (2017) Habitat Suitability and Distribution Models: With Applications in R; Cambridge University Press, University Printing House: Cambridge, UK.

Habel JC, Rasche L, Schneider UA, Engler JO, Schmid E, Rödder D, Meyer ST, Trapp N, del Diego RS, Eggermont H, Lens L (2019) Final countdown for biodiversity hotspots. Conserv Lett 12:e12668

Hao T, Elith J, Guillera-Arroita G, Lahoz-Monfort JJ (2019) A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. Diversity and Distributions 25:839–852

Harris JBC, Dwi Putra D, Gregory SD, Brook BW, Prawiradilaga DM, Sodhi NS, Wei D, Fordham DA (2014) Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Divers Distrib 20:773–785

Hastie T, Tibshirani R (1995) Generalized additive models for medical research. Stat Methods Med Res 4:187–196

Hastie TJ (2017) Generalized additive models. In Statistical models in S (pp. 249–307). Routledge

Heers AM (2018) Flight and locomotion. Ornithology: Foundation, analysis, and application, In: Morrison M L, Rodewald AD, Voelker G, Colón MR, Prather JF (ed) Ornithology: Foundation, analysis, and application. Baltimore: Johns Hopkins University Press, pp.273–308

Hijmans RJ, Phillips S, Leathwick, J, Elith J (2013) dismo: Species distribution modeling. Available from http://cran.r-project.org/package=dismo

Hirzel AH, Le Lay, G (2008). Habitat suitability modelling and niche theory. J Appl Ecol 45:1372–1381

Hosner PA, Tobias JA, Braun EL, Kimball RT (2017) How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes). Proc R Soc B Biol Sci 284: 20170210

Hunter N, Mills M, Cohen C (2019) Elgon Francolin *Scleroptila elgonensis* should be treated as a species distinct from Moorland Francolin *S. psilolaema*. Bull Afr Bird Club 26:92–100

Ihlow F, Dambach J, Engler JO, Flecks M, Hartmann T, Nekum S, Rajaei H, Rödder D (2012). On the brink of extinction? How climate change may affect global chelonian species richness and distribution. Glob Change Biol 18: 1520–1530

Kaky E, Nolan V, Alatawi A, Gilbert, F (2020) A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: A case study with Egyptian medicinal plants. Ecol Inform 60:101150

Kandziora M, Gehrke B, Popp M, Gizaw A, Brochmann C, Pirie MD (2022) The enigmatic tropical alpine flora on the African sky islands is young, disturbed, and unsaturated. Proc Natl Acad Sci 119:e2112737119

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Sci Data 4:1–20

Keane A, Brooke MDL, McGowan PJK (2005) Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). Biol Conserv 126:216–233

Kidane YO, Hoffmann S, Jaeschke A, Beloiu M, Beierkuhnlein C (2022) Ericaceous vegetation of the Bale Mountains of Ethiopia will prevail in the face of climate change. Sci Rep 12(1):1858

Kidane YO, Steinbauer MJ, Beierkuhnlein C (2019) Dead end for endemic plant species? A biodiversity hotspot under pressure. Glob Ecol Conserv 19:e00670

Kimball RT, Hosner PA, Braun, EL (2021) A phylogenomic supermatrix of Galliformes (Landfowl) reveals biased branch lengths. Mol Phylogenet Evol 158: 107091

Landis JR, Koch, GG (1977) The measurement of observer agreement for categorical data. Biometrics 159–174

Lissovsky AA, Dudov SV (2021) Species-distribution modeling: advantages and limitations of its application. 2. MaxEnt. Biol Bull Rev 11(3):265–275

Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah LE (2006) Global warming and extinctions of endemic species from biodiversity hotspots. Conserv Biol 20:538–548

Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence absence models in ecology: the need to account for prevalence. J Appl Ecol 38:921–931

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. Divers Distrib 15:59–69

McGowan PJK, Owens LL, Grainger MJ (2012) Galliformes science and species extinctions: what we know and what we need to know. Anim Biodivers Conserv 35:321–331

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Neate-Clegg MH, Stuart SN, Mtui D, Şekercioğlu ÇH, Newmark WD (2021). Afrotropical montane birds experience upslope shifts and range contractions along a fragmented elevational gradient in response to global warming. PLoS One 16(3):e0248712

Nelder JA, Wedderburn RWM (1972) Generalized linear models. J R Stat Soc Ser A: Gen 135: 370–384

Pearson RG, (2007) Species' distribution modeling for conservation educators and practitioners. Synthesis. Am Mus Nat Hist 50:54–89

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Raxworthy C J, Ingram CM, Rabibisoa N, Pearson R G (2007) Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. Syst Biol 56:907–923

Razgour O, Kasso M, Santos H, Juste J (2020) Up in the air: Threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian Highlands bat. Evol Appl 14:794–806

Ripley BD (2007) Pattern recognition and neural networks. Cambridge University Press.

Rödder D, Schmitt T, Gros P, Ulrich W, Habel, JC (2021) Climate change drives mountain butterflies towards the summits. Sci Rep 11:14382

Seni G, Elder JF (2010) Ensemble methods in data mining: Improving accuracy through combining predictions. Synth Lect Data Min Knowl Discov 2:839–126

Sheard C, Neate-Clegg MH, Alioravainen N, Jones SE, Vincent C, MacGregor HE, Bregman TP, Claramunt S, Tobias JA (2020) Ecological drivers of global gradients in avian dispersal inferred from wing morphology. Nat Commun 11:2463

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293

Teferi E, Uhlenbrook S, Bewket W, Wenninger J, Simane B (2010) The use of remote sensing to quantify wetland loss in the Choke Mountain range, Upper Blue Nile basin, Ethiopia. Hydrol Earth Syst Sci 14:2415–28

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, De Siqueira MF, Grainger A, Hannah L, Hughes L (2004) Extinction risk from climate change. Nature 427:145–148

Thuiller W, Georges D, Engler R, Breiner F, Georges MD, Thuiller, CW (2016) Package 'biomod2'. https://cran.r-project.org/web/packages/biomod2/index.html

Thuiller W, Georges D, Gueguen M, Engler R, Breiner F (2021) Package 'biomod2': Ensemble Platform for Species Distribution Modeling, version 3.5.1

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD–a platform for ensemble forecasting of species distributions. Ecography 32:369–373

Thuiller W, Lavorel S, Araújo, MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. Glob Ecol Biogeogr 14: 347–357

Tilahun S, Edwards S, Egziabher TBG (eds) (1996) Important Bird Areas of Ethiopia: a first inventory. Addis Ababa: Ethiopian Wildlife & Natural History Society.

Töpfer T, Podsiadlowski L, Gedeon K (2014) Rediscovery of the Black-fronted Francolin *Pternistis* (*castaneicollis*) *atrifrons* (Conover, 1930)(Aves: Galliformes: Phasianidae) with notes on biology, taxonomy and conservation. Vertebr Zool 64: 261–271

Töpfer T, Gedeon K (2020) Alpine birds of Africa. Pages 505-517 in M.I. Goldstein and D.A. DellaSala, editors. Encyclopedia of the World's Biomes, Volume 1. Elsevier.

Tôrres NM, De Marco P, Santos T, Silveira L., de Almeida Jácomo AT, Diniz-Filho J A (2012) Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. Divers Distrib 18:615–627

Trew BT, Maclean IM (2021) Vulnerability of global biodiversity hotspots to climate change. Glob Ecol Biogeogr 30:768–783

UNESCO (2023) Bale Mountains National Park. https://whc.unesco.org/en/list/111/

Urban MC (2015). Accelerating extinction risk from climate change. Science 348:571–573

Urbina-Cardona N, Blair ME, Londoño MC, Loyola R, Velásquez-Tibatá J, Morales-Devia H (2019) Species distribution modeling in Latin America: a 25-year retrospective review. Trop Conserv Sci 12:1940082919854058

Valavi R, Guillera-Arroita G, Lahoz-Monfort JJ, Elith J (2022) Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. Ecol Monogr 92:e01486

Winkler, DW, Billerman SM, Lovette I (2015) *Bird families of the world: An Invitation to the Spectacular Diversity of Birds*. Lynx Edicions, Barcelona

Wisz MS, Guisan A (2009) Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. BMC Ecol 9:1–13

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

5.8. Supplementary information

Table S1. Bioclimatic variables selected for habitat suitability modeling (data source: CHELSA (http://chelsa-climate.org).

Variables	Codes	Units	Temporal scales
Annual Mean Temperature	BIO1	Degree Celsius	Annual
Mean Diurnal Range	BIO2	Degree Celsius	Month
Temperature Seasonality	BIO4	Dimensionless	Month
Temperature Annual Range	BIO7	Degree Celsius	Month
Annual Precipitation	BIO12	Millimeter	Annual
Precipitation of Driest Month	BIO14	Millimeter	Month
Precipitation Seasonality	BIO15	Dimensionless	Month
Precipitation of Warmest Quarter	BIO18	Millimeter	Quarter
Precipitation of Coldest Quarter	BIO19	Millimeter	Quarter

Table S2. Pairwise Spearman's correlation coefficient between the selected variables using heat-map.

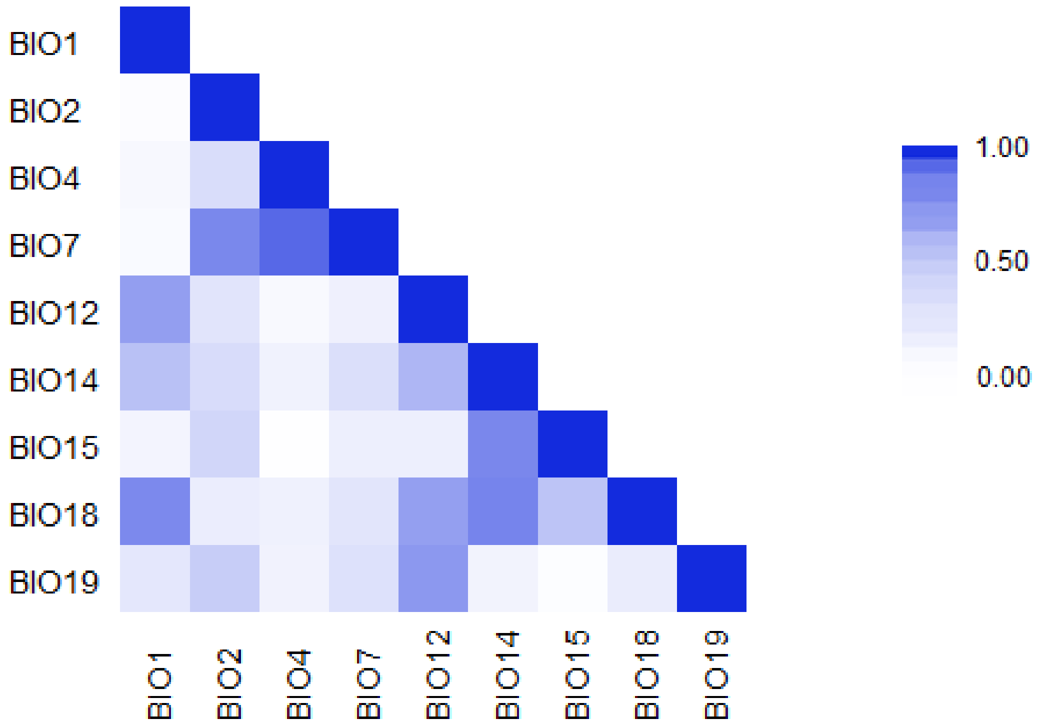

Table S3. The scores of TSS and ROC (AUC) for evaluating predictive performance of each algorithm.

S.No	Run	Algorithm	Metric.eval	Cutoff	Sensitivity	Specificity	Calibration	Validation
1	RUN1	GBM	TSS	583	100	98.488	0.985	0.805
2	RUN1	GBM	ROC	588.5	100	98.55	0.996	0.946
3	RUN1	GLM	TSS	646	100	93.55	0.936	0.834
4	RUN1	GLM	ROC	649	100	93.6	0.977	0.946
5	RUN1	GAM	TSS	71	97.059	95.512	0.926	0.462
6	RUN1	GAM	ROC	72.5	97.059	95.525	0.955	0.73
7	RUN1	CTA	TSS	411	100	79.463	0.795	0.779
8	RUN1	CTA	ROC	415.5	100	79.463	0.897	0.89
9	RUN1	ANN	TSS	929	97.059	96.25	0.933	0.462
10	RUN1	ANN	ROC	928.5	97.059	96.25	0.969	0.803
11	RUN1	MAXENT	TSS	68	100	88.238	0.883	0.853
12	RUN1	MAXENT	ROC	70.5	100	88.488	0.977	0.962
13	RUN2	GBM	TSS	539	100	98.375	0.984	0.852
14	RUN2	GBM	ROC	543.5	100	98.438	0.995	0.933
15	RUN2	GLM	TSS	566	100	92.1	0.921	0.931
16	RUN2	GLM	ROC	566.5	100	92.112	0.975	0.963
17	RUN2	GAM	TSS	222	97.059	94.5	0.916	0.31
18	RUN2	GAM	ROC	229.5	97.059	94.525	0.943	0.647
19	RUN2	CTA	TSS	411	100	79.275	0.793	0.786
20	RUN2	CTA	ROC	415	100	79.275	0.896	0.893
21	RUN2	ANN	TSS	930	97.059	96.512	0.936	0.703
22	RUN2	ANN	ROC	933.5	97.059	96.525	0.973	0.907
23	RUN2	MAXENT	TSS	48	100	85.9	0.86	0.895
24	RUN2	MAXENT	ROC	53.5	100	86.662	0.977	0.967
25	RUN3	GBM	TSS	567	100	98.625	0.986	0.808
26	RUN3	GBM	ROC	570.5	100	98.638	0.995	0.943
27	RUN3	GLM	TSS	667	100	94.138	0.942	0.882
28	RUN3	GLM	ROC	673.5	100	94.213	0.98	0.935
29	RUN3	GAM	TSS	677	97.059	92.325	0.894	0.295
30	RUN3	GAM	ROC	676.5	97.059	92.325	0.924	0.645
31	RUN3	CTA	TSS	408	100	90.762	0.908	0.663
32	RUN3	CTA	ROC	409.5	100	90.762	0.969	0.831
33	RUN3	ANN	TSS	797	100	93.688	0.937	0.444
34	RUN3	ANN	ROC	802.5	100	93.713	0.977	0.854
35	RUN3	MAXENT	TSS	85	97.059	90.738	0.879	0.865
36	RUN3	MAXENT	ROC	86.5	97.059	90.888	0.979	0.952
37	RUN4	GBM	TSS	567	100	98.388	0.984	0.881
38	RUN4	GBM	ROC	568	100	98.4	0.995	0.975
39	RUN4	GLM	TSS	585	100	92.238	0.923	0.927

40	RUN4	GLM	ROC	585.5	100	92.262	0.971	0.979
41	RUN4	GAM	TSS	763	97.059	92.662	0.897	0.547
42	RUN4	GAM	ROC	762.5	97.059	92.663	0.927	0.771
43	RUN4	CTA	TSS	410	100	78.938	0.789	0.8
44	RUN4	CTA	ROC	414	100	78.938	0.895	0.9
45	RUN4	ANN	TSS	897	97.059	94.525	0.916	0.8
46	RUN4	ANN	ROC	896.5	97.059	94.525	0.966	0.919
47	RUN4	MAXENT	TSS	83	100	87.638	0.877	0.899
48	RUN4	MAXENT	ROC	90.5	100	88.225	0.974	0.978
49	RUN5	GBM	TSS	556	100	98.112	0.981	0.905
50	RUN5	GBM	ROC	556.5	100	98.125	0.994	0.975
51	RUN5	GLM	TSS	586	100	92.725	0.927	0.877
52	RUN5	GLM	ROC	587.5	100	92.738	0.973	0.97
53	RUN5	GAM	TSS	641	97.059	93.5	0.906	0.284
54	RUN5	GAM	ROC	639.5	97.059	93.5	0.933	0.633
55	RUN5	CTA	TSS	410	100	79.15	0.792	0.792
56	RUN5	CTA	ROC	414.5	100	79.15	0.896	0.896
57	RUN5	ANN	TSS	909	100	96.088	0.961	0.938
58	RUN5	ANN	ROC	906.5	100	96.088	0.977	0.977
59	RUN5	MAXENT	TSS	94	100	88.138	0.882	0.909
60	RUN5	MAXENT	ROC	97.5	100	88.475	0.973	0.983
61	RUN6	GBM	TSS	606	100	98.812	0.988	0.807
62	RUN6	GBM	ROC	606	100	98.812	0.995	0.902
63	RUN6	GLM	TSS	687	100	93.787	0.938	0.888
64	RUN6	GLM	ROC	693	100	93.863	0.975	0.962
65	RUN6	GAM	TSS	722	97.059	94.7	0.918	0.32
66	RUN6	GAM	ROC	743.5	97.059	94.713	0.945	0.654
67	RUN6	CTA	TSS	417	100	91.012	0.91	0.652
68	RUN6	CTA	ROC	421.5	100	91.012	0.968	0.834
69	RUN6	ANN	TSS	789.5	100	95.65	0.957	0.712
70	RUN6	ANN	ROC	787.5	100	95.65	0.975	0.851
71	RUN6	MAXENT	TSS	48	100	86.55	0.866	0.898
72	RUN6	MAXENT	ROC	85.5	97.059	89.938	0.976	0.967
73	RUN7	GBM	TSS	549	100	98.312	0.983	0.94
74	RUN7	GBM	ROC	550	100	98.325	0.995	0.973
75	RUN7	GLM	TSS	605	100	92.162	0.922	0.95
76	RUN7	GLM	ROC	613.5	100	92.225	0.97	0.976
77	RUN7	GAM	TSS	525	97.059	95.012	0.921	0.578
78	RUN7	GAM	ROC	526.5	97.059	95.012	0.944	0.784
79	RUN7	CTA	TSS	410	100	78.988	0.79	0.798
80	RUN7	CTA	ROC	414	100	78.988	0.895	0.899
81	RUN7	ANN	TSS	802	97.059	91.862	0.889	0.806

82	RUN7	ANN	ROC	802	97.059	91.862	0.967	0.955
83	RUN7	MAXENT	TSS	94	100	87.725	0.878	0.971
84	RUN7	MAXENT	ROC	98.5	100	88.087	0.972	0.987
85	RUN8	GBM	TSS	562	100	98.375	0.984	0.73
86	RUN8	GBM	ROC	566	100	98.388	0.995	0.888
87	RUN8	GLM	TSS	525	100	91.775	0.918	0.909
88	RUN8	GLM	ROC	525.5	100	91.8	0.975	0.958
89	RUN8	GAM	TSS	126	97.059	94.112	0.912	0.19
90	RUN8	GAM	ROC	124	97.059	94.112	0.94	0.592
91	RUN8	CTA	TSS	410	100	79.15	0.792	0.792
92	RUN8	CTA	ROC	414.5	100	79.15	0.896	0.896
93	RUN8	ANN	TSS	881	91.176	92.3	0.835	0.925
94	RUN8	ANN	ROC	886.5	91.176	92.337	0.913	0.967
95	RUN8	MAXENT	TSS	113	94.118	91.175	0.853	0.825
96	RUN8	MAXENT	ROC	115.5	94.118	91.35	0.977	0.954
97	RUN9	GBM	TSS	571	100	98.6	0.986	0.82
98	RUN9	GBM	ROC	567.5	100	98.6	0.995	0.952
99	RUN9	GLM	TSS	677	100	94.2	0.942	0.885
100	RUN9	GLM	ROC	677.5	100	94.213	0.977	0.949
101	RUN9	GAM	TSS	0	100	0	0.9	0.679
102	RUN9	GAM	ROC	1.5	97.059	93.188	0.947	0.824
103	RUN9	CTA	TSS	460	97.059	92.725	0.898	0.547
104	RUN9	CTA	ROC	458	97.059	92.725	0.957	0.684
105	RUN9	ANN	TSS	915	100	95.688	0.957	0.805
106	RUN9	ANN	ROC	914	100	95.688	0.973	0.903
107	RUN9	MAXENT	TSS	45	100	85.7	0.859	0.891
108	RUN9	MAXENT	ROC	50.5	100	86.512	0.978	0.958
109	RUN10	GBM	TSS	543	100	98.238	0.982	0.823
110	RUN10	GBM	ROC	551.5	100	98.3	0.995	0.911
111	RUN10	GLM	TSS	657	100	93.938	0.939	0.877
112	RUN10	GLM	ROC	660.5	100	93.975	0.977	0.951
113	RUN10	GAM	TSS	535	97.059	96.475	0.935	0.449
114	RUN10	GAM	ROC	533.5	97.059	96.475	0.956	0.721
115	RUN10	CTA	TSS	415	100	80.525	0.805	0.665
116	RUN10	CTA	ROC	419.5	100	80.525	0.903	0.833
117	RUN10	ANN	TSS	879	100	93.875	0.939	0.554
118	RUN10	ANN	ROC	878	100	93.875	0.975	0.779
119	RUN10	MAXENT	TSS	103	100	90.825	0.909	0.851
120	RUN10	MAXENT	ROC	108.5	100	91.188	0.978	0.961

Chapter 6

General Discussion

6.1. Broader context

The heterogeneous landscapes of Ethiopia are home to speciose flora and fauna. While mounting evidence on bird species studies in this biodiversity-rich country has emphasized in community ecology (synecology) with a thematic focus on species richness, diversity, and composition, the organismal ecology (autoecology) of several species, especially rare, endemic, and cryptic bird species, has scarcely been quantified, given its importance to deliver appropriate species-specific conservation measures. In other words, there are substantial gaps in knowledge about on how and why birds exist in heterogeneous landscapes featured by diverse plant, climate, topography, and human disturbance in the country. This could be mainly due to budgetary and logistical constraints. Therefore, this chapter provides detailed and combined explanations on how the ecology, breeding biology and climate change impacts underpin conservation implications of two endemic and threatened francolins and their habitats in the Ethiopian highlands. All of these robust inferences were made using appropriate field methods and combined statistical tools.

Habitat characteristics are important factors influencing the occurrence, occupancy and abundance of bird species. These characteristics determine the distribution and association of bird species (Sutherland and Green, 2005) and have a major influence on detectability (Bibby et al., 2000). As in other tropical countries, habitat characteristics defined by topography, hydrography, geology, climate and vegetation determine the evolution and distribution of biodiversity in Ethiopia (Ash and Atkins, 2009; Fashing et al., 2022). The distribution of vegetation, a key factor in the survival of bird species, is hypothesized to be linked to climatic and altitudinal variations and other abiotic factors in the country (Friis et al., 2010). For example, the semi-natural vegetation in agricultural landscapes supports high bird species richness in Ethiopia (Marcacci et al., 2022).

The single-season (static) occupancy model (MacKenzie et al., 2002) and the multi-season (dynamic) occupancy model (MacKenzie et al., 2002) were used for Moorland

Francolins and Harwood’s Francolins, respectively, to scrutinize determinants of occupancy, detectability and dynamic parameters (colonization and extinction). Occupancy models (MacKenzie et al., 2018) and conventional models such as the popular presence-only models (Elith et al., 2006; Phillips et al., 2006) model species-habitat associations. The response variable for the former models is always presence/absence data (widely known as detection/nondetection data) and incorporates missing observations, while the latter can use presence-only or presence/absence data, and these models lack explicit absence data and instead generate background (i.e., pseudo-absence) (VanDerWal et al., 2009; Barbet-Massin et al., 2012). Occurrence data for conventional models, such as the popular MaxEnt model or other algorithms, can be collected from a single field survey or from highbrow literature, as I did for Moorland Francolin. The sampling effort for these models is unknown (Guillera-Arroita, 2017), whereas the design for occupancy models requires repeated field visits to a site by human observers, camera traps or other tools (MacKenzie et al., 2018). Consequently, occupancy models provide robust data that account for imperfect detection to estimate occupancy (i.e., habitat use) and species distribution, making them more flexible and reliable (MacKenzie et al., 2018). For this reason, occupancy models are sometimes referred to as ‘data-hungry models’ and are more suitable for species-specific studies (Jha et al., 2022). In this study, I used camera traps to scrutinize the occupancy of Moorland Francolins and the breeding biology of Harwood’s Francolins. For Harwood’s Francolins, I sometimes used playbacks to enhance detectability of the species in very fragmented habitats and finally combined the data (direct observation and playback) to accurately and precisely estimate the habitat use of the species. Based on this, it is plausible to say that occupancy models allowed us to provide better estimates of habitat use of the rare and cryptic francolin species in the central highlands of Ethiopia.

6.2. Ecology of Moorland Francolin

Moorland Francolin was recently elevated to species level and is endemic to the Ethiopia highlands. The species is restricted to the summits of both highland blocks, except for the northwest highlands (Chapter 5). The species is a member of the red-winged group of francolins in the Afrotropics (Madge and McGowan, 2002). With respect to this group and other endemic pheasant species in this biogeographical realm, very limited information is available on the ecological preferences Moorland Francolin in the alpine and subalpine habitats of the Ethiopian highlands.

Moorland Francolin is a sedentary species and is hard to detect by direct observation, particularly at low-population densities in fragmented and disturbed habitats, and field observers often discount to survey such habitats. This is because these species, like Harwood's Francolin (Chapter 4), have plumage coloration that allows for background matching, similar to other phasianid species (Winkler et al., 2015). The use of camera traps was therefore a reliable tool for understanding the ecology of this species. I conducted repeated surveys in predetermined line transects, which allowed us to collect data effectively by avoiding false absences and false positives of Moorland Francolins. To estimate species occupancy and detection probabilities, true absences and missing observations are of considerable importance in accurately and precisely determining species-habitat associations (MacKenzie et al., 2018). In addition, I measured habitat covariates, including fine-scale covariates, landscape-scale covariates, and climatic covariates. I also added the effects of sampling month and survey occasion (effort) to examine species-habitat associations using static occupancy modeling.

Accordingly, naïve and true occupancy and detection probability estimates were higher in pristine (locally conserved and managed) than in disturbed habitats, suggesting that the species strongly prefers to live in traditionally managed habitats. The historical natural resource management, called the Qero system in the Guassa Community Conservation Area (GCCA) (Ashenafi and Leader-Williams, 2005; Ashenafi et al., 2012), is of global importance for the conservation of the flagship species, the Ethiopian wolf (*Canis simensis*) (Tefera and Sillero-Zubiri, 2006). A recent report has also demonstrated that this carnivore species qualifies for umbrella status, and in this way the species benefits the sympatric biodiversity of the alpine habitat, including Moorland Francolin, and the local community living around the protected area through the wise use of resources (Mekonnen et al., 2024), especially the multipurpose and cultural keystone species called Guassa (*Festuca macrophyhlla*) grass (Chengere et al., 2022).

As hypothesized, based on the average results of the most parsimonious models, predators strongly affect Moorland Francolins in the relatively pristine alpine habitat of

GCCA. Because most Galliformes are ground-dwelling birds, natural predators generally have a negative impact on the species (del Hoyo et al., 1994). The other important covariate that positively influenced the species was herb species richness. Mixed and dense herbaceous vegetation was suitable for feeding, hiding and nesting of the target species. The most preferred herb species were found where the species scratched the ground to feed on seeds, bulbs and roots. Insects and worms were also consumed by the species in the herbaceous vegetation.

Contrary to the hypothesis, Moorland Francolin occupancy decreased with increasing distance from roads in GCCA, while roads and paths had a negative, though non-significant, effect on occupancy in disturbed habitats at other sites. Moorland Francolins responded differently to the same covariates in pristine and disturbed habitats, suggesting that the species avoids fragmented and highly disturbed sites in Sub-Afroalpine habitats. These habitats are dominated by high human population growth, where people are changing the habitats (land use types) into eucalyptus plantations, farmlands, settlements, etc. The detection probability of the species increased significantly as a function of average precipitation and sampling occasion (effort) in the pristine alpine habitat. Moorland Francolins were more active during wet and misty conditions to search for food. This is a typical habit of Galliformes, which prefer rainy and less sunny conditions, especially at dawn and dusk, and spend much of the daytime in quiescent (del Hoyo et al., 1994). Repeated surveys with camera traps were useful to explicitly infer the drivers of species-habitat association.

6.3. Effect of climate change on Moorland Francolin

Moorland Francolin is a cold-adapted species that is likely to be affected by extreme temperatures. Global warming is predicted to have a severe impact on restricted range alpine (i.e., mountaintop) bird species. A plethora of evidence shows that mountaintop endemic bird species are vulnerable to climate change and associated risk factors (e.g., Freeman et al., 2018; Neate-Clegg et al., 2021). Moorland francolin is therefore not a notable exception, as many bird species at risk of extinction often share similar demographic and ecological traits (e.g., endemism, rarity and ground nesting) and extinct bird species also exhibited such trait (Marzluff and Restani, 2018).

Most importantly, most galliform species are poor dispersers due to their morphological traits such as body size and wing shape (Hosner et al., 2017), their chances of persisting the climate change seems unlikely. This is because the currently suitable cold climate will gradually change to a hot one, where generalist bird species from lower elevations will move upward and colonize the mountaintops. Focusing on Moorland Francolin as a candidate species, an ensemble of six algorithms from biomod2 package revealed that the current relatively cool temperature (i.e., annual mean temperature, mean = 9.89 °C, range = 5.82 - 15.98 °C) was the main driver for the occurrence of the species in the alpine habitat of the Ethiopian highlands. Black-fronted Francolin in southern Ethiopia also showed a similar habitat association, where the species preferred to survive only at cold temperatures (Gedeon et al., 2017b). With increasing global warming, no suitable habitat is predicted for the Moorland Francolin in the worst-case scenarios, mainly the Shared Socioeconomic Pathways (SSP 370 in 2061-2080) and (SSP 585 in 2081-2100). From the perspective of the current geographical range of the Moorland Francolin (less than 5,000 km^2), populations are at high risk of extinction due to climate change and habitat loss (livestock grazing, human population growth and agriculture). This study proposed that the species could be listed as Vulnerable on the IUCN Red List based on the results of the area of occupancy (AOO) metric and other assessment criteria.

6.4. Ecology of Harwood’s Francolin

To understand the determinants of spatiotemporal habitat use, I modeled habitat covariates (satellite-based indices of vegetation traits, topography, anthropogenic, climatic, and survey covariates) that could affect the species using dynamic occupancy modeling. Results from the average of the top models showed that Normalized Difference Vegetation Index (NDVI), quadratic slope term (SL^2), and Human Disturbance Index (HDI) significantly negatively influenced the occupancy of Harwood's Francolin in the Upper Blue Nile Basin (UBNB) of Ethiopia.

The species rarely used certain habitats characterized by high NDVI (> 0.5), probably due to the presence of aerial and terrestrial predators, and as such the species averted to dwell in areas dominated by large tree species in habitats such as *Combretum-Terminalia* woodland and wooded grassland (CTW), Dry evergreen Afromontane forest and

Grassland Complex (DAF), and riparian vegetation in UBNB. However, at lower vegetation reflectance, the species is highly persistent in shrub, scrub, and sparsely vegetated habitats (i.e., open woodland and grassland) habitats. Equally interesting, species occupancy decreased as a function of quadratic slope, indicating that species is averse to exiting over steep gradients. The reason could be that potential predators, including raptors, other cliff-nesting birds, primates, and cats, occupy these gradients of mountainous landscapes in Ethiopia (Saavedra, 2009). Steep slopes in Ethiopia are unfavorable for cultivation and lack herbaceous vegetation (Nyssen et al., 2004), making the slopes unsuitable for hiding, feeding, and resting of the target species.

It is not surprising that human pressure, measured in this study as the human disturbance index, poses a serious threat to Harwood's francolins. Hunting, livestock grazing and habitat loss are the main known disturbance factors for the Ethiopian francolin species (e.g. Töpfer et al., 2014; Abrha et al., 2017; Gedeon et al., 2017). Contrary to the report by del Hoyo et al. (1994), pheasant species are discriminately hunted for food and medicinal purposes in Ethiopia, especially Harwood's francolin (Robertson et al., 1997; Abrha et al., 2017). Other bird species are not hunted due to the religious beliefs of local Christians.

As I hypothesized, the detection probability of the species increased with increasing average temperature. The valley, hill and bottom of mountain habitats had low temperature records and these areas have low NDVI and steepness of the gradient. Indeed, there is an inverse correlation between temperature and NDVI across the country (Muir et al., 2021), particular for UBNB (Merga et al., 2022; Moisa et al., 2022).

Based on the model averaging, there were no statistically significant covariates affecting the dynamic parameters (colonization probability and extinction probability of the species) from two seasons data. However, the highest extinction probability was noted in plantations with multiple stressors and the colonization probability was highest at lower vegetation reflectance.

6.5. Breeding biology of Harwood’s Francolin

The mating system of most phasianids is diverse (McGowan, 1994; Madge and McGowan, 2002; Winkler et al., 2015), but polygyny is the most common one (Winkler et al., 2015). The breeding cycle of birds has three distinct forms of parental care: nest building, incubation, and offspring provisioning (Wang et al., 2023). Focusing on phasianids, only female pheasants are responsible for incubating and hatching the eggs (McGowan, 1994; Cockburn, 2006), probably due to the occurrence of sexual selection on males (Lislevand et al., 2009; Winkler et al., 2015; Wang et al., 2023), suggesting that mating success exhibits high skewness in the family. The “offspring provisioning” stage usually excludes chick feeding in precocial birds such as pheasant species (Wang et al., 2023), but it involves intensive care such as brooding in extreme weather conditions, escorting to rich food sources, and giving alarm calls to thwart the risk of predation (del Hoyo et al., 1994; Hansell, 2000).

The mating system of Harwood’s Francolin is polygamous (Robertson et al., 1997; Abrha et al., 2018). Specifically, my results are similar to those reported by Lislevand et al. (2009), where the target species exhibited a non-lekking mating system (i.e., resource-defence polygyny). Female parents were responsible to select and build nests, consistent with many pheasant species (McGowan, 1994; Cockburn, 2006) and they exhibited three key behavioral mechanisms to thwart the risk of predation during the breeding cycles. These included background matching, nest orientation and positioning relative to other unselected microhabitats, and depositional odor trails during feeding. The average female nest attendance was 94.81% per day, indicating that females reduce the risk of predation and temperature drop of the nests. I also confirmed that females approaching hatching stayed for more than two days without leaving the nests, and that the nests had molted soft feathers from ventral parts that could produce brood patches. In breeding birds, molting is induced by continuous fasting (Berry 2003) to facilitate heat transfer from the patch to the egg (Jones, 1971; Gill 2007; Winkler 2016). As in many polygynous phasianid species (Winkler et al., 2015), female parents of Harwood’s Francolins provide all forms of care during the breeding cycle, hence uniparental care. The breeding success of the species was 86.94% and 95.47% at measured and unmeasured (random) sites, respectively. Predation and agricultural activities were the main proximate causes of breeding failure in this species. Repeated nest visits, egg touching and other related activities were also partly considered as indirect factors for hatching failure. Many birds are more sensitive to disturbance during the breeding season (Green, 2004), especially galliform species (Zhao et al., 2020). The results highlight how nest site selection, nest building behavior, and parental care contribute to breeding success in this species.

6.6. Combining results for species-specific conservation approach

The current study on Moorland Francolin provides the first evidence on the ecology of the species in the alpine habitats of Ethiopia. Based on occupancy modeling results, the habitat requirements of the species are mainly mixed herbaceous vegetation in traditionally protected and managed areas at fine and landscape scales. Roads and trails dominated by native grasses and associated herb species are highly preferred by the species. In addition, the presence of (natural) predators also affects the presence of the species in the area. The total suitable area for the species is likely to be less than 5,000 km^2 and this habitat is undergoing massive decline due to human pressure, livestock grazing and other related factors. The endemic plant species restricted to the alpine habitat are expected to become extinct in the face of climate change and will be dominated by a few plant species (Kidane et al., 2022) and the habitat will become highly fragmented (Kandziora et al., 2022). Finally, this means that the current specific habitats (e.g., Mima Mound, *Erica* moorland, *Euryops-Alchemilla* shrubland, *Helichrysum-Festuca* grassland, *Festuca* (Guassa) grassland and wetlands) will no longer occur.

Therefore, to conserve the species and their native and suitable habitats, integrated conservation efforts that include socio-ecological and political perspectives will be effective in mitigating climate change and maintaining the ecological function and services of the alpine habitat. In particular, the conservation efforts of local and international actors for the protection of endangered flagship species (Ethiopian wolf) throughout the Ethiopian highlands and cultural keystone species such as *Festuca* grass in Guassa have been strongly supported to sustain the biological and cultural diversity of the alpine habitats. The indigenous people follow the Qero system on how to use natural resources wisely. The indigenous community use grasses through cut and carry system in Guassa. This grazing-free system could help minimize the incidence of wildfire in the area during the dry season by reducing the amount of accumulated grass debris on the ground. As such, the area has been a stronghold for biodiversity and ecosystem services that are vital for humans as well. Implementing the Qero system into some selected alpine habitats could help sustain the diversity of the species in the face of ongoing climate change and other related stressors. With a focus on this target species, I also recommend captive breeding to mitigate the consequences of predicted climate change.

Similarly, the conservation of Harwood's Francolin depends on its specific habitat requirements and breeding success. The species uses scattered vegetation, bush, scrub and grass dominated habitats adjacent to agricultural areas (hence low NDVI), and it is paramount importance to conserve these areas for the survival of the species and sympatric biodiversity. Therefore, the spatio-temporal occupancy patterns of Harwood's Francolins provide insight into sound conservation and management plans. Specifically, I recommend the following actions:

1) The species, especially breeding females, use areas in and around agricultural fields during the rainy season for food sources. Thus, besides avoidance of disturbance, and access to nesting sites, it is important to constrain mowing of grasses, grazing, and removal of bushes during farming operations (e.g., weeding process).

2) Hunting pressure on this species should be minimized and the perception of discriminatory and unregulated hunting needs serious capacity building and awareness raising to reduce the multifaceted disturbances to the species and its habitats. In turn, the local people should be well informed about alternative sources of income such as ecotourism, employment and sustainable use of resources from the habitats.

3) The government should strongly consider establishing at least one Important Bird and Biodiversity Area (IBA) in the Upper Blue Nile Basin, presumably in the Jema and Jara valleys, in cooperation with the local people, to conserve this endemic species and habitat and thereby benefit the local people.

7. References

Abrha, A. M., Nigus, H. K., Weldetnsae, B. G., Tilahun, M., Nigusse, A.G., & Deribew, K. T. (2017). Effects of human disturbances on two sympatric francolin species in the central highlands of Ethiopia. *Podoces*, *12*(1), 13–21.

Abrha, A. M., and Nigus, H. K. (2017). The ecology of Harwood's Francolin Pternistis harwoodi (Aves: Galliformes: Phasianidae) at Merhabete District, central highlands of Ethiopia: implications for conservation. *Journal of Threatened Taxa, 9*(9), 10633–10641.

Abrha, A. M., Zelelew, S. A., Nigus, H. K., and Alelign, A. (2018). Diurnal activity patterns of Harwood's Spurfowl *Pternistis harwoodi* in relation to habitat types and climatic conditions in the central highlands of Ethiopia. *Ostrich*, *89*(2), 195–201.

Abbate, E., Bruni, P., and Sagri, M. (2015). Geology of Ethiopia: a review and geomorphological perspectives. In: Billi, P. (ed.), Landscapes and Landforms of Ethiopia (pp. 33–64). Springer Netherlands.

Alcock, J. (2016). Avian mating and social behavior. Pages 313-353 in I. J. Lovette and J. W. Fitzpatrick, editor. Handbook of bird biology. John Wiley and Sons.

Antonelli, A., Kissling, W. D., Flantua, S. G., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., Kreft, H., Linder, H. P., Badgley, C., Fjeldså, J., and Fritz, S. A. (2018). Geological and climatic influences on mountain biodiversity. *Nature Geoscience*, *11*(10), 718–725.

Arthur, J. W., Curtis, M. C., Arthur, K. J., Coltorti, M., Pieruccini, P., Lesur, J., Fuller, D., Lucas, L., Conyers, L., Stock, J., and Stretton, S. (2019). The transition from hunting–gathering to food production in the Gamo Highlands of Southern Ethiopia. *African Archaeological Review*, *36*, 5–65.

Ash, J., and J. Atkins, editors. (2009). Birds of Ethiopia and Eritrea: an atlas of distribution. Christopher Helm, London.

Ash, J.S., and Gullick, T.M. (1989). The present situation regarding the endemic breeding birds of Ethiopia. *Scopus*, *13* (1), 90–96.

Ashenafi, Z. T., and Leader-Williams, N. (2005). Indigenous common property resources management in the central highlands of Ethiopia. *Human Ecology*, *33*(4), 539–563.

Ashenafi, Z. T., Leader-Williams, N., and Coulson, T. (2012). Consequences of human land use for an afro-alpine ecological community in Ethiopia. *Conservation and Society*, *10*(3), 209–216.

Atickem, A., and Stenseth, N. C. (2022). The role of rodents in the conservation of endangered species in the Ethiopian highlands. *Therya*, *13*(1), 73–77.

Barbet-Massin, M., Jiguet, F., Albert, C.H. and Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in ecology and evolution*, *3*(2), 327–338.

Ben Mocha, Y., Scemama de Gialluly, S., Griesser, M., and Markman, S. (2023). What is cooperative breeding in mammals and birds? Removing definitional barriers for comparative research. *Biological Reviews*, *98*(6), 1845–1861.

Berry, W. D (2003). The physiology of induced molting. *Poultry Science* 82, 971–980.

Biber, M. F., Voskamp, A. and Hof, C. (2023). Potential effects of future climate change on global reptile distributions and diversity. *Global Ecology and Biogeography*, 32(4), 519–534.

BirdLife International (2004). State of the world's birds 2004: indicators for our changing world. Cambridge, UK: BirdLife International.

BirdLife International (2024) Species factsheet: *Scleroptila psilolaema*. Downloaded on 03/05/2024.

Bladon, A. J., Donald, P. F., Collar, N. J., Denge, J., Dadacha, G., Wondafrash, M., and Green, R. E. (2021). Climatic change and extinction risk of two globally threatened Ethiopian endemic bird species. *PloS one*, *16*(5), e0249633.

Bodin, S. C., Neumann, K., Hensel, E. A., Vogelsang, R., Demissew, S., Casas-Gallego, M., and Hahn, K. (2024). Afromontane forests and human impact after the African Humid Period: wood charcoal from the Sodicho rock shelter, SW Ethiopian highlands. *Vegetation History and Archaeobotany*, 33, 529–543.

Bostwick, K. (2016). Feathers and Plumages. Pages 101-147 in I. J. Lovette and J. W. Fitzpatrick, editor. Handbook of bird biology. John Wiley and Sons.

Bowler, D. E., Bjorkman, A. D., Dornelas, M., Myers-Smith, I. H., Navarro, L. M., Niamir, A., Supp, S. R., Waldock, C., Winter, M., Vellend, M. and Blowes, S.A. (2020). Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People and Nature*, *2*(2), 380–394.

Brandon, K. (1995). People, parks, forests or fields: a realistic view of tropical forest conservation. *Land Use Policy*, *12*, 137–144.

Campos-Cerqueira, M., Arendt, W. J., Wunderle Jr, J. M. and Aide, T. M. (2017). Have bird distributions shifted along an elevational gradient on a tropical mountain? *Ecology and Evolution*, *7*(23), 9914–9924.

Chengere, S. A., Steger, C., Gebrehiwot, K., Nemomissa, S. and Dullo, B. W. (2022). Modeling cultural keystone species for the conservation of biocultural diversity in the Afroalpine. *Environments*, *9*(12), 156.

Chignell, S. M., Laituri, M. J., Young, N. E., and Evangelista, P. H. (2019). Afroalpine wetlands of the Bale Mountains, Ethiopia: Distribution, dynamics, and conceptual flow model. *Annals of the American Association of Geographers*, *109*(3), 791–811.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1592):1375–1383.

Cordier, J. M., Lescano, J. N., Ríos, N. E., Leynaud, G. C. and Nori, J. (2020). Climate change threatens micro-endemic amphibians of an important South American high-altitude center of endemism. *Amphibia-reptilia*, *41*(2), 233–243.

Costion, C. M., Simpson, L., Pert, P. L., Carlsen, M. M., Kress, W. J. and Crayn, D. (2015). Will tropical mountaintop plant species survive climate change? Identifying key knowledge gaps using species distribution modelling in Australia. *Biological Conservation*, *191*, 322–330.

Crowe, T. M., Mandiwana-Neudani, T. G., Little, R. M., and Bowie, R. C. (2022). Why the taxonomy of francolins and spurfowls (Galliformes, Phasianidae) needs revision: responses to Hustler (2021) and Hunter et al. (2021a, b). *Ostrich*, *93*(4), 280–291.

Davies, N. B., J. R. Krebs, and S.A. West. (2012). An introduction to behavioural ecology. John Wiley & Sons.

de Klerk, H. M., Crowe, T. M., Fjeldså, J., and Burgess, N. D. (2002). Biogeographical patterns of endemic terrestrial Afrotropical birds. *Diversity and Distributions*, *8*(3), 147–162.

del Hoyo, J. (1994). Family Cracidae (chachalacas, guans and curassows). Pages 310-363 in J. del Hoyo, A. Elliott and J. Sargatal, editors. Handbook of the Birds of the World, Vol. 2. New Word Vultures to Guineafowl. Lynx Edicions, Barcelona.

del Hoyo, J., A. Elliott, and J. Sargatal, editors. (1994). Handbook of the Birds of the World, Vol. 2. New Word Vultures to Guineafowl. Lynx Edicions, Barcelona.

Donald, P. F., Fishpool, L. D., Ajagbe, A., Bennun, L. A., Bunting, G., Burfield, I.J., Butchart, S. H., Capellan, S., Crosby, M. J., Dias, M. P., and Diaz, D. (2019). Important Bird and Biodiversity Areas (IBAs): the development and characteristics of a global inventory of key sites for biodiversity. *Bird Conservation International*, *29*(2), 177–198.

Dudley, N., and Stolton, S. (1999). Conversion of paper parks to effective management: developing a target.

Ervin, J., Sekhran, N., Dinu, A., Gidda, S., Vergeichik, M., and Mee, J. (2010). Protected Areas for the 21st Century: Lessons from UNDP/GEF’s Portfolio. New York: United Nations Development Programme and Montreal: Convention on Biological Diversity.

Fashing, P. J., Nguyen, N., Demissew, S., Gizaw, A., Atickem, A., Mekonnen, A., Nurmi, N. O., Kerby, J. T., and Stenseth, N. C. (2022). Ecology, evolution, and conservation of Ethiopia’s biodiversity. *Proceedings of the National Academy of Sciences*, *119*(50), e2206635119.

Fierro-Calderón, K., Loaiza-Muñoz, M., Sánchez-Martínez, M. A., Ocampo, D., David, S., Greeney, H. F., and Londono, G. A. (2021). Methods for collecting data about the breeding biology of Neotropical birds. *Journal of Field Ornithology*, *92*(4), pp.315-341.

Fishpool, L.D.C., Evans, M.I. (Eds.) (2001). Important Bird Areas of Africa and associated islands: priority sites for conservation. Pisces Publications/BirdLife International, Newbury/Cambridge, UK.

Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V., and Fitzpatrick, J. W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences*, *115*(47), 11982–11987.

Friis, I., Demissew, S. and van Breugel, P. (2010). Atlas of the Potential Vegetation of Ethiopia. *Biologiske Skrifter 58*, 1–307.

Gaffney, D., Summerhayes, G. R., Luu, S., Menzies, J., Douglass, K., Spitzer, M. and Bulmer, S. (2021). Small game hunting in montane rainforests: Specialised capture and broad spectrum foraging in the Late Pleistocene to Holocene New Guinea Highlands. *Quaternary Science Reviews*, *253*, 106742.

Gedeon, K., Zewdie, C., and Töpfer, T. (2017a). The birds (Aves) of Oromia, Ethiopia–an annotated checklist. *European Journal of Taxonomy*, 306, 1– 69.

Gedeon, K., Rödder, D., Zewdie, C., and Töpfer, T. (2017b). Evaluating the conservation status of the Black-fronted Francolin *Pternistis atrifrons*. *Bird Conservation International, 28(4),* 653–661.

Gedeon, K., Seyring, M., Abrha, A. M, Ejeta, C. Z., Abate, N. T., and Töpfer, T. (2023). Birds of Ethiopia: Checklist and Range Maps. *Bonn zoological Bulletin-Supplementum*, *66*, 1–636.

Gill, F. B. (2007). Ornithology, third edition. W. H. Freeman, New York, NY, USA.

Gill, F., Donsker, D., and Rasmussen, P. editors. (2024). IOC World Bird List (v 13.2). Doi 10.14344/IOC.ML.13.2. http://www.worldbirdnames.org/ (accessed 8 February 2024).

Gowaty, P. A. (2018). Reproductive behavior and mating systems. Pages 493-525 in M.L. Morrison, A.D. Rodewald, G. Voelker, M.R. Colón and J.F. Prather, editors. Ornithology: Foundation, Analysis, and Application. Johns Hopkins University Press.

Groos, A. R., Akçar, N., Yesilyurt, S., Miehe, G., Vockenhuber, C., and Veit, H. (2021). Nonuniform late Pleistocene glacier fluctuations in tropical eastern Africa. *Science Advances*, *7*(11), eabb6826.

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: Advances, challenges and opportunities. *Ecography*, *40*(2), 281–295.

Habel, J. C., Rasche, L., Schneider, U. A., Engler, J. O., Schmid, E., Rödder, D., Meyer, S. T., Trapp, N., Sos del Diego, R., Eggermont, H., and Lens, L. (2019). Final countdown for biodiversity hotspots. *Conservation Letters*, *12*(6), e12668.

Hansell, M. (2000). *Bird nests and construction behaviour*. Cambridge University Press.

Harris, R. B., Birks S. M., and Leaché. A. D. (2014). Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). *Journal of Biogeography* 41(11): 2045-2056.

Hensel, E. A., Vogelsang, R., Noack, T., and Bubenzer, O. (2021). Stratigraphy and chronology of Sodicho Rockshelter–A new sedimentological record of past environmental changes and human settlement phases in southwestern Ethiopia. *Frontiers in Earth Science*, *8*, 611700.

Hoffmann, D., de Vasconcelos, M. F. and Fernandes, G. W. (2020). The fate of endemic birds of eastern Brazilian mountaintops in the face of climate change. *Perspectives in Ecology and Conservation*, 18(4), 257–266.

Hole, D. G., Huntley, B., Arinaitwe, J., Butchart, S. H., Collingham, Y. C., Fishpool, L. D., Pain, D. J., and Willis, S. G. (2011). Toward a management framework for networks of protected areas in the face of climate change. *Conservation Biology*, *25*(2), 305–315.

Hosner, P. A., Tobias, J. A., Braun, E. L. and Kimball, R. T. (2017). How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes). *Proceedings of the Royal Society B: Biological Sciences*, *284*(1854), 20170210.

Hrdina, A., and Romportl, D. (2017). Evaluating global biodiversity hotspots–Very rich and even more endangered. *Journal of Landscape Ecology*, *10*(1), 108–115.

Hunter, N., Mills, M. and Cohen, C. (2019). Elgon Francolin *Scleroptila elgonensis* should be treated as a species distinct from Moorland Francolin *S. psilolaema*. *Bulletin of the African Bird Club*, *26*, 92–100.

Hustler, K. (2021). Taxonomic revision of francolins–reflections from a central African perspective. *Ostrich*, *92*(4), 324–328.

IUCN (2016). A Global standard for the identification of Key Biodiversity Areas, Version 1.0. Gland, Switzerland: IUCN.

Jones, R. E. (1971). The incubation patch of birds. Biological Reviews, 46, 315–339.

Keane, A., Brooke, M. D. L., and McGowan, P. J. K. (2005). Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). *Biological Conservation*, *126* (2), 216–233.

Kimball, R. T., Hosner, P. A., and Braun, E. L. (2021). A phylogenomic supermatrix of Galliformes (Landfowl) reveals biased branch lengths. *Molecular Phylogenetics and Evolution*, *158*, 107091.

Ligon, J. D. (2004). The evolution of avian breeding systems. Oxford University Press.

Lislevand, T., Figuerola, J., and Szekely. T. (2009). Evolution of sexual size dimorphism in grouse and allies (Aves: Phasianidae) in relation to mating competition, fecundity demands and resource division. *Journal of Evolutionary Biology*, *22*(9):1895–1905.

Lovette, J. I. (2016). Avian diversity and classification. Pages 7-61 in I. J. Lovette and J. W. Fitzpatrick, editor. Handbook of bird biology. John Wiley and Sons.

Mekonnen, A., Fashing, P. J., Chapman, C. A., Worku, E. A., Fetene, B., Fekadu, M., Guadie, A., Stenseth, N. C. and Venkataraman, V. V. (2024). The Ethiopian wolf can act as a flagship and umbrella species to protect the Afroalpine ecosystem and foster sustainable development. *Environmental Conservation*, *51*(1), 45–54.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248–2255.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., and Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, *84* (8), 2200–2207.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. (2018). Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier

Madge, S., and McGowan, P. (2002). Pheasants, Partridges and Grouse. Christopher Helm, London.

Mahamued, B. A., Donald, P. F., Collar, N. J., Marsden, S. J., Ndang'ang'a, P.K., Wondafrash, M., Abebe, Y. D., Bennett, J., Wotton, S. R., Gornall, D., and Lloyd, H. (2022). Rangeland loss and population decline of the critically endangered Liben Lark Heteromirafra archeri in southern Ethiopia. *Bird Conservation International*, *32*(1), 64-77.

Mainwaring, M. C., Hartley, I. R., Lambrechts, M. M., and Deeming, D. C. (2014). The design and function of birds' nests. *Ecology and Evolution*, *4*(20), 3909–3928.

Mandiwana-Neudani, T. G., Little, R. M., Crowe, T. M. and Bowie, R. C. (2019a). Taxonomy, phylogeny and biogeography of African spurfowls Galliformes, Phasianidae, Phasianinae, Coturnicini: *Pternistis* spp. *Ostrich*, *90*(2), 145–172.

Mandiwana-Neudani, T. G., Little, R. M., Crowe, T. M. and Bowie, R. C. (2019b). Taxonomy, phylogeny and biogeography of 'true' francolins: Galliformes, Phasianidae, Phasianinae, Gallini; *Francolinus*, *Ortygornis*, *Afrocolinus* gen. nov., *Peliperdix* and *Scleroptila* spp. *Ostrich*, *90*(3), 191–221.

Marcacci, G., Gremion, J., Mazenauer, J., Sori, T., Kebede, F., Ewnetu, M., Christe, P., Arlettaz, R. and Jacot, A. (2022). High semi-natural vegetation cover and heterogeneity of field sizes promote bird beta-diversity at larger scales in Ethiopian Highlands. *Journal of Applied Ecology*, *59*(5), 1219–1230.

Marzluff, J. M., and Restani, M. (2018). Extinction and endangerment. Pages 779-800 in M. L. Morrison, A. D. Rodewald, G. Voelker, M. R. Colón and J. F. Prather, editors. Ornithology: Foundation, Analysis, and Application. Johns Hopkins University Press.

Mata-Guel, E. O., Soh, M. C., Butler, C. W., Morris, R. J., Razgour, O. and Peh, K. S. H. (2023). Impacts of anthropogenic climate change on tropical montane forests: an appraisal of the evidence. *Biological Reviews*, *98*(4), 1200–1224.

McCain, C. M. and Garfinkel, C. F. (2021). Climate change and elevational range shifts in insects. *Current Opinion in Insect Science*, *47*, 111–118.

McGowan, P. J. K. (1994). Family Phasianidae (pheasants and partridges). Pages 434-552 in J. del Hoyo, A. Elliott and J. Sargatal, editors. Handbook of the Birds of the World, Vol. 2. New Word Vultures to Guineafowl. Lynx Edicions, Barcelona.

McGowan, P. J. K., Owens, L. L., and Grainger, M. J. (2012). Galliformes science and species extinctions: what we know and what we need to know. *Animal Biodiversity and Conservation*, *35*(2), 321–331.

Mittermeier, R. A., Robles-Gil, P., Hoffmann, M., Pilgrim, J. D., Brooks, T. B., Mittermeier, C. G., Lamoreux, J. L. and Fonseca, G. A. B. (2004). Hotspots Revisited: Earth’s Biologically Richest and Most Endangered Ecoregions. CEMEX, Mexico City, Mexico.

Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M. and Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. In *Biodiversity hotspots: distribution and protection of conservation priority areas* (pp. 3-22). Berlin, Heidelberg: Springer Berlin Heidelberg.

Moranta, J., Torres, C., Murray, I., Hidalgo, M., Hinz, H., and Gouraguine, A. (2021). Transcending capitalism growth strategies for biodiversity conservation. *Conservation Biology*, *36*(2), e13821.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858.

Neate-Clegg, M. H., Stuart, S. N., Mtui, D., Şekercioğlu, Ç. H. and Newmark, W. D. (2021). Afrotropical montane birds experience upslope shifts and range contractions along a fragmented elevational gradient in response to global warming. *PLoS One*, *16*(3), e0248712.

Nigussie, G., Fekadu, M., Demissew, S., and Warkineh, B. (2019). Impact of conservation management on land change: A case study in Guassa community conservation area for the last 31 years (1986–2015). *Modeling Earth Systems and Environment*, *5*, 1495–1504.

Ossendorf, G., Groos, A. R., Bromm, T., Tekelemariam, M. G., Glaser, B., et al. (2019). Middle stone age foragers resided in high elevations of the glaciated Bale Mountains, Ethiopia. *Science*, *365*(6453), 583–587.

Palomo, I., Montes, C., Martin-Lopez, B., González, J. A., Garcia-Llorente, M., Alcorlo, P. and Mora, M. R. G. (2014). Incorporating the social–ecological approach in protected areas in the Anthropocene. *BioScience*, *64*(3), pp.181-191.

Perez, D. M., Manica, L. T., and Medina, I. (2023). Variation in nest-building behaviour in birds: a multi-species approach. *Philosophical Transactions of the Royal Society B*, *378*(1884), 20220145.

Price-Waldman, R., and Stoddard, M. C. (2021). Avian coloration genetics: recent advances and emerging questions. *Journal of Heredity*, *112*(5), 395–416.

Redman N, Stevenson T, Fanshawe J (2011) Birds of the Horn of Africa: Ethiopia, Eritrea, Djibouti, Somalia and Socotra. Revised and expanded edition. Christopher Helm, London.

Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quarterly review of biology*, *57*(4), 405–435.

Robertson, P. A., Dellelegn, Y., Dejene, S., Shimelis, A., and Alemayehu, M. (1997). Harwood's Francolin *Francolinus harwoodi*: recent observations on its status, distribution, habitat requirements, behaviour and threats. *Bird Conservation International, 7* (3), 275–282.

Spottiswoode, C. N., Wondafrash, M., Gabremichael, M. N., Abebe, Y. D., Mwangi, M. A. K., Collar, N. J., and Dolman, P. M. (2009). Rangeland degradation is poised to cause Africa's first recorded avian extinction. *Animal Conservation*, *12*(3), 249–257.

Stattersfield, A. J., Crosby, M. J., Long, A. J., and Wege, D. C. (1998). Endemic Bird Areas of the world: Priorities for biodiversity conservation. Cambridge UK: BirdLife International.

Talukdar, S., and Gupta, A. (2018). Attitudes towards forest and wildlife, and conservation-oriented traditions, around Chakrashila Wildlife Sanctuary, Assam, India. *Oryx*, *52*(3), 508–518.

Tefera. Z., and Sillero-Zubiri, C. (2006). A flagship species for Afroalpine conservation: An overview of the status and conservation of the Ethiopian wolve. *Walia*, *25*, 13–21.

Tian, S., J. Xu, J. Li, Z. Zhang, and Y. Wang. 2018. Research advances of Galliformes since 1990 and future prospects. *Avian Research*, 9(32), 1–13.

Tidemann, S. C., and Gosler, A. eds. (2010). Ethno-ornithology: birds, indigenous peoples, culture and society. Earthscan London, UK.

Tilahun, S., Edwards, S., and Gebregziabher, T. (1996). Important bird areas of Ethiopia: A first inventory. Ethiopian Wildlife & Natural History Society.

Töpfer, T., and Gedeon. K (2020). Alpine birds of Africa. Pages 505-517 in M.I. Goldstein and D.A. DellaSala, editors. Encyclopedia of the World's Biomes, Volume 1. Elsevier.

Töpfer, T., Podsiadlowski, L., and Gedeon, K. (2014). Rediscovery of the Black-fronted Francolin *Pternistis* (*castaneicollis*) *atrifrons* (Conover, 1930) (Aves: Galliformes: Phasianidae) with notes on biology, taxonomy and conservation. *Vertebrate Zoology*, *64* (2), 261–271.

UNDP-United Nations Development Programme, (2012). Guassa-Menz Community Conservation Area, Ethiopia. Equator Initiative Case Study Series. New York, NY.

UNEP-WCMC (2018). 2018 United Nations List of Protected Areas. Supplement on protected area management effectiveness. UNEP-WCMC: Cambridge, UK.

Urban, E. K., Fry, C. H., and Keith, S. (1986). The birds of Africa, Vol. 2. Academic Press, London.

VanDerWal, J., Shoo, L. P., Graham, C. and Williams, S. E. (2009). Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological modelling*, *220*(4), 589–594.

van den Hout, P. J., Mathot, K. J., Maas, L. R., and Piersma, T. (2010). Predator escape tactics in birds: linking ecology and aerodynamics. *Behavioral Ecology*, *21*(1), 16–25.

Waliczky, Z., Fishpool, L. D., Butchart, S. H., Thomas, D., Heath, M. F., Hazin, C., Donald, P. F., Kowalska, A., Dias, M. P., and Allinson, T.S. (2019). Important Bird and Biodiversity Areas (IBAs): their impact on conservation policy, advocacy and action. *Bird Conservation International*, *29*(2), 199–215.

Wang, D., Zhang, W., Yang, S., and Richter, X. Y. L. (2023). Sex differences in avian parental care patterns vary across the breeding cycle. *Nature communications*, *14*(1), 6980.

Winkler, D. W. (2016). Breeding Biology of Birds. Pages 407-450 in I. J. Lovette and J. W. Fitzpatrick, editor. Handbook of bird biology. John Wiley and Sons.

Winkler, D.W., Billerman, S.M. and Lovette, I., 2015. *Bird families of the world: An Invitation to the Spectacular Diversity of Birds*. Lynx Edicions, Barcelona.

Xiao, H., Hu, Y., Lang, Z., Fang, B., Guo, W., Zhang, Q.I., Pan, X. and Lu, X. (2017). How much do we know about the breeding biology of bird species in the world? *Journal of Avian Biology*, 48(4), 513-518.

Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., Luo, A., Li, Y., Ji, C., Peng, S. and Meng, J. (2021). Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Science of the Total Environment*, *783*, 146896.

8. Publications

The following published articles are part of my doctoral research. The publications corresponding to the chapters are noted at the beginning of each chapter, and the authors' contributions, including those accepted and submitted, are listed at the end of each chapter.

- Chapter 2

Abrha, A.M., Gedeon, K., Podsiadlowski, L., Weldesilasie, D.M., Töpfer T. (2023). Occupancy of the Ethiopian endemic Moorland Francolin in pristine and degraded Afroalpine biome using a camera trap approach. Ecology and Evolution 13(11):e10551. https://doi.org/10.1002/ece3.10551

- Chapter 3

Abrha, A.M., Gedeon, K., Podsiadlowski, L., Töpfer, T. (2023). Dynamic occupancy modeling of a cryptic ground-dwelling pheasant species in the Upper Blue Nile Basin in Ethiopia. Global Ecology and Conservation 48:e02710. https://doi.org/10.1016/j.gecco.2023.e02710

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RESEARCH ARTICLE

Occupancy of the Ethiopian endemic Moorland Francolin in pristine and degraded Afroalpine biome using a camera trap approach

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Abstract

Occupancy modeling is an essential tool for understanding species-habitat associations, thereby helping to plan the conservation of rare and threatened wildlife species. The conservation status and ecology of several avian species, particularly ground-dwelling birds, are poorly known in Ethiopia. We used camera trap-based occupancy modeling to investigate habitat covariate influence on occupancy (Ψ) and detection probability (ρ) estimates of Moorland Francolins *Scleroptila psilolaema* from spatially replicated surveys across both relatively pristine and disturbed landscapes in the Afroalpine biome of Ethiopia. Model-averaged estimate of $\widehat{\Psi}$ across all sites was 0.76 ($SD=0.28$) and $\widehat{\rho}$ was 0.77 ($SD=0.13$) in the pristine landscape. The $\widehat{\Psi}$ of the species in the disturbed landscape was 0.56 ($SD=0.19$) and $\widehat{\rho}$ was 0.48 ($SD=0.06$). As hypothesized, based on our model-averaged beta coefficient estimates ($\beta_{mean} \pm SE$), predators significantly negatively influenced the occupancy of Moorland Francolins in pristine habitat. We also found a significant positive association of occupancy with herb species richness. Contrary to our prediction, distance to road significantly negatively influence the occupancy of the species, suggesting that occupancy probability was highest in proximity to roadsides and trails in the pristine habitat. There was no significant influence of habitat covariates on the occupancy of the species in the disturbed habitat. The most important covariates that significantly influence the detectability of the species in pristine habitat included sampling occasion and precipitation. The greater occupancy and detectability of this endemic species in the pristine habitat could be linked with the particular conservation status and management of this biodiversity hotspot in the central highlands of Ethiopia. Our results suggest that strict legal enforcement is required to sustainably preserve Moorland Francolins and the ecological integrity of the entire Afroalpine biome. We recommend using camera traps in order to develop realistic and effective conservation and management strategies for rare, sensitive, cryptic, and ground-dwelling animals in the region.

KEYWORDS
Afroalpine biome, camera trap, conservation, endemic, moorland francolin, occupancy

TAXONOMY CLASSIFICATION
Agroecology, Autecology, Population ecology, Zoology

1 | INTRODUCTION

Among the 34 Earth's biodiversity hotspots, the Eastern Afromontane hotspot, including the Ethiopian Highlands, ranks fourth by a number of endemic plant and vertebrate families and genera (Mittermeier et al., 2004). Next to the Guinea-Congo Forests biome, the second-highest number of biome-confined bird species are found in the Afrotropical Highlands biome (BirdLife International, 2004). In Ethiopia, all bird species subsist in three biomes: the Afrotropical Highlands (including the Afroalpine and Afromontane), Sudan-Guinea savanna, and Somali-Masai biomes (Fishpool & Evans, 2001; Gedeon, Zewdie, & Töpfer, 2017). The Afroalpine biome of Ethiopia consists of a complex mosaic of grassland, moorland, bushland, and other habitat types which are unique in terms of species distinctiveness. This biome harbors a considerable endemic flora and fauna and is home to a number of range-restricted bird species (Ash & Atkins, 2009; Gedeon, Zewdie, & Töpfer, 2017; Töpfer & Gedeon, 2020), as well as to rodents (Ashenafi et al., 2012; Bryja et al., 2019; Razgour et al., 2021), and medium and large-sized mammals (Ashenafi & Leader-Williams, 2005).

Historically, the oldest records of human high-elevational occupation worldwide are from the Afroalpine biome (Ossendorf et al., 2019), but today human population growth (Reber et al., 2018) is the key threat to wildlife in the Afroalpine and Afromontane (Asefa et al., 2017; Ashenafi et al., 2012; Razgour et al., 2021). Agricultural practices, human-induced climate change, and other threats synergistically affect both the biomes' flora (Asefa et al., 2020) and fauna (Asefa et al., 2017; Razgour et al., 2021; Rodrigues et al., 2021).

Like in other tropical countries, the distribution of vegetation in Ethiopia reflects the interplay among altitudinal variation as well as climatic and other abiotic factors (Friis et al., 2010). The combination of different habitat characteristics, species traits, and their interactions define the occurrence, occupancy, and abundance of wildlife populations and influence their distribution patterns and detectability (Devarajan et al., 2020; Guillera-Arroita, 2017).

Most native bird species of Afroalpine and Afromontane habitats of Ethiopia are poorly studied in terms of their abundance, distribution, and threats (Ash & Atkins, 2009; Gedeon, Zewdie, & Töpfer, 2017). One of them is the Moorland Francolin *Scleroptila psilolaema* (Figure 1), an endemic species of the Ethiopian highlands (BirdLife International, 2023; Gill et al., 2023), where it inhabits both Afroalpine and Afromontane habitats (Töpfer & Gedeon, 2020). Knowledge on its breeding biology, home range size, population abundance, occupancy (i.e., habitat use), and other ecological patterns is still scant. Previous distributional data showed Moorland Francolins to occur in the eastern and western highlands (Ash & Atkins, 2009; Gedeon, Zewdie, & Töpfer, 2017). It is classified as Near Threatened due to the ever-increasing loss of moorland and grassland habitats (BirdLife International, 2023), but its population size and habitat association along its geographical range are insufficiently known.

FIGURE 1 An adult female Moorland Francolin *Scleroptila psilolaema* in the Afroalpine biome, Ethiopia. The feather patterns contribute crypsis through background matching in this species (photo credit: Kai Gedeon).

In biodiversity-rich Sub-Saharan African countries such as Ethiopia, little attention is paid to camera trap-based research (Cordier et al., 2022). To fill this knowledge gap, our sampling protocol for Moorland Francolins occupancy estimates relies on data obtained using camera traps. Although this approach may disturb wildlife and alter their behavior (Caravaggi et al., 2020; Wearn & Glover-Kapfer, 2017, 2019), it is cost-effective and non-invasive to study ecological patterns such as population size and distribution of animals. The centerpiece in most occupancy-based camera trap studies are frequently applied on mammal species (e.g., Burton et al., 2015; Niedballa et al., 2015; Kays et al., 2020; Cremonesi et al., 2021; Wevers et al., 2021; Cordier et al., 2022), yet some studies are conducted on ground-dwelling bird species, mainly pheasants (e.g., O'Brien & Kinnaird, 2008; Sharief et al., 2022; Tanwar et al., 2021; Zou et al., 2019). Most importantly, camera traps are particularly useful to study elusive, cryptic, and rare species (O'Brien & Kinnaird, 2008; Sharief et al., 2022; Si et al., 2014; Winarni et al., 2005) and thus represent the most promising approach to investigate Moorland Francolin. Camera trapping is more efficient than other methods such as traditional distance sampling (Suwanrat et al., 2015; Wearn & Glover-Kapfer, 2019). Moreover, it can provide valuable information to implement sound conservation strategies (O'Brien & Kinnaird, 2008; Sharief et al., 2022; Si et al., 2014; Wearn & Glover-Kapfer, 2017).

We attempt to draw an inference of baseline data on the ecology of Moorland Francolins using an occupancy modeling framework. We used presence/absence (i.e., detection/non-detection) data to analyze two stochastic processes: occupancy and detection probability. Occupancy is a dichotomous state variable that accounts for imperfect detection to minimize unreliable inferences of species distribution and range (Bailey et al., 2014; Guillera-Arroita & Lahoz-Monfort, 2012; Kéry et al., 2010; MacKenzie et al., 2018; Tyre et al., 2003). Occupancy models estimate the probability of a species' presence in a fraction of landscape units (MacKenzie et al., 2002, 2018) and help to understand habitat use within a landscape. They are applied across several animal taxa for the implementation of successful conservation and management strategies (Burton et al., 2015; MacKenzie et al., 2018; Steenweg et al., 2017). Therefore, the objective of this study was to gain insight into the habitat use of Moorland Francolins in its native range for the first time and to investigate the effect of habitat covariates on occupancy and detection probability from spatially replicated surveys.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was performed in two areas (Figure 2): Guassa Community Conservation Area (hereafter GCCA) and an area encompassing Sululta plain, Entoto Natural Park, Ankober-Debresina escarpment, and a few sites between them (hereafter collectively abbreviated SEA). The study areas are part of Ethiopia's central highlands in which several Important Bird and Biodiversity Areas (IBAs) are designated (Tilahun et al., 1996). These highland areas consist of top mountain massifs and volcanic cones (Friis et al., 2010). Most of our study sites (93%) were located in IBAs, including GCCA, Entoto Natural Park, Ankober-Debresina escarpment, and Sululta plain. The remaining sites were located outside these IBAs in Angolela Tera, Assagirt, Sheno, and Mendida districts. However, both IBAs and non-IBAs sites in SEA are under serious anthropogenic threat: farming, livestock grazing, settlement, monocultural plantations, and recreational activities. For instance, ENP has shifted its purpose from conservation implementation (Tilahun et al., 1996) to recreational area where mass tourism (Asefa, 2018; Tesema & Berhan, 2019) and monocultural plantations (Bahru et al., 2021; Tadesse & Tafere, 2017) strongly affect the landscape. Both Sululta plain and Ankober-Debresina escarpment are mainly influenced by livestock grazing, farming, and settlement expansions. Except for Sululta plain, the other areas are dominated by exotic *Eucalyptus* plantation and African juniper *Juniperus procera* (Esayas & Bekele, 2011). Therefore, we distinguished between the two study areas based on their different levels of human disturbance, topography, floristic structure and composition, and conservation status, considering GCCA a relatively pristine and SEA a strongly human-modified area.

GCCA (Figures 2 and 3) covers 78 km^2 (Steger et al., 2020), yet the total land area sums up to 111 km^2 if the adjoining villages and other land use types are included (Ashenafi & Leader-Williams, 2005; Nigussie et al., 2019). This area shows critically important habitat features for many wildlife species (Steger et al., 2020) and comprises both the Ericaceous belt (3000–3200 m a.s.l) and the Afroalpine belt (above 3200 m a.s.l) (Friis et al., 2010). The area has been managed by the local community through a management model called the Qero system (Ashenafi et al., 2012; Ashenafi & Leader-Williams, 2005). Unlike other IBAs of the study areas, the Qero system, coupled with the conservation initiatives of Frankfurt Zoological Society, The Darwin Initiative, European Union, and Ethiopian Wolf Conservation Program have significantly sustained the ecological integrity of GCCA since 2003. In this area, the Ethiopian Wolf *Canis simensis* is the flagship species (Tefera & Sillero-Zubiri, 2006), generating income through ecotourism which is partly plowed back

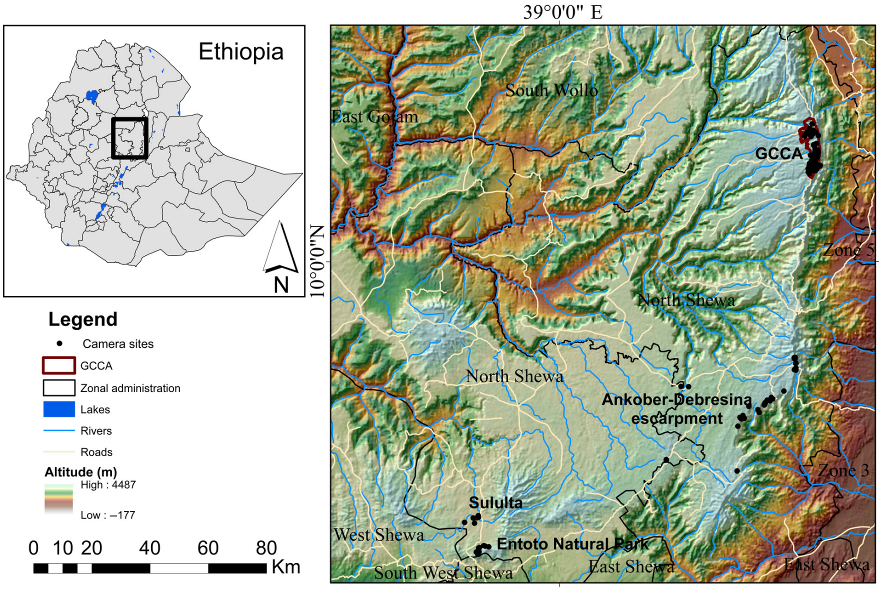

FIGURE 2 The two study areas (GCCA and SEA) and location of camera sites in the central highlands of Ethiopia. GCCA, Guassa Community Conservation Area. The southern sites (including Sululta, Entoto National Park, Ankober-Debresina escarpment, and other areas) form SEA.

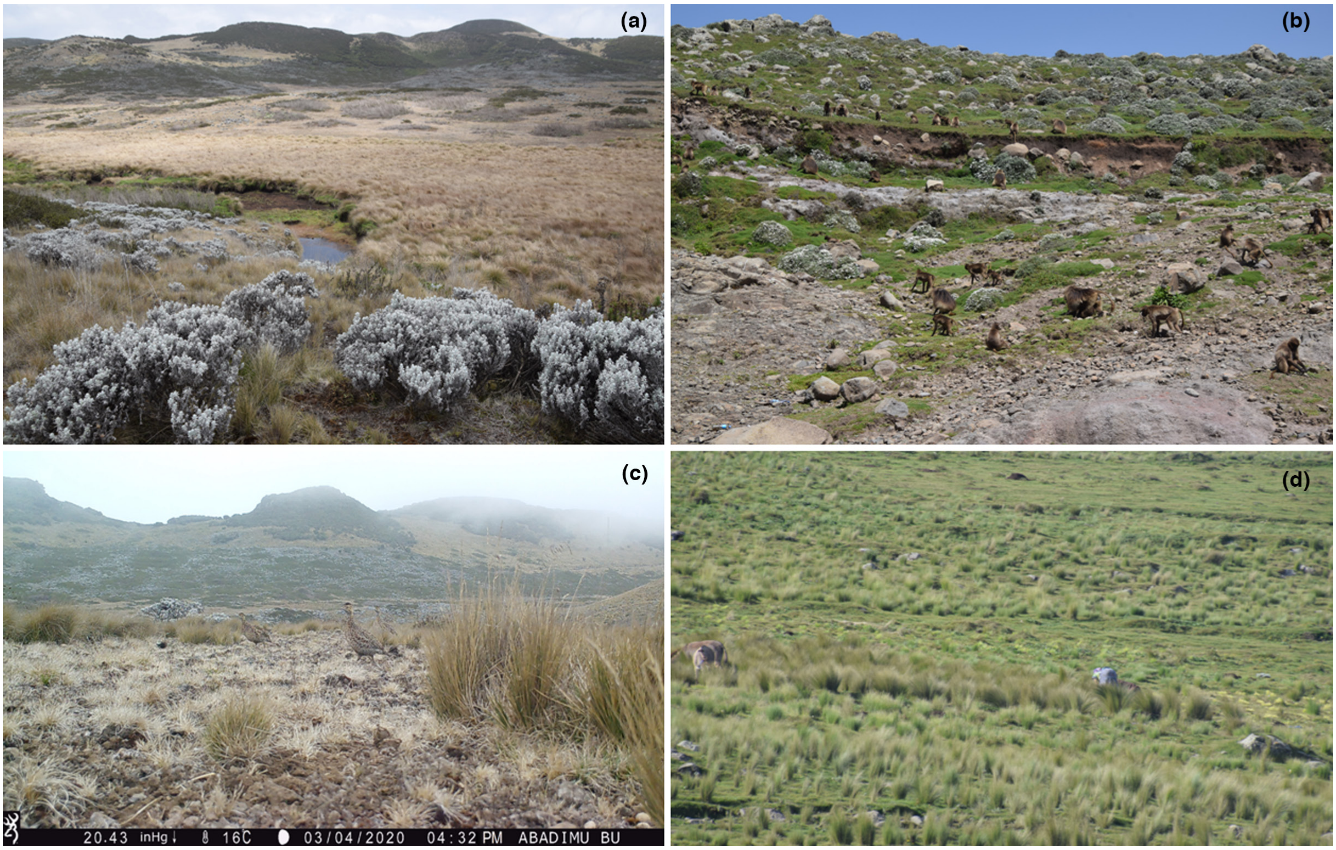

FIGURE 3 Afroalpine habitats in the central highlands of Ethiopia: GCCA with most habitat types (a) and the target species feeding in *Helichrysum-Festuca* grassland (c) and SEA with degraded rocky habitat (b) and grazing land (d).

for the conservation of the species itself (Eshete et al., 2015; Estifanos et al., 2018).

SEA (Figures 2 and 3) forms part of the Afromontane with altitudes generally below 3000 m a.s.l. Very small patches of herbs, shrubs, scattered acacia trees, and exotic trees are common. Here, the Moorland Francolins persist in very small uncultivated and grassland patches of Afromontane habitats.

These highland areas experience a bimodal rainfall pattern with main rain from June to September and smaller amount of rain from October to February (Mohammed et al., 2022). The distinctive habitat features of both of these areas are erratic climatic conditions and a very short dry season (ca. 2 months). The mean annual temperature of GCCA and SEA are 21.26°C (±0.95 SE) and 15.53°C (±0.55 SE), whereas the mean annual precipitation of GCCA and SEA were 2.65 mm (±0.78 SD) and 2.69 mm (±0.90 SD), respectively (Figure S1).

2.2 | Sampling design

Site selection for this study was made randomly. Most sites were obtained through a distribution map from the IUCN, scientific literature, and citizen science data, whereas some sites were chosen without antecedent species records. Following the standard design procedure for allocating optimal sampling occasion (MacKenzie et al., 2018; MacKenzie & Royle, 2005), we initially attempted to conduct a total of 185 camera sites (or preferably sites) ($n = 116$ for GCCA and $n = 69$ for SEA) for a single-season design located in various habitat types. All camera sites were arranged in 39 line transects ($n = 20$ for GGCA and $n = 19$ for SEA), with an average transect length of 2.04 km (±0.80 SD) across both study areas. In this study, we expected that the number of sites (*s*) and occasions (K) were sufficient to determine the stochastic processes. Then, the total survey is simply defined as $s \times K$, and the maximum survey occasion for each site was calculated by minimizing *s*, while taking a standard error of 0.05 for GCCA and 0.065 for SEA. Since both study areas are separated by approximately 150 km independent camera trap data collections were conducted for 5 months for both areas. Along these geographical scales, specific habitat characteristics (i.e., covariates) predicted to influence the occupancy and detection rates of the target species were measured at each site (Table 1).

2.3 | Camera trapping

In December 2019 and the first 3 weeks of January 2020, we made a pilot survey in both areas to assess the study species using camera traps and broadcast playback methods. A total of 20 cameras (Browning Trail Cameras and Bushnell Trophy Cam HD brands) were used for short-term deployments in this study. Since we had a small

TABLE 1 Habitat covariates predicted to affect occupancy and detection probabilities of Moorland Francolins in the central highlands of Ethiopia.

Covariate	Type of data	Measurement and scoring systems	Hypothesized relationship	References tested the effects
Occupancy covariates				
Fine-scale level covariates				
Herb species richness (Hsp)	Continuous	Number of herb species in each site	The species prefers herbaceous sites for feeding, breeding, and concealment.	Jolli et al. (2012); Sukumal et al. (2017)
Species richness (Sprich)[a]	Continuous	Plant species richness (i.e., alpha diversity) in each site	See Hsp	Atikah et al. (2021)
Woody density (WD)	Continuous	Density of tree and shrub vegetation per 0.8 ha	The species is negatively influenced by birds of prey perched on trees and rocky areas.	Sukumal et al. (2017)
Tree canopy cover (T_{caco})	Continuous	Tree canopy cover (CaCo) index estimated using mobile app or digital camera	Francolins avoid tree canopy cover due to the presence of human disturbance and birds of prey and other predators.	Atikah et al. (2021); Chen et al. (2019); Sukumal et al. (2017)
Predator[b]	Binary	Presence of predator (1 = if predator/s was/were recorded and 0 otherwise).	Francolin are negatively influenced by predators.	Abrha et al. (2018); Sukumal et al. (2017)
Landscape-scale covariates				
Elevation (Elev)	Continuous	The elevation of each site is measured in the field using GPS.	Elevation explains climate and vegetation variations that affect species survival and reproduction differently in both sites.	Chen et al. (2019); Holzner et al. (2021); Jolli et al. (2012); O'Brien and Kinnaird (2008); Pardo et al. (2017); Wevers et al. (2021); Whitworth et al. (2018)
Distance to roads (DR)[c]	Continuous	Distance from the center of each site to the nearest paved or unpaved roads	Proximity to road exposes the species to predators and other disturbances.	Dean et al. (2019); Kroeger et al. (2022); Semper-Pascual et al. (2020); Tan et al., (2017); Whitworth et al. (2018)
Distance to settlements (DS)[c]	Continuous	Distance from the center of each site to the nearest settlement	Francolins avoid human settlements where several stressors, including human presence, grazing, mowing, and others are common activities.	Chen et al. (2019); Jolli et al. (2012); Nuttall et al. (2017); O'Brien and Kinnaird (2008); Pardo et al. (2017); Semper-Pascual et al. (2020)
Distance to water point (DW)	Continuous	Distance from the center of each site to the nearest water point (wetlands, streams, madicolous, etc)	Francolins use water points for food and cover in various habitats	Nuttall et al. (2017); Sukumal et al. (2017)
Detection covariates				
Fine-scale level covariates				
Sampling month (M)[a]	Continuous	The survey month for both areas (SEA: Feb and Mar and GCCA: Apr-Jun) in 2020	Detection probability of Moorland Francolins varies between sampling months	Holzner et al. (2021); Jolli et al. (2012)
Survey occasion (E)	Continuous	Number of days for which camera trap was active in each site per sampling occasion also called survey timing-how long?	The francolin detection increases with number of days of cameras deployed	Holzner et al. (2021); Kays et al. (2020); Semper-Pascual et al. (2020); Si et al. (2014); Tan et al., (2017); Wevers et al. (2021)

(Continues)

TABLE 1 (Continued)

Covariate	Type of data	Measurement and scoring systems	Hypothesized relationship	References tested the effects
Climate covariates				
Temperature (T)	Continuous	Temperature of each site while camera trap was active	The francolin detection is influenced by temperature because francolins highly favor cold conditions and adapted to extreme low nocturnal temperature	Abrha et al. (2018); Gedeon, Rödder, et al. (2017)
Precipitation (P)	Continuous	Precipitation of each site while camera trap was active	Francolins have plenty of food resource to easily rake the wet ground and produce continuous calls for breeding during raining or wet season	Abrha et al. (2018); Gedeon, Rödder, et al. (2017)

Note: The first nine predictors are site-specific covariates, whereas the last four are observational-specific covariates.

[a] The spatiotemporal covariates are dropped due to high collinearity (Dormann et al., 2013; Zuur et al., 2010). This study selected herb species richness over total species richness (Sprich) in both study area. Herbaceous and shrubby vegetation were dominant in GCCA (> 80% ground vegetation cover) (Nigussie et al., 2019).

[b] Hunting was not considered as a threat for this species (See Discussion).

[c] Human disturbance factors: grazing, mowing and farming are the major factors in the study sites (Ashenafi et al., 2012; Nigussie et al., 2019; Steger et al., 2020). *Festuca abyssinica* grass (Guassa) intriguingly is valued for fodder for livestock (cut and carrying system and livestock grazing), thatching, wall building mix with mud, and help to make whip, rope, hat, broom (mure) and raincoats (gesa).

number of cameras, some adjoining habitats (see habitat covariates below) were simultaneously assessed and in both study areas cameras were deployed sequentially. Cameras were repositioned to other sites to cover the desired representative home range and to make the field survey more cost-effective. When small camera traps are available, repositioning to new sites is recommended to increase the spatial coverage of target species (Meek et al., 2014; Shannon et al., 2014; Si et al., 2014; Wearn & Glover-Kapfer, 2017).

Each camera trap was placed horizontally (i.e., camera alignment was perpendicular to the ground) within a 50 m radius (~ 0.8 ha) of plot or focal patch size to optimize detectability. Because some terrain settings were very difficult to conduct surveys, cameras were not fixed at the center of each plot instead they were placed approximately 10–30 m distance from the grid center, where freshly raked and possible feeding grounds were noticed. Single camera placement is employed to detect small-medium mammals and bird species (Ferreguetti et al., 2015; Lamelas-López & Salgado, 2021). The camera spacing in continuous habitats in GCCA was approximately 0.3 km (0.2–0.5 km), while in SEA was approximately 0.5 km (0.3–0.8 km) to enhance detectability and to avoid spatial autocorrelation between camera traps. Though telemetry data collection was originally proposed to estimate the home range of the species which enables to estimate camera spacing, we assumed that the camera trapping space was sufficient and representative to study occupancy of this species based on available literature. If the average home range size of a target species is not known, it is recommended to infer spatial extent from congeneric or other related species (Niedballa et al., 2015). Mostly, camera trap spacing, based on home range, for pheasants ranges from 0.2 km (Zou et al., 2019) to 0.7 km (Suwanrat et al., 2015). Therefore, the camera spacing was higher than the home range diameter of the species, which was a similar approach as in other studies (Maffei & Noss, 2008; Niedballa et al., 2015). In our case, camera traps were unbaited but rather were providentially camouflaged with rocks, stones, and Ericaceous heathlands of the study sites. Site selection for camera placement was randomly carried out across various habitats of both study areas, as was proposed by several other studies (e.g., Burton et al., 2015; Cordier et al., 2022; Meek et al., 2014; Tanwar et al., 2021; Wearn & Glover-Kapfer, 2017).

We placed camera traps on tree trunks, attached to thick coarser grasses (*Festuca* spp.) and shrubs, and on wooden stakes at approximately 30–60 cm above the ground, as this standard height is credible to trigger the motion sensor and it is reasonable to detect ground-dwelling bird species (Figure 3; Figure S2). Because some sites were in completely rocky areas, we also put cameras by arranging stacked stones that matched the background of the site. Most cameras had 16 GB memory and some cameras mounted on courser grasses and shrubs had 32 GB SanDisk memory card as they were easily triggered by the movement of vegetation during high wind velocity. However, to enhance good photographs and detectability, prudent vegetation removal was carried out in some sites to avoid false triggering mainly during windy conditions (Meek et al., 2014; Wearn & Glover-Kapfer, 2017). Our primary interest was to capture photos of the target species that can be easily pooled into detection/non-detection binary matrices. In most cases, the video function was discounted, yet some videos were collected from the field to understand the natural behavioral repertoire of the species and its interaction with other species (i.e., predators) in the habitats. Because both camera models had different setting options but similar functions, we set up cameras for the following typical important parameters: (1) camera traps were active for 24 h/day and programmed to capture 1 photo/trigger at 10 s intervals, and some sites with more than one camera traps set to capture 20 s video/trigger, with subsequent videos delayed for 5 min; (2) the sensitivity of the infrared sensor was programmed to be medium or normal; and (3) the quality of photos were adjusted to be medium for both camera brands. The battery life of each camera was checked during data retrieval, storage, and repositioning of cameras. Extreme weather conditions (too hot or too cold) severely affected the sensitivity of sensors in our areas.

2.4 | Habitat covariates

To include representative habitat types in GCCA, we adapted the habitat classifications of Ashenafi et al. (2012). The habitat types were Mima Mound, *Erica* Moorland, *Euryops-Alchemilla* shrubland, *Helichrysum-Festuca* grassland, and *Festuca* (Guassa) Grassland. In their classifications, swamp habitat which is typically characterized by woody vegetation (US definition) and reed swamp or forested fen (European definition) is now replaced by "peatland". In this habitat, the wetland type is normally a moor surrounded by *Erica*, *Festuca* and other plant species and has permanent and ephemeral water fed by precipitation hence called "ombrothropic peatland". Moreover, we identified and added montane forest to the classification as an important other habitat type for wildlife species in the area, though it was not included in the rodent-based study (Ashenafi et al., 2012). Because the sites in SEA study area were human-dominated, the habitat types were homogenous and it was very hard to distinguish and classify in relation to vegetation patterns. Broadly, we categorized the habitats into *Eucalyptus-Juniperus* habitat and grazing lands. The later class obviously incorporated agricultural lands. Overall, this area has been heavily transformed to *Eucalyptus* plantations to meet demand for wood products and improve the livelihoods of local communities (Bahru et al., 2021; Tadesse & Tafere, 2017).

At the sites, we collected 13 covariates derived from habitat features, landscape connectivity metrics, climatic factors, and sampling covariates which were predicted to influence the occupancy and detection probabilities of the target species. Occupancy was modeled as a function of site-specific covariates, including biotic factors (vegetation traits and predators) and landscape connectivity metrics, while detectability was modeled as a function of observational-specific covariates, including survey occasion (hereafter occasion) and climatic factors (precipitation and temperature). The occasion is defined as a total number of days for which each camera was active per site (Table 1).

Specific vegetation traits assumed to influence habitat use were collected from each site using different tools. Due to the occurrence of scattered trees within most sites (with the exception of montane forest adjoining to the moorland habitats and ENP) and complex landscapes varying with soil, climate, topographic, and other features, we used only two $20 \times 20\,\text{m}^2$ randomly placed quadrats for tree species with DBH ≥ 10 cm in woody vegetation sites separated by at least 15 m between quadrat. Meanwhile, in each large quadrat, $5 \times 5\,\text{m}^2$ for shrub and liana species with ≤ 10 cm were nested (Figure S2). Thus, the following vegetation traits were measured accordingly: (1) by placing five $1 \times 1\,\text{m}^2$ quadrats (four in the corner and one in the center) in each nested quadrat; herb and fern species richness was identified and counted; (2) woody species richness and abundance were determined from the larger and nested plots; (3) woody species density (abundance of individual trees, shrubs and lianas/0.8 ha) was also estimated from each site; and (4) average tree canopy cover was estimated using GLAMA (Gap Light Analysis Mobile Application software) from vertically upward looking photos (approximately 8 photos/site) either directly collected in the field or retrieved photographs with a digital camera (Nikon D5300) from sampling sites (Gonsamo et al., 2011; Tichý, 2016).

Landscape connectivity metrics (landscape scale covariates), including elevation, distance to the nearest road (both paved and unpaved roads and trail with at least 1 m wide), distance to nearest water points, and distance to nearest settlements were gauged either directly at the site using a handheld GPS and tape meter or indirectly using Google earth images. Nearest and accessible metrics to some sites were measured in the field. Average on-site ambient temperature and precipitation measurements would have been costly and very difficult to conduct in each site; instead, we obtained climatic data from NASA 2022 (https://power.larc.nasa.gov/data-access-viewer/) to understand species-habitat associations.

2.5 | Data analysis

Single-season occupancy model was applied to understand the influence that habitat covariates have on occupancy and detectability while accounting for imperfect detection (MacKenzie et al., 2002, 2018). The detection history was derived from a sequence of species detection/non-detection dichotomous data (i.e., detection = 1 and non-detection = 0) that were pooled into occasions from consecutive camera days for each site. For occupancy models, data collected by camera traps needs to be divided into sampling occasions (Sollmann, 2018). Such data treatment is important to maximize detectability, maintain spatiotemporal independence among occasions and thereby increases adequacy of model fit. Sensitive analysis was conducted without incorporating any covariates to evaluate the discrepancy of occupancy and detection estimates for different sampling intervals. Based on the input of the analysis, we chose the balance between high parameter estimates and small confidence intervals (see Table S1). Consequently, an occasion was defined as an interval of two camera days for both study areas.

Cameras were active for approximately six consecutive days ($n = 98$, 2–10 days) to obtain an average of three occasions per site at GCCA area. Whereas cameras at SEA area were active for approximately eight consecutive days ($n=48$, 4–12 days) to obtain an average of four occasions per site. Number of camera days varied depending on the probability of detection of the species in the two different areas. Such study duration is recommended for high detectable species (Guillera-Arroita et al., 2010; MacKenzie & Royle, 2005). To account occupancy model assumptions (MacKenzie et al., 2002, 2018), each site was surveyed between one to five repeated occasions ($K_{\text{max}}=5$; $K_{\text{average}}=2.95$) in GCCA from March to June 2020, while in SEA each site was surveyed two to six repeated occasions ($K_{\text{max}}=6$; $K_{\text{average}}=3.46$) from February to March 2020. The discrepancy in number of occasions per site was due to accessibility, logistical constraints, security, weather conditions, and technical problems. We had missed observations in some sites meaning that sampling was not conducted at site i during time t and hence a missed observation represented by hyphen (–) was filled instead in the complete detection history ($\mathbf{h}_i$). This also included data from malfunctioned cameras and blank photos in some cameras.

We used PRESENCE program v.2.13.39 (Hines, 2006) to model occupancy and detection estimates. The parameters were estimated using logit link and a maximum likelihood approach in the program (MacKenzie et al., 2002, 2018). Occupancy probability (Ψ) was modeled as a logit link function of fine-scale level and landscape scale covariates. The structure of model framework of the occupancy probability of a site (i) in association with the site-specific covariates is expressed as:

$$\text{logit}\left(\Psi_i\right) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ \dots \ + \beta_u X_{iu} \tag{1}$$

Likewise, the detection probability (ρ) was modeled as a logit link function of observation-specific covariates. The logit equation derived from the probability of detecting a species at site i, during survey j in association with the covariates is:

$$\text{logit}\left(\rho_{ij}\right) = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ \dots \ + \beta_u X_{iu} + \beta_{u+1} y_{ij1} \ \dots \ \beta_{u+v} y_{ijv}, \tag{2}$$

where $X_{i1} \dots X_{iu}$ refers to site covariates associated with the probability of a site i being occupied and $y_{ij1} \dots y_{ijv}$ refers to sample covariates.

All continuous covariates were normalized by z score conversion (mean = 0 and SD = 1) to help convergence of the maximum likelihood algorithm prior to analysis (Schielzeth, 2010). Such data transformation produces better model performance and interpretability (Gelman & Hill, 2007; Schielzeth, 2010). Since we had spatial data, collinearity was assessed using variance inflation factor (VIF). Covariates with highest VIF were dropped in the analysis and covariates at threshold level VIF < 5 and Spearman's correlation ($r_s<0.7$) were retained (Dormann et al., 2013; Zuur et al., 2010). Of the strongly correlated covariates, we retained ecologically important covariates based on field evidence and existed literature to understand their influence on occupancy and detectability. With a total of 11 covariates, the global model was run, and subsequently competing models were constructed based on plausible additive covariates. The null model (ψ(.),ρ(.)) was also constructed to compare with the relative weight of other additive models which included one or more covariates.

Since the ratio of effective sample size to the number of parameters (n/k) was small, model selection procedures were carried out using Akaike's Information Criterion for small sample bias adjustment (AIC_c) from the competing candidate set of models (Burnham & Anderson, 2002), where the most supported models are top-ranked models with $\Delta\text{AIC}_c \le 2.0$ (Burnham & Anderson, 2002). Summed model weights of each covariate from each model were also calculated to rank the relative importance of the covariates (Burnham & Anderson, 2002). Then, in order to retain ecologically meaningful covariates, models with $\Delta\text{AIC}_c \le 4.0$ were selected to drive model average estimates of occupancy and detection probabilities (Burnham et al., 2011) (Tables 2 and 3). Competitive models were used to estimate Ψ and ρ and calculated parameter estimates, standard errors (SEs), and level of significance based on 95% CI (zero-overlapped method) for each covariate. Uninformative parameters (Arnold, 2010; Leroux, 2019) were also assessed in our model sets. Estimates of the slopes (i.e., β coefficients) for covariates were used to determine the magnitude of their influence on Ψ and ρ.

We used a parametric bootstrap goodness of fit (GOF) using 10,000 permutations to assess the adequacy of fit of the global model (i.e., the most parameterized model) and Pearson's Chi-square test (χ^2) and non-Bayesian p-value were implemented to check overdispersion ($\hat{c}$) (MacKenzie & Bailey, 2004). The degree of overdispersion parameter estimate ($\hat{c}$) or variance inflation factor was assessed using chi-squared (GOF) statistic. It was calculated by dividing the observed test statistic by the average of simulated test statistics.

We computed the number of occasions (K) to enhance the odds of detecting Moorland Francolins in a site. We considered a set of four levels of confidence (ρ^*): 0.7, 0.8, 0.9, and 0.99 by assuming that the species detection probability is always less than one. The occasion (K) was calculated from the detection probability (ρ) of the model averaging to determine the true absence of the species from a site (McGrath et al., 2015; Pellet & Schmidt, 2005; Sewell et al., 2010).

$$K = \frac{\log(1-\rho*)}{\log(1-\rho)}, \tag{3}$$

where ρ is the calculated detection probability and ρ^* is the target detection probability as mentioned above.

Both original and square-root transformed data were used sequentially for normality assumption using Shapiro–Wilk and homoscedasticity tests. Consequently, we used one-way ANOVA to compare mean differences in photos captured among sampling months in GCCA, and a post hoc testing procedure using Bonferroni error adjustment was applied for multiple comparisons. We also used Mann–Whitney U-test to compare mean differences in photos and parameter estimates across spatiotemporal. Similarly, this test was used for occupancy probability estimates comparison in relation to predator presence and absence. This data was analyzed in IBM SPSS statistics (version 20). A two-tailed hypothesis test with an alpha value of 5% was considered.

TABLE 2 Results of model selection for Moorland Francolins occupancy and detection probabilities in the central highlands of Ethiopia.

Model structure	AIC_c	ΔAIC_c	ω_i	K	−2 L	$\hat{c}$
Traditionally protected landscape (GCCA)						
$\Psi(Hsp + T_{caco} + Pre + DR), p(E + T + P)$	257.40	0.00	0.08	9	237.35	0.88
$\Psi(Hsp + Pre + DR), p(E + T + P)$	257.46	0.06	0.07	8	239.84	0.83
$\Psi(Hsp + Pre + Elev + DR), p(E + T + P)$	258.01	0.61	0.06	9	237.96	0.88
$\Psi(WD + Hsp + Pre + DR), p(E + T + P)$	258.07	0.67	0.05	9	238.02	0.80
$\Psi(Hsp + T_{caco} + Pre + DR), p(E + P)$	258.16	0.76	0.05	8	240.54	0.81
$\Psi(Hsp + Pre + Elev + DR), p(E + P)$	258.39	0.99	0.05	8	240.77	0.83
$\Psi(Hsp + Pre + DR), p(E + P)$	258.44	1.04	0.05	7	243.20	0.84
$\Psi(Hsp + T_{caco} + Pre + Elev + DR), p(E + T + P)$	258.47	1.07	0.04	10	235.94	0.82
$\Psi(Hsp + Pre + Elev), p(E + T + P)$	258.94	1.54	0.04	8	241.32	0.88
$\Psi(WD + Hsp + Pre + DR), p(E + P)$	258.96	1.56	0.03	8	241.34	0.83
$\Psi(WD + Hsp + Pre + Elev + DR), p(E + T + P)$	259.17	1.77	0.03	10	236.64	0.83
$\Psi(WD + Hsp + T_{caco} + Pre + DR), p(E + T + P)$	259.18	1.78	0.03	10	236.65	0.80
$\Psi(Hsp + T_{caco} + Pre + DR + DW), p(E + T + P)$	259.35	1.95	0.03	10	236.82	0.77
…						
$\Psi(.), \rho(.)$	298.28	40.88	0.00	2	294.15	1.09
Human-modified landscape (SEA)						
$\Psi(Hsp + Tcaco + DR + DS), p(.)$	182.77	0.00	0.07	6	168.72	0.99
$\Psi(Hsp + DS), p(.)$	183.32	0.55	0.06	4	174.39	1.14
$\Psi(Tcaco + DS), p(.)$	183.37	0.60	0.05	4	174.44	1.15
$\Psi(Hsp + DR + DS), p(.)$	183.62	0.85	0.05	5	172.19	0.97
$\Psi(Hsp + Tcaco + DS), p(.)$	183.75	0.98	0.04	5	172.32	1.15
$\Psi(Tcaco + DS), p(E)$	184.13	1.36	0.04	5	172.70	1.41
$\Psi(Hsp + DS), p(T)$	184.32	1.55	0.03	5	172.89	1.10
$\Psi(Tcaco + DR + DS), p(.)$	184.40	1.63	0.03	5	172.97	1.03
$\Psi(Hsp + Tcaco + DR + DS), p(T)$	184.45	1.68	0.03	7	167.65	0.95
$\Psi(Hsp + DR + DS), p(T)$	184.65	1.88	0.03	6	170.60	0.92
$\Psi(Hsp + Tcaco + DR + DS), p(T)$	184.68	1.91	0.03	7	167.88	1.04
$\Psi(Tcaco), p(.)$	184.76	1.99	0.03	3	178.21	1.15
…						
$\Psi(.), \rho(.)$	186.58	3.81	0.009	2	182.31	1.09

Note: Model rankings are based on the AIC_c values; AIC_c values compared to the top-ranked model (ΔAIC_c); ΔAIC_c scores ≤ 2.0 are the top-ranked model; model weight (ω_i), and number of parameters (K), and $-2L = -2\mathrm{Log}_e L$. $\hat{c}$ = overdispersion parameter to estimate lack of fit.

3 | RESULTS

3.1 | Camera trapping in GCCA and SEA

The deployed camera traps yielded 610 and 361 trap nights in GCCA and SEA, respectively. We failed to collect data from 21 (GCCA) and SEA (18) sites mostly due to battery failure and system malfunctioning. We found a significant difference in average photos captured among sampling months in GCCA ($F_{2,95} = 11.775$, $p < .001$). There was no significant difference in average photos captured between sampling months in SEA (Mann–Whitney test $U = 277.5$, $n = 48$, $p = .893$). Pooling the data across both study areas, the average photos captured in GCCA was approximately four units higher in comparison to SEA (Mann–Whitney test $U = 1365$, $n = 146$, $p < .001$) (Figure S3). Likewise, model-averaged estimates of occupancy probability ($\hat{\Psi}$) and detection probability ($\hat{\rho}$) parameters were significantly higher in the pristine habitat than in the disturbed landscape (Figure 4).

3.2 | Habitat use modeling for traditionally managed habitat

We captured a total of 2632 photos (7–141 photos per site) from all sampling occasions in GCCA. Moorland Francolins were detected at 68 of 98 sites, which resulted in a naïve occupancy (proportion of sites that recorded at least one photograph on the whole camera

TABLE 3 Summed model weight ($\Sigma\omega_i$) and influence of covariates calculated from model-averaged beta coefficient estimates and standard errors ($\beta_{mean} \pm SE$).

Site	Covariate	$\Sigma\omega_i$	$\beta_{mean} \pm SE$	95% CIs Lower	95% CIs Upper	*p*-Value
GCCA	Occupancy (Ψ)					
	Predator	**0.97**	**−2.12 ± 0.84**	**−3.76**	**−0.48**	**.011**
	Herb species richness	**0.97**	**1.40 ± 0.68**	**0.07**	**2.74**	**.039**
	Distance to road	**0.78**	**−0.74 ± 0.35**	**−1.44**	**−0.05**	**.034**
	Tree canopy cover	0.46	−0.58 ± 0.37	−1.30	0.13	.117
	Elevation	0.35	0.79 ± 0.60	−0.39	1.97	.189
	Woody density	0.22	−0.46 ± 0.42	−1.29	0.37	.277
	Distance to water	0.10	0.21 ± 0.41	−0.59	1.00	.621
	Distance to settlement	0.06	0.36 ± 0.49	−0.60	1.33	.472
	Detection (ρ)					
	Occasion	**0.99**	**0.68 ± 0.23**	**0.23**	**1.13**	**.003**
	Precipitation	**0.92**	**0.75 ± 0.36**	**0.05**	**1.45**	**.037**
	Temperature	0.70	0.40 ± 0.23	−0.04	0.84	.082
SEA	Occupancy (Ψ)					
	Distance to settlement	**0.76**	**0.74 ± 0.41**	**−0.07**	**1.55**	**.071**
	Tree canopy cover	0.72	−0.84 ± 0.48	−1.77	0.09	.080
	Herb species richness	0.60	0.83 ± 0.48	−0.11	1.77	.083
	Distance to road	0.37	0.62 ± 0.41	−0.18	1.42	.131
	Predator	0.09	1.10 ± 1.23	−1.31	3.51	.378
	Woody density	0.03	0.23 ± 0.44	−0.63	1.09	.614
	Detection (ρ)					
	Occasion	0.26	0.39 ± 0.30	−0.19	0.98	.195
	Temperature	0.23	0.34 ± 0.27	−0.19	0.86	.210
	Precipitation	0.18	0.21 ± 0.21	−0.21	0.63	.322

Note: Lower and upper 95% confidence intervals of the coefficients were constructed. Non-overlapping with zero (bold) shows significance values of β estimates.

sites) estimate of 0.69. In GCCA, at the habitat-specific level, the findings showed that the highest habitat use was obtained in Mima Mound, *Euryops-Alchemilla* shrubland, and *Helichrysum-Festuca* grassland. Conversely, the least was shown across the tree belt (i.e., montane forest and *Eucalyptus* plantation) (Figure S4).

The null model ($\psi(.)$, $\rho(.)$) appeared to be the least important model to explain the stochastic processes (Table 2; Table S2). The Ψ for this model was 0.73 (SE = 0.05) with a 95% CI of 0.63–0.82 and ρ of 0.85 (SE = 0.03) with 95% CI of 0.79–0.89. In GCCA, some evidence of breeding activity was observed from the camera traps, such as three juveniles were provisioned by both parents.

We constructed candidate sets without interactions between covariates to model Ψ and *p* in the order of parsimony models using ΔAIC_c. The bootstrapping procedure and χ^2 test revealed that the global model ($\psi(WD + Hsp + T_{caco} + Pre + Elev + DR + DS + DW)$, $\rho(E + T + P)$) lacks overdispersion ($\chi^2 = 35.95$; $p = .35$; $\hat{c} = 0.85$), showing independence among sites. Subsequently, the combinations of occupancy and detection covariates of the top models were tested based on the lowest ΔAIC_c values. The bootstrapped top 13 models also showed adequate model fit ($\hat{c} \sim 1$, Table 2). The summed weight of the top-ranked models ($\Delta AIC_c \leq 2.0$) was 0.61 and the most parsimonious model ($\psi(Hsp + T_{caco} + Pre + DR)$,$\rho(E + T + P)$) had only 0.08 model weight, suggesting more plausible competing models existed to explain the occupancy and detection estimates (Table 2). We used model averaging to improve inference as the top model clearly

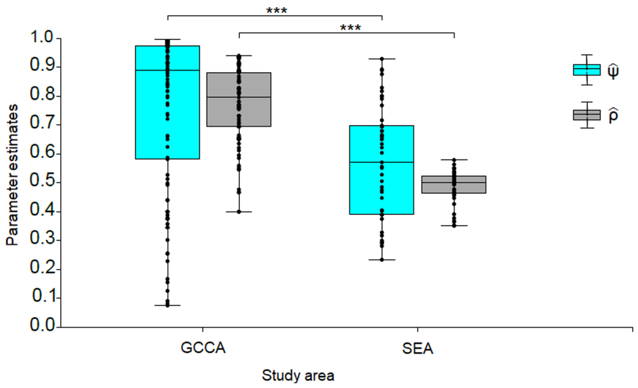

FIGURE 4 Parameter estimates (occupancy and detectability) of Moorland Francolin derived from model averaging. The asterisks (***) denote a strong statistically significant difference between parameter estimates in the study area at $p < .001$ level.

showed model selection uncertainty (Symonds & Moussalli, 2011). Due to the ecological importance of individual covariates included in the top models, we discounted models with less than five $\Delta\mathrm{AIC}_c$ to increase model weight (Richards, 2005) and we considered the top-ranked models with summed model weight of 0.95 (Symonds & Moussalli, 2011).

Model-averaged estimate of $\hat{\Psi}$ across all sites was 0.76 (SD = 0.28) and $\hat{\rho}$ was 0.82 (SD = 0.05). The overall occupancy was 10% greater than the naïve occupancy estimates when detection probability is accounted for. As we hypothesized, predators negatively associated with the Ψ of Moorland Francolins in GCCA ($\beta_{\mathrm{mean}} \pm \mathrm{SE} = -2.12 \pm 0.84$; 95% CI: −3.76; −0.48) and the summed ω_i was 97% (Table 3). There was a higher average occupancy probability in the absence of predators in comparison to the presence of predators (Mann–Whitney *U*-test = 244.5, $n = 98$, $p < .001$) (Figure 5). These predators were avian and mammalian species. We observed Yellow-billed Kite *Milvus aegyptius*, Augur Buzzard *Buteo augur*, Verreaux's Eagle *Aquila verreauxii*, and Common Kestrel *Falco tinnunculus* to be common potential aerial predators of Moorland Francolins in the area. The most important potential mammalian predators were African Civet *Civettictis civetta*, Honey Badger *Mellivora capensis*, Black-backed Jackal *Canis mesomelas*, Serval *Leptailurus serval* and White-tailed Mongoose *Ichneumia albicauda*.

We also found that herb species richness showed a significantly positive influence the occupancy of the species based on model averaging estimates ($\beta_{\mathrm{mean}} \pm \mathrm{SE} = 1.40 \pm 0.68$, 95% CI: 0.07–2.74) and the summed ω_i was 97% (Table 3; Figure 6). Contrary to our prediction, distance to road was significantly negatively influenced the Ψ of the species and the model weight of the covariate was 78% ($\beta_{\mathrm{mean}} \pm \mathrm{SE} = -0.74 \pm 0.35$; 95% CI: −1.44, −0.05), suggesting that occupancy probability decreased as the distance to road increased in the pristine habitat (Table 3; Figure 6).

As depicted in the top models, the ability to detect Moorland Francolins was modeled as a function of survey occasion, precipitation, and temperature with summed model weight of 0.95, 0.92, and 0.70, respectively. The most important covariates supported by our hypotheses, however, included sampling occasion ($\beta_{\mathrm{mean}} \pm \mathrm{SE} = 0.68 \pm 0.23$, 95% CI: 0.23–1.13) and precipitation ($\beta_{\mathrm{mean}} \pm \mathrm{SE} = 0.75 \pm 0.36$, 95% CI: 0.05–1.45), both of which significantly positively influenced the detectability of the species (Table 3; Figure 6). Although the detectability of the species was increasing with temperature, the beta coefficient estimate ($\beta_{\mathrm{mean}} \pm \mathrm{SE} = 0.40 \pm 0.23$; 95% CI: −0.04 to 0.84) overlapped zero which exhibited a positive association but non-significant difference with habitat use of the species.

3.3 | Habitat use modeling for human-modified landscape

In the human-modified landscape, a total of 339 photos (2–29 photos per site) from 23 sites were trapped, yielding a naïve occupancy estimate of 0.48. The Ψ estimate without any covariate was 0.54 (SE = 0.08) with a 95% CI of 0.38–0.70 and ρ of 0.54 (SE = 0.06) with a 95% CI of 0.42–0.65. In this study area, based on the above considerations, the null model was included in the top important models with $\boldsymbol{\omega}_i = 0.95$ to explain the stochastic processes. The global model ($\psi(\mathrm{WD}+\mathrm{Hsp}+\mathrm{T}_{\mathrm{caco}}+\mathrm{Pre}+\mathrm{Elev}+\mathrm{DR}+\mathrm{DS}+\mathrm{DW}),\rho(\mathrm{E}+\mathrm{T}+\mathrm{P})$) showed no evidence of lack of fit ($\chi^2 = 118.13$; $p = .35$; $\hat{c} = 1.07$). The most parsimonious model ($\Psi(\mathrm{Sprich}+\mathrm{T}_{\mathrm{caco}}+\mathrm{DR}+\mathrm{DS}),\rho(.)$) had 0.07 model weight. Hence, all top models ($\Delta\mathrm{AIC}_c \leq 2.0$) were equally supported to influence habitat use modeling in the case of SEA-disturbed sites (Table 2; Table S2).

Model-averaged estimate of $\hat{\Psi}$ across all sites in SEA was 0.56 (SD = 0.19) and $\hat{\rho}$ was 0.48 (SD = 0.06). The overall occupancy was underestimated by approximately 17% when detection probability is not accounted for. Distance to settlement, tree canopy cover, herb species richness, distance to road, predator, and woody density appeared in the competing models to explain habitat use of the target species in this area. As predicted, distance to settlement ($\boldsymbol{\omega}_i = 0.76$; $\beta_{\mathrm{mean}} \pm \mathrm{SE} = 0.74 \pm 0.41$; 95% CI: −0.07 to 1.55) positively associated with habitat use of the species, yet its respective 95% CIs slightly overlapped zero. Other covariates also showed non-significant associations with occupancy of the species (Table 3).

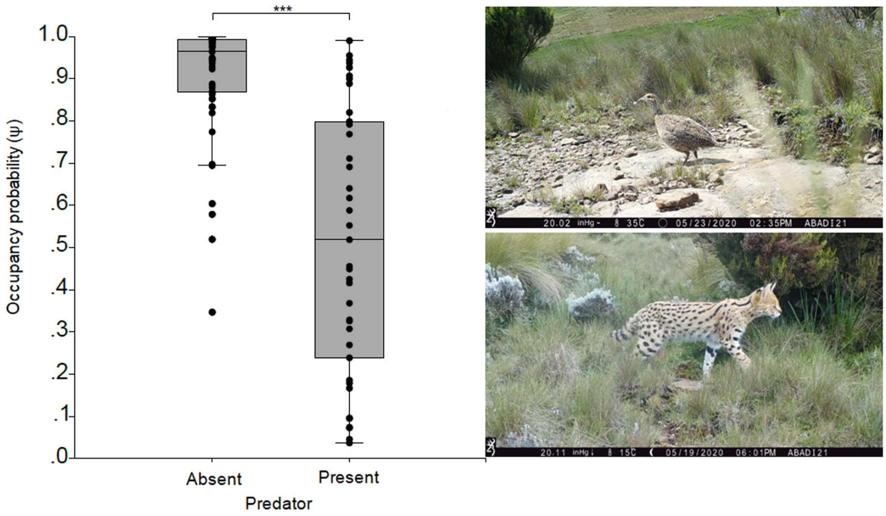

FIGURE 5 Occupancy probability of Moorland Francolin in association with predator presence/absence in GCCA. Cameras placed in woody plant species frequently had photos of predators like Serval *Leptailurus serval*. Error bars indicate standard errors of occupancy probability, ***$p < .001$.

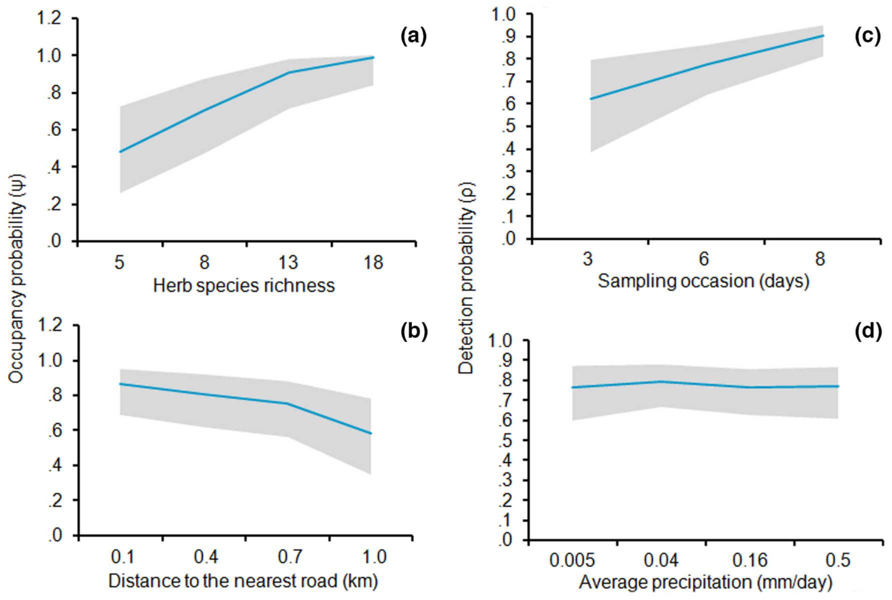

FIGURE 6 (a, b) Occupancy probability (ψ) of Moorland Francolin in association with herb species richness and distance to the nearest road (km) and (c, d) Detection probability (ρ) of the species in association with sampling occasion and average precipitation (mm/day), respectively. The estimates for the parameters are created from the most parsimonious model that holds these covariates and the shaded area in each graph shows 95% confidence intervals.

In this study area, detectability was more supported without covariates based on the top models. Thus, the sample covariates predicted to influence detectability had relatively low summed weight and 95% of CIs overlapped zero. In this disturbed habitat, detection probability was not significantly affected by sample covariates but all covariates depicted positive association with detectability. The summed model weight of each covariate was below 0.30 (Table 3).

3.4 | Recommended number of sampling occasions (K)

The sampling occasion (K) needed at GCCA was ranged from 1 to 3, this meaning that a single occasion (mean 0.86 and 1.14, respectively) was needed for a targeted confidence level of probabilities of 0.7 and 0.8 and two (mean 1.64) and three (mean 3.27) occasions sequentially were sufficient for 0.9 and 0.99 detection probabilities to estimate the true absence of the species at a given site. Similarly, we found that 2, 3, 4, and 7 occasions sequentially were needed at SEA.

4 | DISCUSSION

4.1 | Occupancy and detection probability estimates using camera trap

Our study delivers the first insights into the habitat use of Moorland Francolins using a camera trap approach. Camera traps for this elusive and cryptic species helped us to avoid false-positive detection, which also corroborates the respective assumption for the occupancy model. The overall or true occupancy estimates in both study areas were greater than the naïve occupancy (ψ) estimates when detection probability is accounted for. These suggest that models incorporate imperfect detections to discount underestimating of overall occupancy (Guillera-Arroita et al., 2014; MacKenzie et al., 2018). Since we had small sample sizes and low density of individuals in SEA, we increased the sampling by one more occasion to minimize the effect of false-negative detections of the target species. Increasing of sampling occasion helps to increase the precision and accuracy of detectability of species (MacKenzie & Royle, 2005; Moore et al., 2014).

In many tropical African countries, the protected areas are called "paper parks"-existing in name only as they poorly counter habitat and species loss (Dudley & Stolton, 1999). However, GCCA as a traditionally protected area is exceptional in this case as the indigenous knowledge for conservation of natural resources, the Qero system, has supported several wildlife species for almost four centuries (Ashenafi & Leader-Williams, 2005; Nigussie et al., 2019). Occupancy and detection probability estimates of Moorland Francolins were higher in traditionally protected areas than in unprotected areas, suggesting the persistent and high conservation effort supporting the Ethiopian Wolf (*Canis simensis*) by the local community in association with international organizations signifies the integrity and functionality of the whole community. Flagship species like this play a vital role in biodiversity conservation at local and global scales (Jarić et al., 2023), which is demonstrated by its positive side effects for Moorland Francolins and other species in GCCA, too. Unlike other carnivore species, this species is a rodent specialist (Ashenafi et al., 2012; Atickem & Stenseth, 2022; Vial et al., 2011).

4.2 | Determinants of occupancy and detection probabilities

Based on beta estimates and moderate model weight, Moorland Francolins revealed an aversion to montane forest habitat due to the presence of predators in the tree canopies. The Afroalpine highlands are suitable habitats for predators (Clouet et al., 2000), and habitat use of many ground-dwelling birds is negatively influenced by the presence of predators in and around the forest habitats (Abrha et al., 2018; Sukumal et al., 2017). In concordance with these findings, our results confirm that predators (both aerial and ground predators) may strongly negatively influence the habitat use of Moorland Francolins in GCCA, although the main diet of several raptors is rodents (Clouet et al., 2000).

Though hunting pressure is one of the key factors for decreasing francolin populations nationwide (Abrha et al., 2017; Gedeon, Rödder, et al., 2017; Töpfer et al., 2014) and globally (McGowan et al., 2012), this threat was only of minor importance to Moorland Francolins in GCCA. However, in both study areas, but essentially in SEA, hunters preferably target to capture Erckel's Francolin *Pternistis erckelii* that usually subsist in habitats below the tree line in GCCA (Demis & Tesfaye, pers. comm.), and sympatrically with Moorland Francolins in SEA. Hunting pressure apparently is much more pronounced on *P. erckelii* due to its larger size and because of the different perceptions by the local communities toward both highland francolins.

Herb species richness was also supported based on model weight and top models. The protected grassland of GCCA covers almost 60% of its total area (Steger et al., 2020) and holds several range-restricted species (Ashenafi et al., 2012; Ashenafi & Leader-Williams, 2005). As expected, the occupancy probability of Moorland Francolins increased with herb species richness in GCCA, in line with other reports on pheasant species (Jolli et al., 2012; Sukumal et al., 2017). This vegetation type is widespread in the plateau of Afroalpine biome of Ethiopia (Nigussie et al., 2019; Steger et al., 2020) and it is the source of food and provides essential shelter for many grassland specialists (Töpfer & Gedeon, 2020). It had also a positive influence on the habitat use of Moorland Francolins at SEA, but the 95% confidence interval of the β-coefficient estimate overlapped zero showing less support for its influence on the species. This is because the area has been increasingly transformed into a monocultural plantation (Bahru et al., 2021; Tadesse & Tafere, 2017), and is subject to tourism activities (Asefa, 2018; Tesema & Berhan, 2019), overgrazing and other human-induced disturbances in the plateau of central highlands (Asefa et al., 2020). For instance, a recent report showed that the natural grassland of Entoto Natural Park has decreased over the last three decades and that the area is now dominated by an *Eucalyptus* plantation (Tesema & Berhan, 2019). In such areas, Moorland Francolins showed a pronounced aversion toward modified habitat types. This implies that Afromontane grassland and shrubland specialists, especially Moorland Francolins might gradually become locally extinct.

Distance to road was also the other strongest covariate influencing the occupancy probability of Moorland Francolins, similar to other reports in ground-dwelling bird species (Whitworth et al., 2018). The occupancy probability of the species was higher along the edge of roadsides and trails than at sites located in remote in GCCA, in concordance with other reports on wildlife species (Kroeger et al., 2022; Paemelaere et al., 2023). This is unexpected because roads can attract hunters and predators, delivering also other human-induced perturbations (Dean et al., 2019; Kroeger et al., 2022). In GCCA, we observed that proximity to road attracts the species as there were food items mainly on the unpaved road, including grains and fruits thrown through window by passengers. Most roadsides have also dense native herbaceous vegetation, which may also help Moorland Francolins to survive. On the contrary, occupancy increased as the distance to road increased in SEA habitat but did not show a significant association with roads. This suggests that Moorland Francolins avoid roads and trails in a human-modified landscape. Thus, roads may have positive effects on bird species in more pristine habitats (Kroeger et al., 2022) and in areas where hunting pressure is controlled as a management strategy (Whitworth et al., 2018). Local low temperatures and high ground vegetation cover (Nigussie et al., 2019; Steger et al., 2020) may lead the species to use the roadsides and trails: (1) to enhance foraging opportunities; (2) to stay more vigilant to avoid risk of predation; (3) as a heat source; (4) to facilitate mating, connectivity and communication.

Avoidance of human settlements is likely related to livestock grazing causing herb species richness to shrink at the GCCA periphery (i.e., human occupation). Similarly, the effect of distance to settlement as a type of human disturbance posed a positive effect on Moorland Francolins in SEA. There was no significant difference for the covariate in this area, yet relatively high model-averaged beta coefficient estimate; model weight and confidence intervals reveal irregularity in association with the species, most presumably due to lack of habitat heterogeneity, a small sample size, limited number of cameras, and small sampling occasions, as compared to recommended occasions. Hence distance to settlement had a slightly significant positive influence on the species in SEA, agreeing with previous studies on pheasants (Chen et al., 2019; Jolli et al., 2012; Nuttall et al., 2017; O'Brien & Kinnaird, 2008), other bird (Pardo et al., 2017) and mammal species (Paemelaere et al., 2023; Semper-Pascual et al., 2020).

In line with our hypothesis, sampling occasion significantly positively influences the detectability of the species in GCCA. Conversely, in SEA, this covariate appeared in one of the most parsimonious models and it positively influenced detectability but it had low model weight and the beta coefficient estimates showed statistically non-significance association. The detectability may be affected by spatial variations and sample sizes. Our hypothesis that species detection increases with number of days of cameras deployed showed consistency with other findings in bird (Paemelaere et al., 2023; Si et al., 2014) and mammal species (Holzner et al., 2021; Semper-Pascual et al., 2020; Shannon et al., 2014; Si et al., 2014; Wevers et al., 2021). The magnitude of sampling occasion on detection probability estimate demonstrates species-specific response (Iannarilli et al., 2021).

In Ethiopia, after a long dry season, both a small and a main rain season occurs in most highland areas (Mohammed et al., 2022). Several francolin species are adapted to this seasonally changing precipitation regime (Abrha et al., 2018; Gedeon, Rödder, et al., 2017), which allows the areas to replenish food resources and ecosystem greenness vital for breeding (Abrha et al., 2018). This is because francolins may find plenty of food by easily raking and scratching the wet ground (Abrha et al., 2018). Moreover, during rain seasons, birds of prey soar less, and agro-pastoral encroachments seem lower compared to the dry season (pers. obs). Elsewhere in tropics, the breeding season of birds is reported to be associated with the beginning of precipitation and this is linked to the abundance in food and cover resources (Cox et al., 2013; França et al., 2020; Jansen & Crowe, 2005). In our species, some camera traps have documented chicks being fed by their parents in GCCA, and this implies that the breeding season of the species may coincide with the short and mild precipitation distribution from February to June. Similarly, temperature positively influenced the detectability of the species, but there was little support for our hypothesis based on models. This may suggest that the species avoids extreme temperatures. Collectively, climate factors are very important for the detectability of the target species in the central highlands of Ethiopia.

4.3 | Camera trapping for assessment of cryptic bird species

The Moorland Francolins, similar to other pheasants in the region, could potentially go visually undetected, particularly in areas of low population density and in disturbed habitats. Extreme weather conditions, seasonality, expert experience, and other factors may also obscure the ability of detecting the species. This is because the birds usually remain silent, hidden, and squatted when people approach them. Thus, false-negative detection could bias inferences about the occupancy and detection probability estimates and other parameters. However, the deployment of non-invasive modern approaches like remotely triggered camera traps can avoid such ecological concerns. This approach also helps to discover new geographical ranges, other wildlife species (including predators) and thereby helping to understand the interactions of the Moorland Francolins in its natural habitat. Another positive feature of the camera trapping technique is that it is cost and time-effective. Our results strongly support the deployment of camera traps for the detection of cryptic and little-known species in a topographically complex region. Camera traps provide reliable comprehension and precision of occupancy of Moorland Francolins in the Afroalpine Biome. Such camera trap data (O'Brien & Kinnaird, 2008; Sharief et al., 2022; Si et al., 2014; Steenweg et al., 2017; Wearn & Glover-Kapfer, 2017) ultimately promotes the proper conservation of the target species.

5 | CONCLUSIONS

The findings demonstrate that habitat use of Moorland Francolins is higher in the more pristine habitats compared to the strongly human-influenced in SEA. This suggests that a community-based conservation area (i.e., GCCA) is a crucial remnant habitat of endangered and data-deficient wildlife species in Ethiopia. Since such community-based conservation approaches obviously support sustainable species-habitat conservation, strengthening the existing Qero system and expanding the model to other potential hotspot sites and/or IBAs is strongly recommended to circumvent the mounting anthropogenic disturbances in the region (Asefa et al., 2017; Chengere et al., 2022; Razgour et al., 2021; Rodrigues et al., 2021).

Our results also show that the species uses various herb species, roadsides and trails for resting, hiding, survival, and reproduction. Conversely, predators threatened the francolins predominantly in native and plantation forests, thus Moorland Francolins tend to avoid tree canopy cover and human settlements in both study areas. In the human-modified SEA areas, most covariates had a weak influence on the occupancy and detection estimates of our target species because habitats are dominated by *Eucalyptus* plantations, fragmented meadow hill patches, and farmlands, unlike the heterogeneous and protected habitats in GCCA.

We confirm that camera trap deployment corroborates the presence or absence of shy ground-dwelling birds not only in known areas but also in understudied areas. The detectability of francolins was determined by the sampling occasion and precipitation. Further research using single or multi-season modeling is required to understand the influence of habitat covariates, seasonal colonization, and local extinction from spatiotemporally replicated surveys.

AUTHOR CONTRIBUTIONS

Abadi Mehari Abrha: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); project administration (equal); software (lead); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Kai Gedeon:** Conceptualization (equal); funding acquisition (equal); methodology (supporting); project administration (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (equal). **Lars Podsiadlowski:** Methodology (supporting); project administration (supporting); supervision (equal); writing – review and editing (equal). **Demis Mamo Weldesilasie:** Data curation (supporting); project administration (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Till Töpfer:** Conceptualization (equal); funding acquisition (equal); methodology (supporting); project administration (equal); supervision (equal); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Abrha, A. M., Nigus, H. K., Weldetnsae, B. G., Tilahun, M., Nigusse, A. G., & Deribew, K. T. (2017). Effects of human disturbances on two sympatric francolin species in the central highlands of Ethiopia. *Podoces*, *12*(1), 13–21.

Abrha, A. M., Zelelew, S. A., Nigus, H. K., & Alelign, A. (2018). Diurnal activity patterns of Harwood's spurfowl *Pternistis harwoodi* in relation to habitat types and climatic conditions in the central highlands of Ethiopia. *Ostrich*, *89*(2), 195–201.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management*, *74*(6), 1175–1178.

Asefa, A. (2018). Avifauna of Entoto Mountain Forest, Ethiopia: Diversity and potential for tourism development. *Journal of Science and Sustainable Development*, *6*(2), 16–28.

Asefa, A., Davies, A. B., McKechnie, A. E., Kinahan, A. A., & van Rensburg, B. J. (2017). Effects of anthropogenic disturbance on bird diversity in Ethiopian montane forests. *The Condor: Ornithological Applications*, *119*(3), 416–430.

Asefa, M., Cao, M., He, Y., Mekonnen, E., Song, X., & Yang, J. (2020). Ethiopian vegetation types, climate and topography. *Plant Diversity*, *42*(4), 302–311.

Ash, J., & Atkins, J. (2009). *Birds of Ethiopia and Eritrea: An atlas of distribution*. Bloomsbury Publishing.

Ashenafi, Z. T., & Leader-Williams, N. (2005). Indigenous common property resources management in the central highlands of Ethiopia. *Human Ecology*, *33*(4), 539–563.

Ashenafi, Z. T., Leader-Williams, N., & Coulson, T. (2012). Consequences of human land use for an afro-alpine ecological community in Ethiopia. *Conservation and Society*, *10*(3), 209–216.

Atickem, A., & Stenseth, N. C. (2022). The role of rodents in the conservation of endangered species in the Ethiopian highlands. *Therya*, *13*(1), 73–77.

Atikah, S. N., Yahya, M. S., Norhisham, A. R., Kamarudin, N., Sanusi, R., & Azhar, B. (2021). Effects of vegetation structure on avian biodiversity in a selectively logged hill dipterocarp forest. *Global Ecology and Conservation*, *28*, e01660.

Bahru, T., Kidane, B., & Tolessa, A. (2021). Prioritization and selection of high fuelwood producing plant species at Boset District, Central Ethiopia: An ethnobotanical approach. *Journal of Ethnobiology and Ethnomedicine*, *17*, 1–15.

Bailey, L. L., MacKenzie, D. I., & Nichols, J. D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution*, *5*(12), 1269–1279.

BirdLife International. (2004). *State of the world's birds 2004: Indicators for our changing world*. BirdLife International.

BirdLife International. (2023). Species factsheet: *Scleroptila psilolaema*. Downloaded from http://www.birdlife.org on 28/04/2023.

Bryja, J., Meheretu, Y., Šumbera, R., & Lavrenchenko, L. A. (2019). Annotated checklist, taxonomy and distribution of rodents in Ethiopia. *Folia Zoologica*, *68*(3), 117–213.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer-Verlag.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*, 23–35.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675–685.

Caravaggi, A., Burton, A. C., Clark, D. A., Fisher, J. T., Grass, A., Green, S., Hobaiter, C., Hofmeester, T. R., Kalan, A. K., Rabaiotti, D., & Rivet, D. (2020). A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conservation Science and Practice*, *2*(8), e239.

Chen, L., Shu, Z., Yao, W., Ma, Y., Xiao, W., & Huang, X. (2019). Combined effects of habitat and interspecific interaction define co-occurrence patterns of sympatric Galliformes. *Avian Research*, *10*(1), 1–13.

Chengere, S. A., Steger, C., Gebrehiwot, K., Nemomissa, S., & Dullo, B. W. (2022). Modeling cultural keystone species for the conservation of biocultural diversity in the Afroalpine. *Environments*, *9*(12), 156.

Clouet, M., Barrau, C., & Goar, J. L. (2000). The diurnal afro-alpine raptor community of the Ethiopian Balé highlands. *Ostrich*, *71*(3–4), 380–384.

Cordier, C. P., Smith, D. A. E., Smith, Y. E., & Downs, C. T. (2022). Camera trap research in Africa: A systematic review to show trends in wildlife monitoring and its value as a research tool. *Global Ecology and Conservation*, *e02326*, e02326.

Cox, D. T., Brandt, M. J., McGregor, R., Ottosson, U., Stevens, M. C., & Cresswell, W. (2013). The seasonality of breeding in savannah birds of West Africa assessed from brood patch and juvenile occurrence. *Journal of Ornithology*, *154*, 671–683.

Cremonesi, G., Bisi, F., Gaffi, L., Zaw, T., Naing, H., Moe, K., Aung, Z., Mazzamuto, M. V., Gagliardi, A., Wauters, L. A., Preatoni, D. G., & Martinoli, A. (2021). Camera trapping to assess status and composition of mammal communities in a biodiversity hotspot in Myanmar. *Animals*, *11*(3), 880.

Dean, W. R. J., Seymour, C. L., Joseph, G. S., & Foord, S. H. (2019). A review of the impacts of roads on wildlife in semi-arid regions. *Diversity*, *11*(5), 81.

Devarajan, K., Morelli, T. L., & Tenan, S. (2020). Multi-species occupancy models: Review, roadmap, and recommendations. *Ecography*, *43*(11), 1612–1624.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46.

Dudley, N., & Stolton, S. (1999). Conversion of paper parks to effective management: developing a target.

Esayas, K., & Bekele, A. (2011). Species composition, relative abundance and distribution of the avian fauna of Entoto Natural Park and escarpment, Addis Ababa. *SINET: Ethiopian Journal of Science*, *34*(2), 113–122.

Eshete, G., Tesfay, G., Bauer, H., Ashenafi, Z. T., de Iongh, H., & Marino, J. (2015). Community resource uses and Ethiopian wolf conservation in mount Abune Yosef. *Environmental Management*, *56*, 684–694.

Estifanos, T., Polyakov, M., Pandit, R., Hailu, A., & Burton, M. (2018). *Protection of the Ethiopian wolf: What are tourists willing to pay for?* Working paper 1803, Agricultural and Resource Economics, The University of Western Australia, Crawley, Australia.

Ferreguetti, Á. C., Tomás, W. M., & Bergallo, H. G. (2015). Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil. *Journal of Mammalogy*, *96*(6), 1245–1254.

Fishpool, L. D. C., & Evans, M. I. (2001). *Important bird areas of Africa and associated islands: Priority sites for conservation*. Pisces Publications/BirdLife International.

França, L. F., Figueiredo-Paixão, V. H., Duarte-Silva, T. A., & Santos, K. B. D. (2020). The effects of rainfall and arthropod abundance on breeding season of insectivorous birds, in a semi-arid neotropical environment. *Zoologia*, *37*, 1–7.

Friis, I., Demissew, S., & van Breugel, P. (2010). Atlas of the potential vegetation of Ethiopia. *Biologiske Skrifter*, *58*, 1–307.

Gedeon, K., Rödder, D., Zewdie, C., & Töpfer, T. (2017). Evaluating the conservation status of the black-fronted francolin *Pternistis atrifrons*. *Bird Conservation International*, *28*(4), 653–661.

Gedeon, K., Zewdie, C., & Töpfer, T. (2017). The birds (Aves) of Oromia, Ethiopia–an annotated checklist. *European Journal of Taxonomy*, *306*, 1–69.

Gelman, A., & Hill, J. (2007). *Data analysis using regression and hierarchical/multilevel models*. Cambridge University Press.

Gill, F., Donsker, D., & Rasmussen, P. (2023). IOC World Bird List (v 13.1). https://doi.org/10.14344/IOC.ML.13.1. http://www.worldbirdnames.org/

Gonsamo, A., Walter, J. M. N., & Pellikka, P. (2011). CIMES: A package of programs for determining canopy geometry and solar radiation regimes through hemispherical photographs. *Computers and Electronics in Agriculture*, *79*(2), 207–215.

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: Advances, challenges and opportunities. *Ecography*, *40*(2), 281–295.

Guillera-Arroita, G., & Lahoz-Monfort, J. J. (2012). Designing studies to detect differences in species occupancy: Power analysis under imperfect detection. *Methods in Ecology and Evolution*, *3*(5), 860–869.

Guillera-Arroita, G., Lahoz-Monfort, J. J., MacKenzie, D. I., Wintle, B. A., & McCarthy, M. A. (2014). Ignoring imperfect detection in biological surveys is dangerous: A response to 'fitting and interpreting occupancy models'. *PLoS ONE*, *9*(7), e99571.

Guillera-Arroita, G., Ridout, M. S., & Morgan, B. J. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, *1*(2), 131–139.

Hines, J. E. (2006). PRESENCE-software to estimate patch occupancy and related parameters. USGS-PWRC Available: http://www.mbr-pwrc.usgs.gov/software/presence.html

Holzner, A., Rayan, D. M., Moore, J., Tan, C. K. W., Clart, L., Kulik, L., Kühl, H., Ruppert, N., & Widdig, A. (2021). Occupancy of wild southern pig-tailed macaques in intact and degraded forests in peninsular Malaysia. *PeerJ*, *9*, e12462.

Iannarilli, F., Erb, J., Arnold, T. W., & Fieberg, J. R. (2021). Evaluating species-specific responses to camera-trap survey designs. *Wildlife Biology*, *2021*(1), 1–12.

Jansen, R., & Crowe, T. M. (2005). Relationship between breeding activity and rainfall for Swainson's spurfowl, *Pternistis swainsonii*, within southern Africa, with specific reference to the Springbok flats, Limpopo Province, South Africa. *Ostrich-Journal of African Ornithology*, *76*(3–4), 190–194.

Jarić, I., Normande, I. C., Arbieu, U., Courchamp, F., Crowley, S. L., Jeschke, J. M., Roll, U., Sherren, K., Thomas-Walters, L., Verissimo, D., & Ladle, R. J. (2023). Flagship individuals in biodiversity conservation. *Frontiers in Ecology and the Environment*. https://hal.science/hal-03935818v1/document

Jolli, V., Srivastav, A., & Thakur, S. (2012). Patch occupancy for cheer pheasant *Catreus wallichii* in the great Himalayan national park conservation area. *International Journal of Galliformes Conservation*, *2*, 74–81.

Kays, R., Arbogast, B. S., Baker-Whatton, M., Beirne, C., Boone, H. M., Bowler, M., Burneo, S. F., Cove, M. V., Ding, P., Espinosa, S., Gonçalves, A. L. S., Hansen, C. P., Jansen, P. A., Kolowski, J. M., Knowles, T. W., Lima, M. G. M., Millspaugh, J., McShea, W. J., Pacifici, K., … Spironello, W. R. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution*, *11*(6), 700–713.

Kéry, M., Gardner, B., & Monnerat, C. (2010). Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography*, *37*(10), 1851–1862.

Kroeger, S. B., Hanslin, H. M., Lennartsson, T., D'Amico, M., Kollmann, J., Fischer, C., Albertsen, E., & Speed, J. D. (2022). Impacts of roads on bird species richness: A meta-analysis considering road types, habitats and feeding guilds. *Science of the Total Environment*, *812*, 151478.

Lamelas-López, L., & Salgado, I. (2021). Applying camera traps to detect and monitor introduced mammals on oceanic islands. *Oryx*, *55*(2), 181–188.

Leroux, S. J. (2019). On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. *PLoS ONE*, *14*(2), e0206711.

MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, *9*, 300–318.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248–2255.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2018). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. Elsevier.

MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, *42*(6), 1105–1114.

Maffei, L., & Noss, A. J. (2008). How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. *Biotropica*, *40*(1), 71–75.

McGowan, P. J. K., Owens, L. L., & Grainger, M. J. (2012). Galliformes science and species extinctions: What we know and what we need to know. *Animal Biodiversity and Conservation*, *35*(2), 321–331.

McGrath, T., Guillera-Arroita, G., Lahoz-Monfort, J. J., Osborne, W., Hunter, D., & Sarre, S. D. (2015). Accounting for detectability when surveying for rare or declining reptiles: Turning rocks to find the grassland earless dragon in Australia. *Biological Conservation*, *182*, 53–62.

Meek, P. D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D. E., Tobler, M., & Townsend, S. (2014). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation*, *23*, 2321–2343.

Mittermeier, R. A., Robles-Gil, P., Hoffmann, M., Pilgrim, J. D., Brooks, T. B., Mittermeier, C. G., Lamoreux, J. L., & Fonseca, G. A. B. (2004). *Hotspots revisited: Earth's biologically richest and Most endangered ecoregions*. CEMEX.

Mohammed, J. A., Gashaw, T., Tefera, G. W., Dile, Y. T., Worqlul, A. W., & Addisu, S. (2022). Changes in observed rainfall and temperature extremes in the upper Blue Nile Basin of Ethiopia. *Weather and Climate Extremes*, *37*, 100468.

Moore, A. L., McCarthy, M. A., Parris, K. M., & Moore, J. L. (2014). The optimal number of surveys when detectability varies. *PLoS ONE*, *9*(12), e115345.

Niedballa, J., Sollmann, R., Mohamed, A. B., Bender, J., & Wilting, A. (2015). Defining habitat covariates in camera-trap based occupancy studies. *Scientific Reports*, *5*(1), 17041.

Nigussie, G., Fekadu, M., Demissew, S., & Warkineh, B. (2019). Impact of conservation management on land change: A case study in Guassa community conservation area for the last 31 years (1986–2015). *Modeling Earth Systems and Environment*, *5*, 1495–1504.

Nuttall, M., Nut, M., Ung, V., & O'Kelly, H. (2017). Abundance estimates for the endangered green peafowl *Pavo muticus* in Cambodia: Identification of a globally important site for conservation. *Bird Conservation International*, *27*, 127–139.

O'Brien, T. G., & Kinnaird, M. F. (2008). A picture is worth a thousand words: The application of camera trapping to the study of birds. *Bird Conservation International*, *18*(S1), S144–S162.

Ossendorf, G., Groos, A. R., Bromm, T., Tekelemariam, M. G., Glaser, B., Lesur, J., Schmidt, J., Akçar, N., Bekele, T., Beldados, A., Demissew, S., Kahsay, T. H., Nash, B. P., Nauss, T., Negash, A., Nemomissa, S., Veit, H., Vogelsang, R., Woldu, Z., … Miehe, G. (2019). Middle stone age foragers resided in high elevations of the glaciated Bale Mountains, Ethiopia. *Science*, *365*(6453), 583–587.

Paemelaere, E. A., Mejía, A., Quintero, S., Hallett, M., Li, F., Wilson, A., Barnabas, H., Albert, A., Li, R., Baird, L., Pereira, G., & Melville, J. (2023). The road towards wildlife friendlier infrastructure: Mitigation planning through landscape-level priority settings and species connectivity frameworks. *Environmental Impact Assessment Review*, *99*, 107010.

Pardo, L. E., Lafleur, L., Spinola, R. M., Saenz, J., & Cove, M. (2017). Camera traps provide valuable data to assess the occurrence of the great curassow *Crax rubra* in northeastern Costa Rica. *Neotropical Biodiversity*, *3*(1), 182–188.

Pellet, J., & Schmidt, B. R. (2005). Monitoring distributions using call surveys: Estimating site occupancy, detection probabilities and inferring absence. *Biological Conservation*, *123*(1), 27–35.

Razgour, O., Kasso, M., Santos, H., & Juste, J. (2021). Up in the air: Threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian highlands bat. *Evolutionary Applications*, *14*(3), 794–806.

Reber, D., Fekadu, M., Detsch, F., Vogelsang, R., Bekele, T., Nauss, T., & Miehe, G. (2018). High-altitude rock shelters and settlements in an African alpine ecosystem: The Bale Mountains national park, Ethiopia. *Human Ecology*, *46*(4), 587–600.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology*, *86*(10), 2805–2814.

Rodrigues, P., Dorresteijn, I., Guilherme, J. L., Hanspach, J., De Beenhouwer, M., Hylander, K., Bekele, B., Senbeta, F., Fischer, J., & Nimmo, D. (2021). Predicting the impacts of human population growth on forest mammals in the highlands of southwestern Ethiopia. *Biological Conservation*, *256*, 109046.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113.

Semper-Pascual, A., Decarre, J., Baumann, M., Camino, M., Di Blanco, Y., Gómez-Valencia, B., & Kuemmerle, T. (2020). Using occupancy models to assess the direct and indirect impacts of agricultural expansion on species' populations. *Biodiversity and Conservation*, *29*, 3669–3688.

Sewell, D., Beebee, T. J., & Griffiths, R. A. (2010). Optimising biodiversity assessments by volunteers: The application of occupancy modelling to large-scale amphibian surveys. *Biological Conservation*, *143*(9), 2102–2110.

Shannon, G., Lewis, J. S., & Gerber, B. D. (2014). Recommended survey designs for occupancy modelling using motion-activated cameras: Insights from empirical wildlife data. *PeerJ*, *2*, e532.

Sharief, A., Singh, H., Joshi, B. D., Singh, I., Mukherjee, T., Chandra, K., Thakur, M., & Sharma, L. K. (2022). Understanding distribution and occupancy of Himalayan monal in Uttarkashi district, Uttarakhand for conservation and management planning. *Wildlife Biology*, *2022*(2), e01013.

Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. *PeerJ*, *2*, e374.

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, *56*(4), 740–749.

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., Townsend, S. E., Carbone, C., Rowcliffe, J. M., Whittington, J., Brodie, J., Royle, J. A., Switalski, A., Clevenger, A. P., Heim, N., & Rich, L. N. (2017). Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, *15*(1), 26–34.

Steger, C., Nigussie, G., Alonzo, M., Warkineh, B., Van Den Hoek, J., Fekadu, M., Evangelista, P. H., & Klein, J. A. (2020). Knowledge coproduction improves understanding of environmental change in the Ethiopian highlands. *Ecology and Society*, *25*(2), 1–19. https://par.nsf.gov/servlets/purl/10167618

Sukumal, N., Dowell, S. D., & Savini, T. (2017). Micro-habitat selection and population recovery of the endangered Green peafowl *Pavo muticus* in western Thailand: Implications for conservation guidance. *Bird Conservation International*, *27*(3), 414–430.

Suwanrat, S., Ngoprasert, D., Sutherland, C., Suwanwaree, P., & Savini, T. (2015). Estimating density of secretive terrestrial birds (Siamese Fireback) in pristine and degraded forest using camera traps and distance sampling. *Global Ecology and Conservation*, *3*, 596–606.

Symonds, M. R., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*, 13–21.

Tadesse, S. A., & Tafere, S. M. (2017). Local people's knowledge on the adverse impacts and their attitudes towards growing *eucalyptus* woodlot in Gudo beret kebele, Basona Worena district, Ethiopia. *Ecological Processes*, *6*(1), 1–13.

Tanwar, K. S., Sadhu, A., & Jhala, Y. V. (2021). Camera trap placement for evaluating species richness, abundance, and activity. *Scientific Reports*, *11*(1), 23050.

Tefera, Z., & Sillero-Zubiri, C. (2006). A flagship species for Afroalpine conservation: An overview of the status and conservation of the Ethiopian wolf. *Walia*, *25*, 13–21.

Tesema, A. D., & Berhan, G. (2019). Assessment of biodiversity conservation in Entoto Natural Park, Ethiopia for ecotourism development. *Asian Journal of Ethnobiology*, *2*(1), 22–37.

Tichý, L. (2016). Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. *Journal of Vegetation Science*, *27*, 427–435.

Tilahun, S., Edwards, S., & Gebregziabher, T. (1996). *Important bird areas of Ethiopia: A first inventory*. Ethiopian Wildlife & Natural History Society.

Töpfer, T., & Gedeon, K. (2020). Alpine birds of Africa. *Encyclopedia of the World's Biomes*, *1*, 505–516.

Töpfer, T., Podsiadlowski, L., & Gedeon, K. (2014). Rediscovery of the black-fronted francolin *Pternistis (castaneicollis) atrifrons* (Conover, 1930)(Aves: Galliformes: Phasianidae) with notes on biology, taxonomy and conservation. *Vertebrate Zoology*, *64*(2), 261–271.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. *Ecological Applications*, *13*, 1790–1801.

Vial, F., Macdonald, D. W., & Haydon, D. T. (2011). Limits to exploitation: Dynamic food web models predict the impact of livestock grazing on Ethiopian wolves *Canis simensis* and their prey. *Journal of Applied Ecology*, *48*(2), 340–347.

Wearn, O. R., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: A guide to best-practices. *WWF Conservation Technology Series*, *1*(1), 181.

Wearn, O. R., & Glover-Kapfer, P. (2019). Snap happy: Camera traps are an effective sampling tool when compared with alternative methods. *Royal Society Open Science*, *6*(3), 181748.

Wevers, J., Beenaerts, N., Casaer, J., Zimmermann, F., Artois, T., & Fattebert, J. (2021). Modelling species distribution from camera trap by-catch using a scale-optimized occupancy approach. *Remote Sensing in Ecology and Conservation*, *7*(3), 534–549.

Whitworth, A., Beirne, C., Flatt, E., Pillco Huarcaya, R., Cruz Diaz, J. C., Forsyth, A., Molnár, P. K., & Vargas Soto, J. S. (2018). Secondary forest is utilized by great curassows (*Crax rubra*) and great Tinamous (*Tinamus major*) in the absence of hunting. *The Condor: Ornithological Applications*, *120*(4), 852–862.

Winarni, N. L., Carroll, J. P., & O'Brien, T. G. (2005). The application of camera traps to the study of Galliformes in southern Sumatra, Indonesia. In R. A. Fuller & S. J. Browne (Eds.), *Galliformes 2004: Proceedings of the 3rd international Galliformes symposium* (pp. 109–121). World Pheasant Association.

Zou, F., Zhang, Q., Zhang, M., Lee, M. B., Wang, X., Gong, Y., & Yang, C. (2019). Temporal patterns of three sympatric pheasant species in the Nanling Mountains: N-mixture modeling applied to detect abundance. *Avian Research*, *10*, 1–10.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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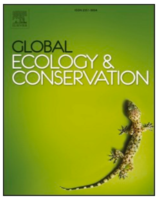

Dynamic occupancy modeling of a cryptic ground-dwelling pheasant species in the Upper Blue Nile Basin in Ethiopia

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ABSTRACT

Modeling the occupancy of species in the context of habitat components is a crucial step to deliver an appropriate conservation strategy. Accounting for imperfect detection in occupancy models helps to conclude on true species distribution and occupancy. We used dynamic occupancy modeling to investigate the influence of habitat covariates on occupancy dynamics of the Near Threatened Harwood's Francolin (*Pternistis harwoodi*) in the Upper Blue Nile Basin in Ethiopia. We used direct observation and playback technique to collect presence/absence data both during a wet and a dry season in 2019 and 2020. By accounting for species' imperfect detection, the model averaged estimates of occupancy probabilities (mean ± SE) across respective seasons were 0.81 ± 0.08 and 0.79 ± 0.07 and detection probabilities were 0.47 ± 0.08 and 0.62 ± 0.06. The colonization and local extinction probability estimates between seasons were 0.59 ± 0.20 and 0.12 ± 0.07, respectively. We demonstrate that occupancy probability significantly decreased with increasing both Normalized Difference Vegetation Index (NDVI: $\beta_{mean} \pm SE = -1.83 \pm 0.66$; 95% CI: −3.12, −0.54) and quadratic term of slope ($SL^2 = -1.51 \pm 0.62$; 95% CI: −2.73, −0.29) in the study area. Furthermore, human disturbance index (HDI: = −1.06 ± 0.54; 95% CI: −2.12, −0.004) significantly negatively influenced the occupancy of the species. As we hypothesized, the detection probability increased significantly as a function of average temperature (0.37 ± 0.13; 95% CI: 0.12, 0.63). There were no statistically significant associations among covariates and the dynamic parameters, yet important covariates such as NDVI slightly negatively influenced colonization, whereas HDI positively influenced local extinction. The aversion of the species towards human disturbance and its persistence at lower NDVI and lower slopes has important implications for conservation strategy in the area. The current study demonstrates empirical evidence of dynamic occupancy modeling for a cryptic ground-dwelling pheasant species in the Upper Blue Nile Basin. Further study is recommended to understand spatiotemporal species-habitat association at fine and landscape scales.

1. Introduction

Occupancy modeling of a species in the context of habitat components is critically important for successful conservation and management of ecological systems (Lahoz-Monfort et al., 2014; MacKenzie et al., 2018). The species-habitat associations and

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distributions are commonly modeled using species distribution models (SDMs) (e.g., Elith et al., 2006; Phillips et al., 2006; Elith and Leathwick, 2009). These models integrate occurrence or count data of species with habitat covariate (i.e., environmental covariate) data to make ecological inferences on species distribution (Elith et al., 2006; Elith et al., 2011). Nevertheless, most of these conventional SDMs use presence-background, true absence or pseudo-absence data without accounting for imperfect detection to predict species distributions (e.g., Guisan and Zimmermann, 2000; Elith et al., 2006; Elith et al., 2011). Such type of models generates biased estimates of true distribution of species as a function of habitat covariates (Kéry et al., 2010). The consideration of imperfect detection for species occupancy and distributions in ecological data is essential to create robust inferences (MacKenzie et al., 2003, 2018; Lahoz-Monfort et al., 2014; Guillera-Arroita et al., 2014; Guillera-Arroita, 2017).

Unlike conventional models such as the popular presence-only models, occupancy models are 'data hungry models' and perform better (Jha et al., 2022). Occupancy models need accurate and precise presence/absence data and environmental factors to produce sound conservation and management strategies for wildlife species (MacKenzie et al., 2002, 2018). These factors determine species-habitat associations (Kearney, 2006; Morrison et al., 2012) and are generally classified into resources, risks and conditions (Matthiopoulos et al., 2020). Among these factors, Normalized Difference Vegetation Index (NDVI) as a surrogate for vegetation or ecosystem greenness (Leveau et al., 2018; Green et al., 2019; Debela et al., 2021; Wu et al., 2021), topography (Burner et al., 2019; Campos-Cerqueira et al., 2021; Debela et al., 2021; Jean-Pierre et al., 2022), anthropogenic disturbances (Ramesh and Downs, 2014; McGowan et al., 2012; Abrha et al., 2017; Devarajan et al., 2020), disease (Bailey et al., 2014; Blanco et al., 2019; Chaudhary et al., 2020; Keesing and Ostfeld, 2021), climatic conditions (Debela et al., 2021; Jean-Pierre et al., 2022) and others affect species in spatiotemporal dynamics (Devarajan et al., 2020).

Harwood's Francolin (other name: Harwood's Spurfowl) *Pternistis harwoodi* is an endemic and Near Threatened pheasant species in Ethiopia (BirdLife International, 2018). In Ethiopia, most pheasants, especially francolins, are highly threatened bird species due to hunting and habitat loss (Töpfer et al., 2014; Abrha et al., 2017; Gedeon et al., 2017). Galliformes face multiple anthropogenic threats (Keane et al., 2005; McGowan et al., 2012; Tian et al., 2018) with hunting (Keane et al., 2005; McGowan et al., 2012), livestock grazing (Wang et al., 2021) and other habitat losses (Bagaria et al., 2021) and climate change (Zahoor et al., 2022; Liu et al., 2023) being the key menacing factors globally. For instance, around 66% of Galliform species are threatened by these synergetic effects (McGowan et al., 2012).

Harwood's Francolin was first discovered in 1899 at Ahiya Fej at south of Jama district in the central highlands of Ethiopia. The subsequent field expeditions that focused on identification of new localities for the species were conducted at Kalo Ford (Cheeseman

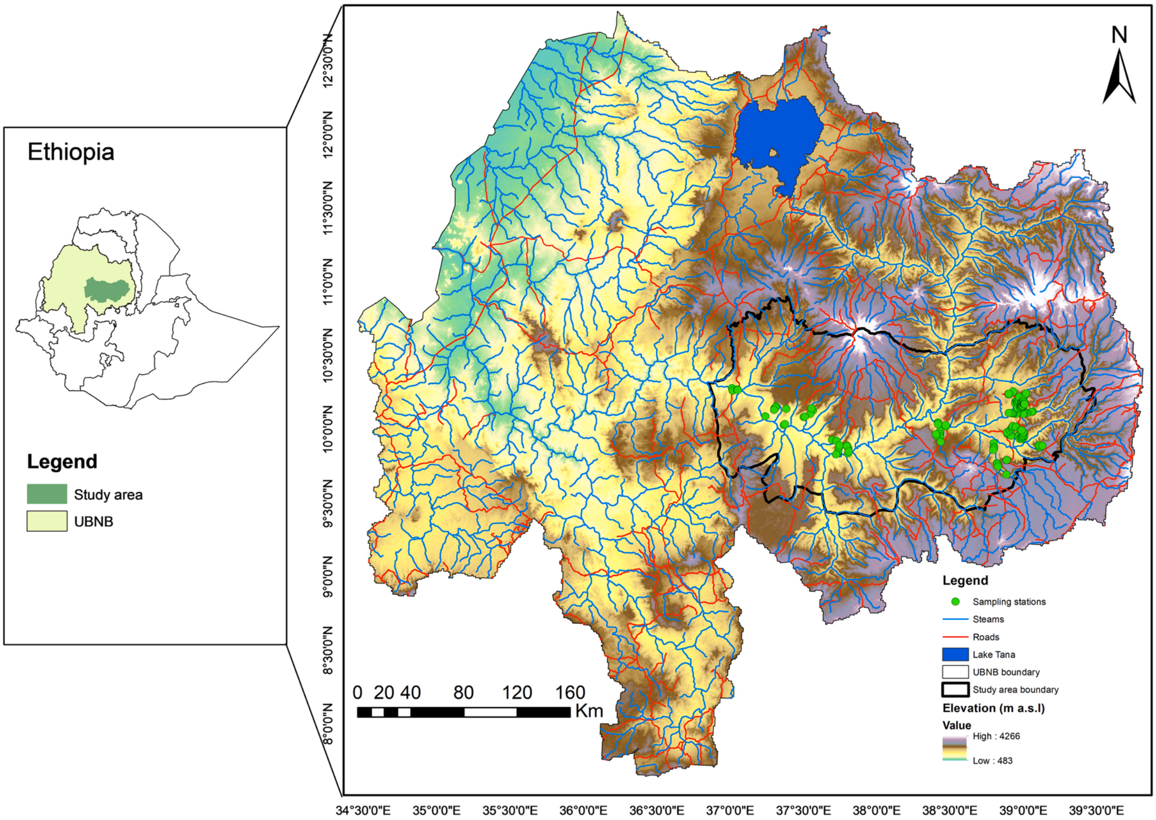

Fig. 1. Study area in the Upper Blue Nile Basin (UBNB) based on digital elevation model (DEM) (SRTM Global elevation data- https://earthexplorer.usgs.gov). All sampling stations (n = 144) are included in the map.

and Sclater, 1935; Urban et al., 1986), near Bichana, and Muger River sub-basins (Urban et al., 1986). The most recent study on the ecology of the species has been frequently reported from Jema and Jara sub-basins (Robertson et al., 1997; Ash and Atkins, 2009; Abrha and Nigus, 2017; Abrha et al., 2017, 2018). Most of these earlier studies were limited by time and research funds. There is scarcity of information about the mechanisms explaining distribution and spatiotemporal habitat use dynamics of Harwood's Francolins so far. Currently, the conservation status of the species is downlisted from 'Vulnerable' to 'Near Threatened' category on the IUCN Red List (BirdLife International, 2018); yet empirical evidence supported spacious geographical range and conservation action that has practically reduced the threats of the target species at site level are lacking. The species is one of the three endemic bird species that could be prioritized for future flagship conservation and management action plans in Ethiopia (Ash and Atkins, 2009).

Even though most studies on ground-dwelling birds of Africa are derived from static occupancy modeling (e.g., Ramesh and Downs, 2014; Maseko et al., 2017; Smith et al., 2017; Gumede et al., 2022; Abrha et al., 2023; Bitani et al., 2023), studies using dynamic occupancy modelling are lacking, in particular on habitat use of galliform species from Ethiopia. Here, we collected presence/absence data of Harwood's Francolins using a combination of techniques from two-season surveys which ranged from Mida Woremo to Amuru, Yaso and Bure districts in the Upper Blue Nile Basin (UBNB). We also collected some spatiotemporal sets of covariates from ground truthing (i.e., field surveyed) and remotely sensed levels in the area. Using dynamic (multi-season) occupancy modeling (MacKenzie et al., 2003), we modeled occupancy and associated parameters governing the processes of the system to draw inferences about occupancy dynamics of the target species in its native range. Therefore, the objective was to determine factors influencing probabilities of occupancy, seasonal colonization, local extinction and detection of the target species across large spatiotemporal scales in UBNB.

2. Methods

2.1. Study area

Ethiopia harbors two large blocks of highlands: the Western and Eastern highlands segmented by the East African Rift Valley. The study area is part of the Western highlands which stretches from Mida Woremo district in north Shewa zone of Amhara to the junction among Amuru, Yaso and Bure districts of Oromia, Benishangul-Gumuz and Amhara regions, respectively. The elevation of the study area ranges from 840 to 2520 m a.s.l (Fig. 1). The dominant habitat vegetation types (for simplicity habitat types) are *Combretum-Terminalia* woodland and wooded grasslands (CTW), Dry evergreen Afromontane forest and grassland complex (DAF), riparian vegetation (RV) and farmland mosaics (Friis et al., 2010). We also included mixed plantations (commonly different fruits and vegetables) scattered along the course of Jema, Wenchit and Jara Rivers as an additional habitat type in this study.

In UBNB, two Important Bird and Biodiversity Areas (hereafter IBAs) including the Mid-Abbay (Blue Nile) River Basin and Jema and Jara Valleys are designated particularly because of the occurrence of endemic species, including Harwood's Francolin (Tilahun et al., 1996; BirdLife International, 2023a). According to the biome classification of Fishpool and Evans (2001), the Mid-Abbay is part of the Sudan-Guinea Savanna biome, whereas Jema and Jara Valleys belongs to the Afrotropical Highlands biome. Multifaceted anthropogenic disturbances are common phenomena across the Ethiopia highlands (Nyssen et al., 2004), particularly in the habitat of the target species (Robertson et al., 1997; Abrha et al., 2017). Generally, the dominant land cover type of UBNB is farmland mosaics (Tekleab et al., 2013). The mean annual temperature of Jema and Jara Valleys and the Mid-Abbay IBAs is 18.61 °C (± 0.09 SE) and 20.34 °C (± 0.11 SE), and the mean annual precipitation is 3.45 mm (± 4.57 SD) and 5.36 mm (± 8.54 SD), respectively. The area is characterized by a high degree of rainfall variability, with the main rain season from June to September (Mohammed et al., 2022).

2.2. Sampling design

2.2.1. Presence/Absence data

Field surveys were conducted during two periods, reflecting a dry (26 October 2019 to 29 March 2020) and a wet season (26 August to 14 November 2020). We conducted direct observation approach (Buckland et al., 2004; Sutherland, 2006) to collect presence/absence data in UBNB. It is a valuable field approach for occupancy modeling studies, particularly for bird monitoring (Zamora-Marín et al., 2021; Zwerts et al., 2021). We also conducted indirect observations such as auditory detections with stimulus and molted feather occurrences. Including indirect methods helps to produce robust estimates of occupancy and associated parameters for cryptic, shy and rare species (MacKenzie et al., 2018; De Rosa et al., 2022; Goldman et al., 2023), such as Harwood's Francolin.

Sampling stations (hereafter stations) (Fig. 1) were selected randomly from predetermined line transects across five habitat types in UBNB. We had 61 line transects (average = 2.1 km ± 1.2 SD) and along these transects a total of 144 stations were allocated. Each station was a 50 m radius with a minimum distance of 0.7 km between them. The number of stations (i.e., effective sample size) allocated across habitats types were based on the standard design procedure (excluding survey cost) for multi-season occupancy study (MacKenzie and Royle, 2005; MacKenzie et al., 2018). Thus stations were selected according to proportion of each habitat size and habitat preferences of the Harwood's Francolins in UBNB (CTW = 42, DAF = 44, farmland = 32, plantations = 12 and RV = 14). The evergreen scrub vegetation habitat is part of DAF in this study (Friis et al., 2010). Four trained field observers participated and each observer assigned to visit new stations during the entire study to avoid potential observer effect. Data collections were mostly performed in the morning (6:00–10:00) and in the late afternoon (15:00–18:00) as the species exhibits optimum activity patterns in both time blocks (Abrha and Nigus, 2017; Abrha et al., 2018) and this could potentially help to minimize false negative detections. In each station, the observers spent 10-minute bouts to record presence/absence (i.e., detection/non-detection) of Harwood's Francolins.

The same stations were surveyed in both non-consecutive seasons. The distance between stations in the continuous habitat ranged from 0.7 to 3.0 km along transects to maintain independence among stations and minimize spatial autocorrelation. Sampling effort was between one to three repeated surveys with an average survey ($K_{average}$) of 1.95 and 2.56 in both seasons, respectively. Repeated surveys in each site were conducted in alternate order based on morning and late afternoon time blocks. Thus, data were collected in an interval of 4–7 days at each station. The total number of surveys (s stations surveyed K times) was 864. However, due to logistic and time constraints, adverse weather conditions, COVID and security reasons, we visited only 581 stations.

Because direct observation produces low data quality for cryptic and shy species (Zwerts et al., 2021), we used the playback technique (De Rosa et al., 2022) at some of the stations to ascertain the presence of elusive Harwood's Francolins. The target species could remain silent and go undetected due its behavior essentially in some low-density populations as well as highly disturbed habitat types. In such conditions, we applied a playback call using Sony speaker (Sony SRS-XB10 portable wireless speaker, Sony Electronics Inc.) immediately after having failed to observe visually. We confirmed that Harwood's Francolins are easily attracted by a playback call during a preliminary assessment survey in 2018 (Gedeon and Abrha, pers. obs). We conducted the survey with alternation of a 5 s playback call followed by 1 min of silence to aurally detect the target species. This call survey repeated for three times until the target species lured by the stimulus. The device was held at about 2 m high and rotated for 360° until the target species responded to the stimulus. We applied it carefully to lure the target species by minimizing unnecessary disturbance on the behavior of the species and the entire community. We did not perform playback when there was an obvious reaction towards our presence or an anti-predator behavior by congenerics, other bird and mammal species in the area. Playback was used during morning and late afternoon time block to match with the normal time for calling and the amplitude of the loudspeaker was adjusted to be low to medium depending on the proximity to the center of the station; medium amplitude was adjusted when observers were at the edge of the stations and there was no disturbance on the nearest station.

Ultimately, we combined direct and indirect observations to minimize false absence of the target species. Data were recorded as detection history of a sequence of binary spatial occupancy patterns (detection=1 and 0 otherwise).

2.2.2. Habitat covariates

We considered habitat covariates both at fine scale and landscape scale levels and climatic conditions. Because fine-scale data have limited spatiotemporal coverage and accessibility (Cisneros-Araujo et al., 2021), most of our covariates were accessed from remotely sensed data (Table 1). Our key interests to consider some covariates were mainly derived from previous studies on anthropogenic disturbances (Robertson et al., 1997; Abrha et al., 2017), activity patterns in the context of climate factors (Abrha et al., 2018), and habitat preferences (Abrha and Nigus, 2017) of the target species. We also incorporated ecologically significant climate covariates from previous studies on congeneric species in Ethiopia (Gedeon et al., 2017). Accordingly, six covariates were collected from each

Table 1

Description of habitat covariates influencing initial occupancy probability (ψ_1), colonization probability (γ), extinction probability (ε), and detection probability (ρ). Some empty cells in the table indicate that the value of coefficients (i.e., beta-β) was not checked for some parameters.

Covariate	Units	Description and source	Predicted effect on dependent variable				Hypotheses and references
			ψ_1	γ	ε	ρ	
NDVI	Dimensionless	Extracted for each station from Landsat 8 Operational Land Imager (OLI) / Thermal Infrared Sensor (TIRS) images. Downloaded from: https://earthexplorer.usgs.gov/	-	-	+	-	Ecosystem greenness influences the occurrence bird species (Leveau et al., 2018; Green et al., 2019; Debela et al., 2021; Wu et al., 2021). Harwood's Francolins prefer shrubs, herbs and sparse trees in and around farmlands (Abrha and Nigus, 2017) where food source are available.
Elevation	m	Extracted for each station from Digital Elevation Model (DEM) of Shuttle Radar and Topography Mission (SRTM-DEM). Downloaded from: https://earthexplorer.usgs.gov/	+	+	-		Elevation influences the occupancy of bird species (Burner et al., 2019; Campos-Cerqueira et al., 2021; Jean-Pierre et al., 2022). Harwood's Francolins' occupancy increases with elevation because increasing elevation may decrease human disturbance in most parts of the area.
Slope	Percent	See elevation	+	+	-		Topographic variables such as slope affect bird species (Debela et al., 2021). The target species avoids extremely steep and extremely slopes in various habitat types (Abrha and Nigus, 2017).
HDI	Dimensionless	The index of human disturbance across stations (i.e., at fine scale level)	-	-	+	-	Anthropogenic disturbances influence occupancy of bird species (Ramesh and Downs, 2014; Abrha et al., 2017; Devarajan et al., 2020).
Season	Julian date	The dry and wet seasons during data collection				+ /-	Seasons influence detectability of Harwood's Francolins due to seasonal variation in food availability.
Temperature	°C	Daily temperature extracted for each station from NASA/POWER) satellite-based weather system. Downloaded from: https://power.larc.nasa.gov/data-access-viewer/				+	Temperature and precipitation influence detectability of Harwood's Francolins (Abrha et al., 2018), since these factors affect reproductive success of bird species (Skagen and Adams, 2012; Mares et al., 2017). Hence, the odds of detecting the target species may increase.
Precipitation	mm	See temperature				+	

station to model occupancy, detection and dynamic parameters (i.e., colonization and extinction).

In our data sets, we used two remotely sensed spatiotemporal datasets (https://earthexplorer.usgs.gov/, accessed on 31 August 2022) including: 1) time-series Normalized Difference Vegetation Index (NDVI; per station at 30 m resolution and 16-day frequency) derived from Landsat 8 OLI/TIRS images (raster band 4 and 5) for the periods of 2019 and 2020. Thus, NDVI = (NIR-RED)/(NIR+RED), where NIR and RED imply near-infrared and red (visible) spectral reflectance, respectively (Kriegler et al., 1969); 2) Elevation and slope were derived from Digital Elevation Model (DEM) of Shuttle Radar and Topography Mission (SRTM-DEM) of 1 arc-second for global coverage (~30 m resolution). We downloaded NDVI by minimizing the aerosols and cloud cover noises. Even though elevation was recorded from ground truthing data using handheld Global Positioning System (GPS, with accuracy ~ ± 3 m, Garmin eTrex 30), we ultimately took it from the STRM-DEM data for consistency purpose. All remotely sensed data were derived for each station and the satellite-based vegetation index (i.e., NDVI) was extracted for both seasons. The average NDVI for each station was computed. We calculated all these habitat covariates in QGIS (version 3.26.1) software (http://www.qgis.org/). Enhanced Vegetation Index (EVI) may be preferred over NDVI (Qiu et al., 2018) due to its capability to enhance vegetation monitoring and considers adjustments to reduce the effect of soil and atmospheric noises (Huete et al., 1997; Tuanmu and Jetz, 2015), yet it is not encouraged to apply it in topographically complex area (Matsushita et al., 2007), like Ethiopian Highlands. NDVI has been extensively used in Ethiopia as a surrogate for aboveground net primary productivity or ecosystem greenness (Muir et al., 2021) and forage availability (Worku et al., 2023), particularly for UBNB (Merga et al., 2022; Moisa et al., 2022). Elevation, slope and average temperature (hereafter temperature) covariates were also in quadratic terms to test the nonlinear influence on occupancy and dynamic parameters.

Following the procedure of Abrha et al. (2017) on the same species, the average human disturbance index (HDI) was determined from each station. HDI covariate was measured after the detection/non-detection data was completed in each station, as this field activity could hamper species detection and impose unnecessary disturbance. The type of human disturbances were classified as: 1) vegetation influence based on local people (VIP) which included cutting, debarking, mowing and thatching; 2) vegetation influence based on livestock grazing pressure (LG); 3) vegetation influence based on fire introduction (VIF) for charcoal preparation, farming activities and honey production and 4) hunting practices (HP). In this study, other minimal anthropogenic disturbances (Abrha et al., 2017) and natural predation effects were not measured due to logistical constraints. Some of these threats were also site-specific in the basin. The HDI covariate of each station was calculated as:

$$HDI = VIP \times 0.4 + LG \times 0.3 + HP \times 0.25 + VIF \times 0.15 \tag{1}$$

The extent of disturbance weight for each disturbance class was assigned based on the previous research findings in the Jema Valley sub-basin (Abrha et al., 2017). We followed the protocol of Barber-Meyer et al. (2013) for quantifying and assigning of HDI weight for dynamic occupancy modeling of Harwood's Francolins.

We obtained remotely-sensed climatic data such as temperature and precipitation from National Aeronautics and Space Administration/Prediction of World Wide Energy Resources (NASA/POWER) satellite-based weather system (https://power.larc.nasa.gov/data-access-viewer/, accessed on 27 August 2022). Because meteorological stations were absent near to the stations, with exception close to Gohatsion (Mohammed et al., 2022), we preferred remotely sensed data. Both data were extracted based on daily average values exactly corresponding to the Julian day of repeated surveys in each station. We lacked ground truthing climatic data and there was no literature related to our focus in Ethiopia to perform bias correction for our data.

We modeled initial occupancy probability (ψ_1) as a function of site-specific covariates including NDVI, slope, elevation, and HDI and the quadratic terms of both topographic covariates. Detection probability (ρ) was modeled as a function of sample covariates such as temperature and its quadratic term, precipitation and season. In addition, detection probability was modeled as a function of NDVI and HDI. Here, seasonal variation in ecosystem or vegetation greenness (i.e., NDVI) and HDI were also hypothesized to influence the detectability of Harwood's Francolins. Accordingly, we tested the influence of covariates on occupancy, detection, local colonization and extinction parameters (Table 1).

2.3. Data analyses

The dynamic occupancy modeling was performed using the program PRESENCE 12.38 (Hines, 2006). The modeling (MacKenzie et al., 2003) was used to determine the effect of habitat covariates on each parameter estimate (ψ_1, γ, ε, and ρ) of Harwood's Francolins. This modeling approach explicitly integrates changes in occupancy rate of a site over time with dynamic parameters: colonization and local extinction probabilities. The colonization probability (γ) is defined as that an unoccupied station in season t is occupied by the species in season $t + 1$; and extinction (ε) is defined as the probability that a station occupied in season t is unoccupied by the species in season $t + 1$ (MacKenzie et al., 2003, 2018). The assumptions of this modeling approach (MacKenzie et al., 2003, 2018) are: 1) No unmodeled heterogeneity in all parameters; 2) Occupancy state is static within a season; 3) Independence of detection of species and detection history in each station and 4) Absence of false positive detections.

Prior to analyses, all continuous covariate data were normalized to increase the software performance. We used Pearson's correlation coefficients (r) and variance inflation factor (VIF) to assess for multicollinearity between independent covariates in IBM SPSS statistics (version 20) (Table S1). All covariates did not show strong correlation ($r < 0.7$) (Dormann et al., 2013). Because the VIF values were less than three, there were no confounding effects between independent covariates. Hence, all covariates were retained for the subsequent competing model sets. Then, based on previous ecological studies on francolin species (Robertson et al., 1997; Abrha and Nigus, 2017; Abrha et al., 2017; Gedeon et al., 2017; Abrha et al., 2018), we tested combinations of habitat covariates effect on each parameter. The null model ($\psi_1(.),\gamma(.),\varepsilon(.),\rho(.)$) was also analyzed for comparison in the candidate sets.

The ratio of effective sample size (n) to the number of parameters (K) (i.e., n/K) was determined. Then we used Akaike's information criteria corrected for small sample sizes (AIC_c) as $n/K \leq 40$ (Burnham and Anderson, 2002). This procedure helped for model selection by producing competing modeling with combinations of covariates of interest in the order of parsimony and cumulative model weight of each covariate (Burnham and Anderson, 2002). We built a total of 33 models depending on biological and ecological hypotheses about habitat preference, threat, and behavior of Harwood's Francolins. Because most candidate models revealed similar level of support, our models did not show "better" representation of the data (MacKenzie et al., 2018). Meanwhile, we incorporated competing models constituted from the top to the bottom, i.e., continuing the list until the cumulative Akaike Weight (ωi) of all models was at least 0.95 (Symonds and Moussalli, 2011). The level of significance was based on 95% CI (zero-overlapping method) and beta (β) coefficient estimates were used to understand the magnitude and effect of covariates on initial occupancy, colonization, local extinction and detectability. We also checked the presence of uninformative parameters using information criterion (IC) in the candidate model sets (Arnold, 2010; Leroux, 2019). Finally, model averaging approach was employed to calculate averaged β coefficient estimates ($\beta_{mean} \pm SE$) (Burnham and Anderson, 2002; Symonds and Moussalli, 2011).

2.4. *Research ethics clearance*

This part of AMA's PhD work was permitted by Ethiopian Wildlife Conservation Authority (EWCA) in Amhara (Ref. N̲o̲: 31/74/12), Oromia (Ref. N̲o̲: 31/79/12) and Benishangul-Gumuz (Ref. N̲o̲: 31/70/12) national regional states.

3. Results

3.1. *Spatiotemporal patterns in occupancy and dynamic parameters*

Harwood's Francolins were detected at 71 and 93 stations throughout the three sampling efforts in the first and second seasons, respectively. This yielded naïve occupancy estimates of 0.49 and 0.65 without correcting for imperfect detection. Based on the null model $((\psi_1(.),\gamma(.),\varepsilon(.),\rho(.))$, initial occupancy, detection, colonization, and extinction probability estimates were 0.76 (95%: 0.64–0.86), 0.58 (95%: 0.52–0.63), 0.50 (95% 0.25–0.75), and 0.12 (0.04–0.28), respectively (Table S2). By accounting for imperfect detection, the average estimates of initial occupancy across seasons were greater than the naïve occupancy. Following the inclusion of covariates in the models, the estimates of initial occupancy across habitat types were similar across habitats, except for plantations. The detection probability was similar across the habitats. The colonization estimates were similar in most habitat types but was lower in plantations. The local extinction estimates were similar in most habitats but slightly greater in plantation habitat (Fig. 2).

The averaged estimates of occupancy probability ($\widehat{\psi}$) Harwood's Francolins across seasons were 0.81 ± 0.08 and 0.79 ± 0.07, respectively and averaged detection probability ($\widehat{\rho}$) estimates were 0.47 ± 0.07 and 0.62 ± 0.06, respectively. The average detectability increased by 32% from 0.47 in 2019–0.62 in 2020 (Fig. 3A). The seasonal colonization and local extinction probability estimates during study seasons were 0.59 ± 0.20 and 0.12 ± 0.07, respectively (Fig. 3B).

The null model was not included among the top candidate sets. In the top-ranked models HDI, NDVI, slope and its quadratic term, temperature and the effect of seasons were incorporated. These competing models were largely built without interactions (except for quadratic fit of elevation, slope and temperature) to model underlying dynamic processes and are ranked in the order of the lowest ΔAIC_c. The cumulative weight ($\Sigma\omega_i$) of the top-ranked models ($\Delta AIC_c \leq 2.0$) were 0.53 and the first ranked model $(\psi_1(HDI+NDVI+SL+SL^2),\gamma(NDVI),\varepsilon(.),\rho(S+T))$ received 0.11 model weight separately which reasonably imply the presence of other

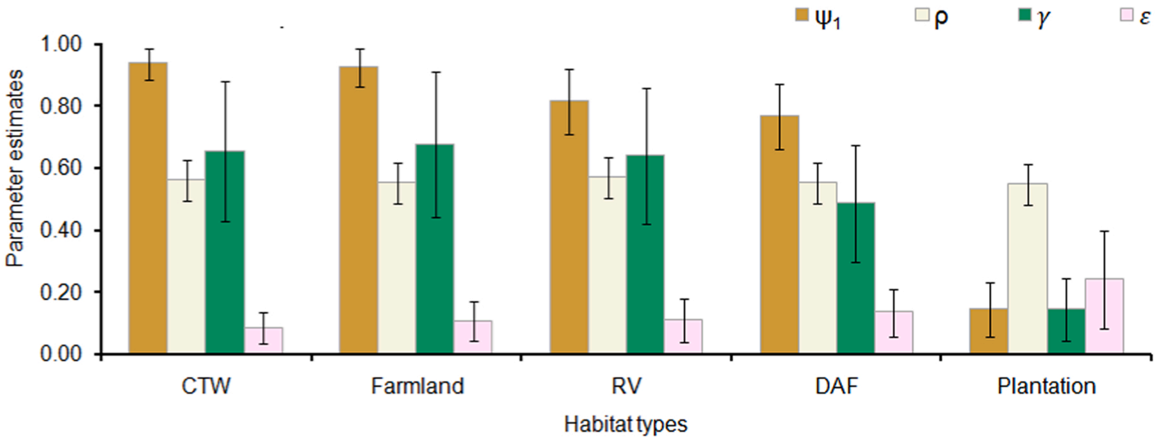

Fig. 2. Average estimates of initial occupancy probability (ψ_1), detection probability (ρ), colonization probability (γ) and extinction probability (ε) across different habitat types in the Upper Blue Nile Basin (estimation calculated from models with $\Delta AIC_c < 4.00$). Error values are standard errors. Abbreviations: CTW-*Combretum-Terminalia* woodland and wooded grasslands; DAF-Dry evergreen Afromontane forest and grassland complex and RV-riparian vegetation.

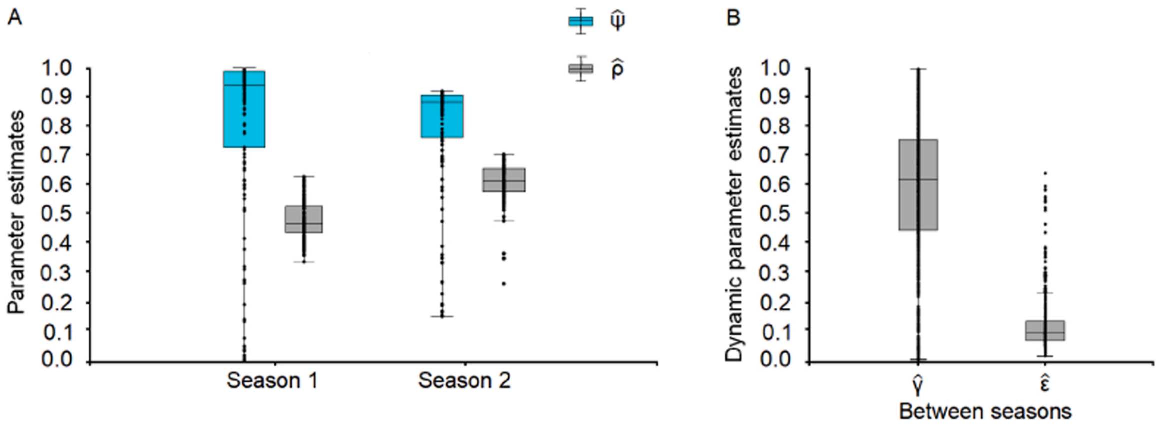

Fig. 3. Model averaged estimates of occupancy probability ($\widehat{\psi}$) and detection probability ($\widehat{\rho}$) (A) across seasons and dynamic parameters ($\widehat{\gamma}$-colonization and $\widehat{\varepsilon}$-extinction) (B) between seasons. Estimations were calculated from top models with $\Delta AIC_c < 4.00$.

competing models to draw inferences about the occupancy and underlying dynamic processes (Table 2). In other words, our competing models showed model selection uncertainty and hence weak support for the *a priori* hypotheses. Therefore, to improve the representation of our data, we applied model averaging, which contained all competing models with $\Delta AIC_c < 4.00$ to produce strongest statistical inferences following the recommendation of Symonds and Moussalli (2011). Moreover, the model weight (ω_i) of covariates appeared in the top-ranked models were increased by removing other models with ΔAIC_c less than six (Richards, 2005; Richards et al., 2011).

3.2. *Influence of habitat covariates on Harwood's Francolins*

As we hypothesized, NDVI correlated significantly negatively with the initial occupancy probability of Harwood's Francolins at the stations in UBNB ($\beta_{mean} \pm SE = 1.83 \pm 0.66$; 95% CI: 3.12,0.54). Thus, the occupancy probability estimates decreased by 76% with increasing NDVI. The habitat use of the target species was also decreased with increasing quadratic slope, suggesting that the species revealed avoidance towards steep and extremely steep slopes ($\beta_{mean} \pm SE = 1.51 \pm 0.62$; 95% CI: 2.73,0.29). We also observed that the occupancy probability decreased by 47% across the quadratic slope gradient. The occupancy probability of Harwood's Francolins significantly decreased with increasing HDI ($\beta_{mean} \pm SE = 1.06 \pm 0.54$; 95% CI: 2.12,0.004) and was decreased by 17% across HDI gradient (Table 3, Fig. 4).

As expected, temperature was significantly positively correlated with the detectability of Harwood's Francolins across stations and it was increased by 64% ($\beta_{mean} \pm SE = 0.37 \pm 0.13$; 95% CI: 0.12, 0.63) (Table 3, Fig. 4). We found a positive association between season and detectability and there was also a negative association between vegetation greenness and detectability, albeit non-significant values among them (Table 3). The colonization probability was associated negatively with NDVI, but 95% CI overlapped zero ($\beta_{mean} \pm SE = 1.39 \pm 1.00$; 95% CI: 3.34, 0.56). The local extinction probability was positively correlated with human disturbance index and NDVI, but found no statistical support (Table 3).

Our models also show that elevation and its quadratic effect had generally negligible influence on occupancy and related

Table 2
Model selection with covariates for dynamic occupancy analysis. Model rankings are based on the Akaike information criterion (AIC) corrected for small sample size (AIC_c) values and only candidate models with $\Delta AIC_c < 2.00$ and null model are reported. Model weight (ω_i), number of parameters (K), and twice of the negative log-likelihood (−2 l) are reported.

Model	AIC_c	ΔAIC_c	ω_i	K	-2 l
ψ_1(HDI+NDVI+SL+SL^2), γ(NDVI), ε(.),ρ(S+T)	727.85	0.00	0.11	15	694.10
ψ_1(HDI+NDVI+SL+SL^2), γ(NDVI), ε(.),ρ(NDVI+S+T)	728.42	0.57	0.08	16	692.14
ψ_1(HDI+NDVI+SL+SL^2), γ(NDVI), ε(NDVI),ρ(S+T)	728.75	0.90	0.07	16	692.47
ψ_1(HDI+NDVI+SL+SL^2), γ(NDVI), ε(.),ρ(HDI+S+T)	728.90	1.05	0.06	16	692.62
ψ_1(HDI+NDVI+SL+SL^2), γ(.),ε(.),ρ(NDVI+S+T)	729.05	1.20	0.06	15	695.30
ψ_1(HDI+NDVI+SL+SL^2), γ(.),ε(.),ρ(S+T)	729.35	1.50	0.05	14	698.09
ψ_1(HDI+NDVI+SL+SL^2), γ(NDVI), ε(HDI),ρ(NDVI+S+T)	729.46	1.61	0.05	17	690.60
ψ_1(HDI+NDVI+SL^2), γ(NDVI), ε(.),ρ(S+T)	729.51	1.66	0.05	14	698.25
…					
ψ_1(.),γ(.),ε(.),ρ (.)	772.65	44.80	0.00	4	764.36

Abbreviations: ψ_1(psi) = initial occupancy probability, γ = colonization probability, ε = extinction probability, and ρ = detection probability, HDI = human disturbance index, NDVI = Normalized Difference Vegetation Index, SL= slope, SL^2 = quadratic term of slope, S = season and T = temperature.

Table 3
Cumulative model weight ($\Sigma\omega_i$) and influence of covariates calculated from the model-averaged beta coefficient estimates and standard errors (β_{mean} ± SE). β estimates values are shown 95% confidence intervals and p values. Zero overlapping shows non-significant values. Only fixed influences are included.

Covariate	$\Sigma\omega_i$	β_{mean} ± SE	95% CIs Lower	Upper	P value
Occupancy (Ψ_1)					
Normalized Difference Vegetation Index	**1.00**	**-1.83 ± 0.66**	**-3.12**	**-0.54**	**0.0056**
Quadratic Slope	**1.00**	**-1.51 ± 0.62**	**-2.73**	**-0.29**	**0.0148**
Human disturbance index	**0.96**	**-1.06 ± 0.54**	**-2.12**	**-0.004**	**0.0484**
Slope	0.88	0.94 ± 0.52	-0.08	1.96	0.0831
Colonization (γ)					
Normalized Difference Vegetation Index	0.62	-1.39 ± 1.00	-3.34	0.56	0.1652
Extinction (ε)					
Human disturbance index	0.15	0.50 ± 0.44	-0.36	1.35	0.2587
Normalized Difference Vegetation Index	0.10	0.86 ± 0.63	-0.38	2.10	0.1731
Detection (ρ)					
Season (pooled)	1.00	0.19 ± 0.27	-0.34	0.73	0.4914
Temperature	**1.00**	**0.37 ± 0.13**	**0.12**	**0.63**	**0.0045**
Normalized Difference Vegetation Index	0.38	-0.24 ± 0.16	-0.55	0.07	0.1338

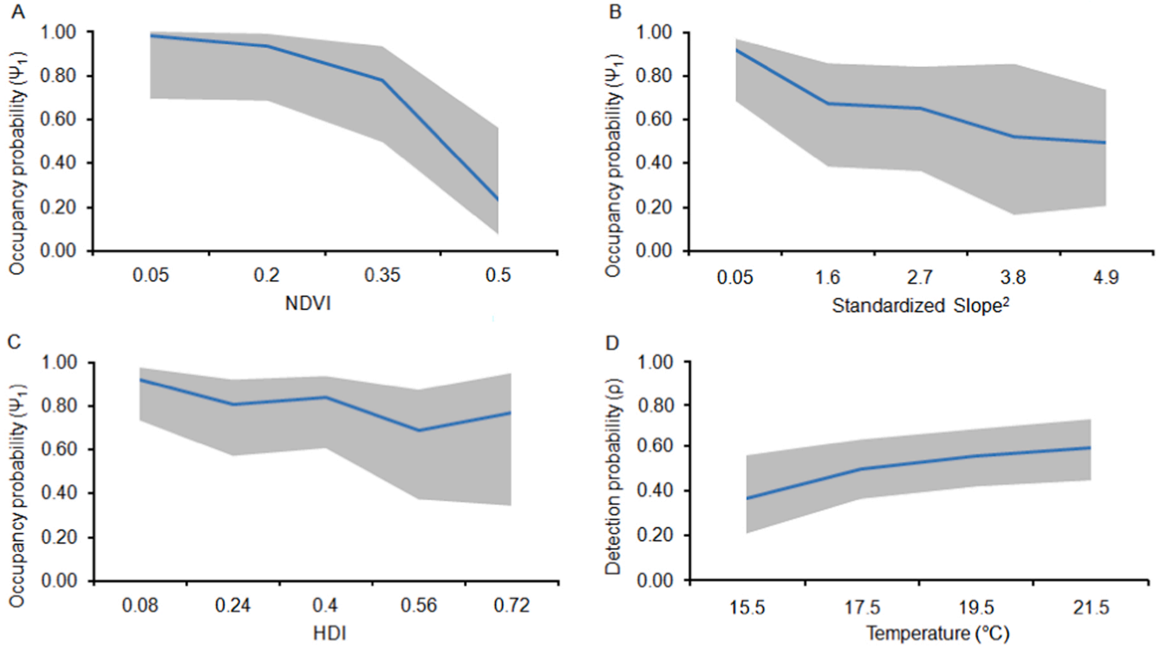

Fig. 4. Model averaged estimates of initial occupancy (ψ_1) and detection (ρ) probabilities for Harwood's Francolins. The left column (A and C) and right column (B) indicate the influence of NDVI, quadratic term of standardized slope and HDI on initial occupancy probability (ψ_1), respectively. The bottom right (D) indicates the influence of temperature (°C) on detection probability (ρ) of the species in UBNB. Parameter estimates were derived from the top-ranked models and the shaded area in each graph indicates 95% confidence intervals.

parameters. Similarly, precipitation and quadratic temperature had insignificant influence on the detectability of Harwood's Francolins during our study seasons. Quadratic slope did not seem to be important covariate to affect the dynamic parameters. From the model averaged estimate perspective, we also showed occupancy and detection probability patterns as a function of significant covariates across stations (Fig. S1).

4. Discussion

4.1. Dynamic occupancy patterns of Harwood's Francolin

The dynamic occupancy modeling is applied for the first time in Ethiopia (see also Devarajan et al., 2020) to study habitat use and distribution of Harwood's Francolins across a huge geographical scale in the Upper Blue Nile Basin (UBNB). In this study, we also incorporated previously poorly documented populations from west of the Mid-Abbay IBA dominated by *Combretum-Terminalia* woodland and wooded grasslands (CTW) in the Sudan-Guinea savanna biome. The nearest and the only locality recorded (*c*.140 km) to our new stations was found at Kalo Ford by Cheesman and Sclater (1935) and recently confirmed by Ash and Atkins (2009), which is near to the junction between Muger and Abbay River. Our results show that the target species essentially uses a mosaic of habitats across several sub-basins, comprising a larger geographic scale than previously known (Ash and Gullick, 1989; Robertson et al., 1997; Abrha and Nigus, 2017; Abrha et al., 2017). Most of our localities for this species also supported the exhaustive field survey of Ash and Atkins (2009).

By pooling seasons, the averaged detection probability of Harwood's Francolins (0.55 ± 0.07 SE) was more than doubled in occupancy modeling than reported using conventional distance sampling (CDS) method from Jema Valley in the Afrotropical Highlands biome (Abrha and Nigus, 2017). This suggests that occupancy modeling delivers more reliable estimations for this restricted range species than other method which do not explicitly account for imperfect detection, in concordance with other reports across different taxa (Kéry et al., 2010; Thapa and Kelly, 2017; Taylor et al., 2021).

Dynamic occupancy modeling also demonstrated to model explicitly colonization and extinction probabilities of Harwood's Francolins with and without covariates. Even though colonization probability was greater than extinction probability (Fig. 3B), the overall level of occupancy of Harwood's Francolins was decreasing between seasons. This is because the estimated net probability of extinction was larger than the estimated net probability of colonization depending on the inference of population trajectory (MacKenzie et al., 2018). The highest extinction probability at plantations was not surprising because this habitat is highly disturbed due to human activities (including hunting, cutting, burning, etc.) and livestock grazing (Abrha et al., 2017). Natural predation, which is a known threat for ground-dwelling pheasants (Little and Crowe, 2004), could also be a possible cause for local extinction of Harwood's Francolins. Our results also revealed that extinction probability was positively associated with both HDI and NDVI (Table S1).

Drawing inference from a two-season dataset could yield erroneous parameter estimates, yet our preliminary study showed important findings for occupancy and the dynamic parameters of Harwood's Francolins. Interestingly, the employed field techniques enabled to scrutinize about the mechanisms that drive the spatiotemporal occupancy patterns and dynamics of the target species across two contiguous biomes in UBNB. Similarly, it has been reported that using combined methods generate effective parameter estimates and facilitates appropriate bird conservation plans and recommendation for future studies (De Almeida-Rocha et al., 2019; Zamora-Marín et al., 2021; Zwerts et al., 2021).

4.2. *Influence of covariates on habitat use of Harwood's Francolins*

Bird species occupancy is influenced by finer-scale and landscape scale covariates (e.g., Harms et al., 2017; Smith et al., 2017; Green et al., 2019; Morante-Filho et al., 2021; Gumede et al., 2022), particularly for galliform species (Ramesh and Downs, 2014; Maseko et al., 2017; Abrha et al., 2023; Bitani et al., 2023). Our results showed that NDVI significantly negatively affected the occupancy of Harwood's Francolins (Fig. 4A). NDVI shows seasonal phenological dynamics in UBNB (Muir et al., 2021; Moisa et al., 2022). The average NDVI derived from wet and dry season data ranged from 0.05 to 0.45 (mean = 0.22; SD = 0.1), implying that stations were dominated by herbaceous and sparse vegetation. The lowest occupancy probability was recorded in plantations habitats along the course of tributary rivers which had highest spectral reflectance of vegetation. Therefore, occupancy probability decreased with increasing NDVI, meaning that Harwood's Francolins preferred low vegetation or sparse trees, evergreen scrub vegetation and herbaceous dominated habitats in CTW and its transformed habitat to farmland mosaics, in concordance with previous results on the ecology of the target species (Abrha and Nigus, 2017), the endangered Black-fronted Francolin (*Pternistis atrifrons*) (Töpfer et al., 2014; Gedeon et al., 2017) in south Ethiopia and other francolin species in Africa (van Niekerk, 2017; Lerm et al., 2019). The distribution of evergreen vegetation is identified on the lower edge of the DAF (Friis et al., 2010) and it is treated as DAF vegetation habitat in this study. Our results also show that forest habitat (DAF) had high NDVI and were shelters for Harwood's Francolins particularly during dry season, yet the habitat was not highly preferred as human, livestock grazing and other stressors considerably existed as compared to other habitats.

Our results also emphasize that quadratic term of slope significantly limit the occupancy probability, suggesting that Harwood's Francolins preferred flat, gentle and moderate slopes over steep and extremely steep slopes (Fig. 4B), similar to the results of Li et al. (2009); Abrha and Nigus (2017) and Abrha et al. (2018). Across most stations, flat, gentle and moderate slopes were characterized by herbaceous, scatter trees and bushy vegetation important for food and nesting grounds (pers. obs.). Flat low and high-elevation habitats are highly disturbed areas, whereas steep and extremely steep slopes are less disturbed due to inaccessible for human encroachment (Abrha and Nigus, 2017). The flat terrain and plateau of UBNB are dominated by farming activities (Tekleab et al., 2013). The steep and extremely steep slopes featured by rocks and escarpments are home of raptors, primates and carnivores in the Western highlands of Ethiopia (Saavedra, 2009). Our results show that Harwood's Francolins mostly avoided these gradients possibly due to 1) the presence of potential predators and in such distinctive gradients, for instance, Leopards (*Panthera pardus*) are reported to prey upon francolins in the Abune Yosef massif (Saavedra et al., 2009) and Gelada monkeys (*Theropithecus gelada*) in the Guassa Community Conservation Area (Lin et al., 2020); 2) because steep slopes are grass free stripes and are rarely cultivated in the highlands of Ethiopia (Nyssen et al., 2004).

Globally, mass extinction of vertebrate species is intensified by anthropogenic disturbances (Dirzo et al., 2014; Ceballos et al., 2015; Ceballos et al., 2020). For instance, most bird species are threatened by human disturbances (Hilton-Taylor et al., 2009), particularly for Galliformes (Keane et al., 2005; McGowan et al., 2012; Tian et al., 2018; Ramesh and Downs, 2014). In Ethiopia, anthropogenic disturbances increasingly threatened birds (Asefa et al., 2017), particularly for francolin species (Töpfer et al., 2014; Abrha and Nigus, 2017; Abrha et al., 2017; Gedeon et al., 2017). Not surprisingly, our results show that human-induced disturbances posed a significant threat on Harwood's Francolins occurrence at the fine scale level (Fig. 4C), which supports the *a priori* hypothesis. In this study, we did not include the effect of mining on the species due to budget and time constraints. Similar to our target species, the multitude of threats the Critically Endangered Djibouti Francolin (*Pternistis ochropectus*) faces are overgrazing, forest fragmentation, hunting and death of *Juniperus procera* trees (Fisher et al., 2009; BirdLife International, 2023b). Previously, it was also reported that Harwood's Francolins avoid various threat factors (Robertson et al., 1997), specifically owing to vegetation disturbances, livestock grazing, burning, and hunting in Jema and Jara Valleys (Abrha et al., 2017).

Colonization probability was also inversely correlated with HDI; albeit non-significant association. To confirm these findings, our hypothesis also supports that colonization probability decreased with increasing human disturbances. Our results also show a non-significant negative association between NDVI and colonization of Harwood's Francolins. However, a relative high 95% CIs, and beta coefficient for the model-averaged estimate of NDVI shows that colonization probability was greater in lower vegetation reflectance characterized by shrubby, bush and herbaceous stations in the area. There were no significant determinant covariates for colonization and extinction, suggesting little variation in the dynamic processes governing changes in the species-habitat association in spatiotemporal patterns.

In terms of temperature, we found a significant positive association of detection probability (Fig. 4D), suggesting that Harwood's Francolins detectability was higher at higher temperature, similar to the findings of Skagen and Adams (2012). We encountered the target species commonly in scrub vegetation and herbaceous covers intermingled with sparse trees in CTW and adjacent vegetation habitats. Such land use is commonly characterized by low NDVI and high temperature and this phenomenon strongly facilitates the habitat use of Harwood's Francolins. Like our findings, temperature and NDVI are inversely correlated in Ethiopia (Muir et al., 2021), particular for UBNB (Merga et al., 2022; Moisa et al., 2022). Therefore, across our study area, detectability increased with increasing temperature, and it was lower at stations with higher NDVI.

4.3. Conservation implications and future directions

Even though we did not contrast various methods for the occurrence data as it was not our focus, the combination of multiple field methods collects reliable and comprehensive datasets, thereby draws fundamental inference for conservation purpose of this cryptic species. There were no false positive detections in our surveys and false negative detections were minimized by study design, essentially the application of playback technique. However, we cannot rule out entirely that, due to topography of the study area, our playback sometimes may have disturbed the target species located at other stations. Future studies should consider potential disturbances if stations are placed too close to each other.

The persistence of Harwood's Francolins at lower ecosystem greenness and lower slope gradients has important implications for in-situ conservation strategy. The detection probability of the target species was strongly influenced by temperature, suggesting that the target species favors lowland areas featured by high temperature in UBNB. Ultimately, this factor could have important contribution of the breeding phenology of the species.

Determination of minimum and maximum of survey efforts (K) to increase species detectability (Pellet and Schmidt, 2005; Sewell et al., 2010; McGrath et al., 2015) is a critical step for future research design. Accordingly, the appropriate survey effort for the target species needed at 0.60 target detection probability is a single effort and a maximum of six efforts is required at 0.99 detection probability to confirm true absence of the species in a station.

To conclude, our results highlight that Harwood's Francolins exist across a large geographical scale in UBNB. The dynamic occupancy modeling informs effective conservation and management implications for the target species. Nonetheless, the target species could also be affected by other covariates, particularly at a finer scale (e.g., plant species richness, canopy cover, shrub height etc.) which we did not incorporate in this study due to budget limitations and time constraints.

Most IBAs in Ethiopia, particularly for UBNB are not protected and have little contribution for globally important restricted range species, such as Harwood's Francolins and other biodiversity. We urge special attention for conservation and management of this threatened pheasant species in *Combretum-Terminalia* woodland and grassland, farmland mosaics, evergreen scrub and riparian vegetation habitats across several sub-basins. We also recommend further study to test the influence of fine-scaled, landscape-scaled and climatic covariates on occupancy dynamics of Harwood's Francolin across spatiotemporally replicated surveys.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02710.

References

Abrha, A.M., Nigus, H.K., 2017. The ecology of Harwood's Francolin *Pternistis harwoodi* (Aves: Galliformes: Phasianidae) at Merhabete District, central highlands of Ethiopia: implications for conservation. J. Threat. Taxa 9 (9), 10633–10641. https://doi.org/10.11609/jott.3189.9.9.10633-10641.

Abrha, A.M., Zelelew, S.A., Nigus, H.K., Alelign, A., 2018. Diurnal activity patterns of Harwood's Spurfowl *Pternistis harwoodi* in relation to habitat types and climatic conditions in the Central Highlands of Ethiopia. Ostrich 89 (2), 1–7. https://doi.org/10.2989/00306525.2018.1429505.

Abrha, A.M., Gedeon, K., Podsiadlowski, L., Weldesilasie, D.M., Töpfer, T., 2023. Occupancy of the Ethiopian endemic Moorland Francolin in pristine and degraded Afroalpine biome using a camera trap approach. Ecol. Evol. 13, e10551 https://doi.org/10.1002/ece3.10551.

Abrha, A.M., Nigus, H.K., Weldetnsae, B.G., Tilahun, M., Nigusse, A.G., Deribew, K.T., 2017. Effects of human disturbances on two sympatric francolin species in the Central Highlands of Ethiopia. Podoces 12 (1), 13–21. 〈https://wesca.net/Podoces/podoces12.1.html〉.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manag. 74 (6), 1175–1178. https://doi.org/10.2193/2009-367.

Asefa, A., Davies, A.B., McKechnie, A.E., Kinahan, A.A., van Rensburg, B.J., 2017. Effects of anthropogenic disturbance on bird diversity in Ethiopian montane forests. Condor 119 (3), 416–430. https://doi.org/10.1650/CONDOR-16-81.1.

Ash, J.S., Gullick, T.M., 1989. The present situation regarding the endemic breeding birds of Ethiopia. Scopus 13 (1), 90–96. 〈https://biostor.org/reference/135205〉.

Ash, J.S., Atkins, J., 2009. Birds of Ethiopia and Eritrea: An Atlas of Distribution. Christopher Helm, London.

Bagaria, P., Thapa, A., Sharma, L.K., Joshi, B.D., Singh, H., Sharma, C.M., Sarma, J., Thakur, M., Chandra, K., 2021. Distribution modelling and climate change risk assessment strategy for rare Himalayan Galliformes species using archetypal data abundant cohorts for adaptation planning. Clim. Risk Manag. 31, 100264 https://doi.org/10.1016/j.crm.2020.100264.

Bailey, L.L., MacKenzie, D.I., Nichols, J.D., 2014. Advances and applications of occupancy models. Methods Ecol. Evol. 5 (12), 1269–1279. https://doi.org/10.1111/2041-210X.12100.

Barber-Meyer, S.M., Jnawali, S.R., Karki, J.B., Khanal, P., Lohani, S., Long, B., MacKenzie, D.I., Pandav, B., Pradhan, N.M.B., Shrestha, R., Subedi, N., 2013. Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J. Zool. 289 (1), 10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x.

BirdLife International, 2018. *Pternistis harwoodi*. The IUCN Red List of Threatened Species 2018: e.T22678815A131514381. 〈https://www.iucnredlist.org/fr/species/22678815/131514381〉. Accessed on 27 June 2023.

BirdLife International, 2023a. Important Bird Area factsheet: Mid-Abbay (Blue Nile) river basin. Downloaded from 〈http://datazone.birdlife.org/site/factsheet/6250〉. Accessed on 10 May 2023.

BirdLife International, 2023b. Species factsheet: *Pternistis ochropectus*. Downloaded fromhttp://datazone.birdlife.org/species/factsheet/djibouti-francolin-pternistis-ochropectus. Accessedon 19 June 2023.

Bitani, N., Cordier, C.P., Smith, D.A.E., Smith, Y.C.E., Downs, C.T., 2023. Microhabitat requirements and occupancy of understorey bird forest specialists in Southern Mistbelt Forests of KwaZulu-Natal, South Africa. Ecol. Manag. 549, 121484 https://doi.org/10.1016/j.foreco.2023.121484.

Blanco, G., Cortés-Avizanda, A., Frías, Ó., Arrondo, E., Donázar, J.A., 2019. Livestock farming practices modulate vulture diet-disease interactions. Glob. Ecol. Conserv 17, e00518. https://doi.org/10.1016/j.gecco.2018.e00518.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2004. Advanced distance sampling: estimating abundance of biological populations. OUP,, Oxford.

Burner, R.C., Styring, A.R., Rahman, M.A., Sheldon, F.H., 2019. Occupancy patterns and upper range limits of lowland Bornean birds along an elevational gradient. J. Biogeogr. 46 (11), 2583–2596. https://doi.org/10.1111/jbi.13691.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York.

Campos-Cerqueira, M., Robinson, W.D., Augusto Leite, G., Mitchell Aide, T., 2021. Bird Occupancy of a Neotropical forest fragment is mostly stable over 17 years but influenced by forest age. Diversity 13 (2), 50. https://doi.org/10.3390/d13020050.

Ceballos, G., Ehrlich, P.R., Raven, P.H., 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. Proc. Natl. Acad. Sci. 117 (24), 13596–13602. https://doi.org/10.1073/pnas.1922686117.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1 (5), e1400253. 〈https://www.science.org/doi/full/10.1126/sciadv.1400253〉.

Chaudhary, V., Wisely, S.M., Hernández, F.A., Hines, J.E., Nichols, J.D., Oli, M.K., 2020. A multi-state occupancy modelling framework for robust estimation of disease prevalence in multi-tissue disease systems. J. Appl. Ecol. 57 (12), 2463–2474. https://doi.org/10.1111/1365-2664.13744.

Cisneros-Araujo, P., Goicolea, T., Mateo-Sánchez, M.C., García-Viñás, J.I., Marchamalo, M., Mercier, A., Gastón, A., 2021. The role of remote sensing data in habitat suitability and connectivity modeling: insights from the cantabrian brown bear. Remote Sens 13 (6), 1138. https://doi.org/10.3390/rs13061138.

De Almeida-Rocha, J.M., Monsalvo, J.A.B., Oliveira, L.D.C., 2019. Diet specialisation reduces the occupancy of cocoa agroforests by diurnal raptors. Bird. Conserv. Int. 29 (4), 558–574. https://doi.org/10.1017/s0959270919000017.

De Rosa, A., Castro, I., Marsland, S., 2022. The acoustic playback technique in avian fieldwork contexts: a systematic review and recommendations for best practice. Ibis 164 (2), 371–387. https://doi.org/10.1111/ibi.13033.

Debela, M.T., Wu, Q., Li, Z., Sun, X., Omeno, O., Li, Y., 2021. Habitat suitability assessment of wintering herbivorous anseriformes in Poyang Lake, China. Diversity 13 (4), 171. https://doi.org/10.3390/d13040171.

Devarajan, K., Morelli, T.L., Tenan, S., 2020. Multi-species occupancy models: review, roadmap, and recommendations. Ecography 43 (11), 1612–1624. https://doi.org/10.1111/ecog.04957.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J., Collen, B., 2014. Defaunation in the Anthropocene. Science 345 (6195), 401–406. 〈https://www.science.org/doi/abs/10.1126/science.1251817〉.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17 (1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.

Elith, J., H. Graham, C., Anderson, P., Dudík, R., Ferrier, M., Guisan, S., Hijmans, A., J., Huettmann, R., Leathwick, F., R., Lehmann, J., Li, J, A., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29 (2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

Fisher, Z.S., Cartwright, S., Bealey, C., Rayaleh, H.A., McGowan, P., Milner-Gulland, E.J., 2009. The Djibouti francolin and juniper forest in Djibouti: the need for both ecosystem and species-specific conservation. Oryx 43 (4), 542–551. https://doi.org/10.1017/S0030605309990214.

Fishpool, L.D.C., Evans, M.I. (Eds.), 2001. Important Bird Areas of Africa and associated islands: priority sites for conservation. Pisces Publications/BirdLife International, Newbury/Cambridge, UK.

Friis, I., Demissew, S., Breugel, P.V., 2010. Atlas of the potential vegetation of Ethiopia. Biol. Skr. 58, 1–307.

Gedeon, K., Rödder, D., Zewdie, C., Töpfer, T., 2017. Evaluating the conservation status of the Black-fronted Francolin *Pternistis atrifrons*. Bird. Conserv. Int 27, 1–9. https://doi.org/10.1017/S0959270917000363.

Goldman, M.R., Shinderman, M., Jeffress, M.R., Rodhouse, T.J., Shoemaker, K.T., 2023. Integrating multiple sign types to improve occupancy estimation for inconspicuous species. Ecol. Evol. 13 (5), e10019 https://doi.org/10.1002/ece3.10019.

Green, A.W., Pavlacky Jr, D.C., George, T.L., 2019. A dynamic multi-scale occupancy model to estimate temporal dynamics and hierarchical habitat use for nomadic species. Ecol. Evol.. 9 (2), 793–803. https://doi.org/10.1002/ece3.4822.

Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. Ecography 40 (2), 281–295. https://doi.org/10.1111/ecog.02445.

Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A., McCarthy, M.A., 2014. Ignoring imperfect detection in biological surveys is dangerous: A response to 'fitting and interpreting occupancy models'. PloS One 9 (7), e99571. https://doi.org/10.1371/journal.pone.0099571.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135 (2–3), 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9.

Gumede, S.T., Smith, D.A.E., Smith, Y.C.E., Ngcobo, S.P., Sosibo, M.T., Maseko, M.S., Downs, C.T., 2022. Occupancy of two forest specialist birds in the Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa. Bird. Conserv. Int. 32 (1), 27–42. https://doi.org/10.1017/S0959270920000544.

Harms, T.M., Murphy, K.T., Lyu, X., Patterson, S.S., Kinkead, K.E., Dinsmore, S.J., Frese, P.W., 2017. Using landscape habitat associations to prioritize areas of conservation action for terrestrial birds. PLoS One 12 (3), e0173041. https://doi.org/10.1371/journal.pone.0173041.

Hilton-Taylor, C., Pollock, C.M., Chanson, J.S., Butchart, S.H., Oldfield, T.E., Katariya, V., 2009. State of the world's species. In: Vié, J.C., Hilton-Taylor, C., Stuart, S.N. (Eds.), Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species: IUCN, pp. 15–41.

Hines, J.E. (2006). PRESENCE-software to estimate patch occupancy and related parameters. USGS-PWRC. ⟨http://www.mbr-pwrc.usgs.gov/software/presence.html⟩.

Huete, A.R., Liu, H.Q., Batchily, K.V., Van Leeuwen, W.J.D.A., 1997. A comparison of vegetation indices over a global set of TM images for EOS-MODIS. Remote Sens. Environ. 59 (3), 440–451. https://doi.org/10.1016/S0034-4257(96)00112-5.

Jean-Pierre, A., Loranger-Merciris, G., Cézilly, F., 2022. Spatial occupancy, local abundance and activity rhythm of three ground dwelling columbid species in the forests of guadeloupe in relation to environmental factors. Diversity 14 (6), 480. https://doi.org/10.3390/d14060480.

Jha, A., Praveen, J., Nameer, P.O., 2022. Contrasting occupancy models with presence-only models: Does accounting for detection lead to better predictions? Ecol. Model. 472, 110105 https://doi.org/10.1016/j.ecolmodel.2022.110105.

Keane, A., Brooke, M.D.L., McGowan, P.J.K., 2005. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes. Biol. Conserv. 126 (2), 216–233. https://doi.org/10.1016/j.biocon.2005.05.011.

Kearney, M., 2006. Habitat, environment and niche: what are we modelling. Oikos 115 (1), 186–191. https://doi.org/10.1111/j.2006.0030-1299.14908.x.

Keesing, F., Ostfeld, R.S., 2021. Impacts of biodiversity and biodiversity loss on zoonotic diseases. Proc. Natl. Acad. Sci. 118(17), e2023540118. https://doi.org/10.1073/pnas.2023540118.

Kéry, M., Gardner, B., Monnerat, C., 2010. Predicting species distributions from checklist data using site-occupancy models. J. Biogeogr. 37 (10), 1851–1862. https://doi.org/10.1111/j.1365-2699.2010.02345.x.

Kriegler, F.J., Malila, W.A., Nalepka, R.F., Richardson, W., 1969. Preprocessing transformations and their effect on multispectral recognition. Remote Sens. Environ. VI 97–132.

Lahoz-Monfort, J.J., Guillera-Arroita, G., Wintle, B.A., 2014. Imperfect detection impacts the performance of species distribution models. Glob. Ecol. Biogeogr. 23 (4), 504–515. https://doi.org/10.1111/geb.12138.

Lerm, R.E., Jansen, R., Underhill, L.G., 2019. Bird distribution dynamics - Indigenous francolins in South Africa, Lesotho, and Swaziland. Biodivers. Obs. 10, 1–31. https://doi.org/10.15641/bo.v10i0.599.

Leroux, S.J., 2019. On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. PLoS One 14 (2), e0206711. https://doi.org/10.1371/journal.pone.0206711.

Leveau, L.M., Isla, F.I., Bellocq, M.I., 2018. Predicting the seasonal dynamics of bird communities along an urban-rural gradient using NDVI. Landsc. Urban Plan. 177, 103–113. https://doi.org/10.1016/j.landurbplan.2018.04.007.

Li, H.Q., Lian, Z.M., Chen, C.G., 2009. Winter foraging habitat selection of brown-eared pheasant (*Crossoptilon mantchuricum*) and the common pheasant (*Phasianus colchicus*) in Huanglong Mountains, Shaanxi Province. Acta Ecol. Sin. 29 (6), 335–340. https://doi.org/10.1016/j.chnaes.2009.09.013.

Lin, B., Foxfoot, I.R., Miller, C.M., Venkatamaran, V.V., Kerby, J.T., Bechtold, E.K., Kellogg, B.S., Nguyen, N., Fashing, P.J., 2020. Leopard predation on gelada monkeys at Guassa, Ethiopia. Am. J. Primatol. 82 (2), e23098 https://doi.org/10.1002/ajp.23098.

Little, R.M., Crowe, T.M., 2004. Effects of a predator control experiment on Grey-winged Francolin (*Scleroptila africanus*) populations. Ostrich 75 (4), 285–287. https://doi.org/10.2989/00306520409485456.

Liu, Z., Tian, S., Lu, S., Zhu, Z., Peng, Y., Li, J., Xu, J., Wang, Y., 2023. Climate and land-use changes threaten the effectiveness of protected areas for protecting Galliformes in Southeast Asia. Front. Ecol. Evol. 11, 1216769. https://doi.org/10.3389/fevo.2023.1216769.

Mackenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42, 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84 (8), 2200–2207. https://doi.org/10.1890/02-3090.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2018. Occupancy Estimation And Modeling: Inferring Patterns And Dynamics Of Species Occurrence, second edition. Elsevier.

Mares, R., Doutrelant, C., Paquet, M., Spottiswoode, C.N., Covas, R., 2017. Breeding decisions and output are correlated with both temperature and rainfall in an arid-region passerine, the sociable weaver. R. Soc. Open Sci. 4 (9), 170835 https://doi.org/10.1098/rsos.170835.

Maseko, M.S., Ramesh, T., Kalle, R., Downs, C.T., 2017. Response of Crested Guinea-fowl (*Guttera edouardi*), a forest specialist, to spatial variation in land use in iSimangaliso Wetland Park, South Africa. J. Ornithol. 158, 469–477. https://doi.org/10.1007/s10336-016-1406-7.

Matsushita, B., Yang, W., Chen, J., Onda, Y., Qiu, G., 2007. Sensitivity of the enhanced vegetation index (EVI) and normalized difference vegetation index (NDVI) to topographic effects: a case study in high-density cypress forest. Sensors 7 (11), 2636–2651. https://doi.org/10.3390/s7112636.

Matthiopoulos, J., Fieberg, J.R., & Aarts, G., 2020. Species Habitat Associations: Spatial Data, Predictive Models, and Ecological Insights. 2nd edition. University of Minnesota Libraries Publishing.

McGowan, P.J.K., Owens, L.L., Grainger, M.J., 2012. Galliformes science and species extinctions: what we know and what we need to know. Anim. Biodivers. Conserv. 35 (2), 321–331. ⟨https://raco.cat/index.php/ABC/article/view/259218⟩.

McGrath, T., Guillera-Arroita, G., Lahoz-Monfort, J.J., Osborne, W., Hunter, D., Sarre, S.D., 2015. Accounting for detectability when surveying for rare or declining reptiles: turning rocks to find the grassland earless dragon in Australia. Biodivers. Conserv 182, 53–62. https://doi.org/10.1016/j.biocon.2014.11.028.

Merga, B.B., Moisa, M.B., Negash, D.A., Ahmed, Z., Gemeda, D.O., 2022. Land surface temperature variation in response to land-use and land-cover dynamics: a case of Didessa River sub-basin in Western Ethiopia. Earth Syst. Environ. 1–13. https://doi.org/10.1007/s41748-022-00303-3.

Mohammed, J.A., Gashaw, T., Tefera, G.W., Dile, Y.T., Worqlul, A.W., Addisu, S., 2022. Changes in observed rainfall and temperature extremes in the Upper Blue Nile Basin of Ethiopia. Weather Clim. Extrem. 37, 100468 https://doi.org/10.1016/j.wace.2022.100468.

Moisa, M.B., Gabissa, B.T., Hinkosa, L.B., Dejene, I.N., Gemeda, D.O., 2022. Analysis of land surface temperature using Geospatial technologies in Gida Kiremu, Limu, and Amuru District, Western Ethiopia. Artif. Intell. Agric. 6, 90–99. https://doi.org/10.1016/j.aiia.2022.06.002.

Morante-Filho, J.C., Benchimol, M., Faria, D., 2021. Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. Landsc. Ecol. 36 (1), 105–117. https://doi.org/10.1007/s10980-020-01121-6.

Morrison, M.L., Marcot, B., Mannan, W., 2012. Wildlife-Habitat Relationships: Concepts and Applications, third ed. Island Press.

Muir, C., Southworth, J., Khatami, R., Herrero, H., Akyapı, B., 2021. Vegetation dynamics and climatological drivers in Ethiopia at the turn of the century. Remote Sens 13 (16), 3267. https://doi.org/10.3390/rs13163267.

Nyssen, J., Poesen, J., Moeyersons, J., Deckers, J., Haile, M., Lang, A., 2004. Human impact on the environment in the Ethiopian and Eritrean highlands-a state of the art. Earth-Sci. Rev. 64 (3–4), 273–320. https://doi.org/10.1016/S0012-8252(03)00078-3.

Pellet, J., Schmidt, B.R., 2005. Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. Biol. Conserv. 123 (1), 27–35. https://doi.org/10.1016/j.biocon.2004.10.005.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190 (3–4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Qiu, J., Yang, J., Wang, Y., Su, H., 2018. A comparison of NDVI and EVI in the DisTrad model for thermal sub-pixel mapping in densely vegetated areas: a case study in Southern China. Int. J. Remote Sens. 39 (8), 2105–2118. https://doi.org/10.1080/01431161.2017.1420929.

Ramesh, T., Downs, C.T., 2014. Land use factors determining occurrence of Red-necked Spurfowl (*Pternistis afer*) in the Drakensberg Midlands. South Afr. J. Ornithol. 155, 471–480. https://doi.org/10.1007/s10336-013-1028-2.

Richards, S.A., 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86 (10), 2805–2814. https://doi.org/10.1890/05-0074.

Richards, S.A., Whittingham, M.J., Stephens, P.A., 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. Behav. Ecol. Sociobiol. 65 (1), 77–89. https://doi.org/10.1007/s00265-010-1035-8.

Robertson, P.A., Dellelegn, Y., Dejene, S., Shimelis, A., Alemayehu, M., 1997. Harwood's Francolin *Francolinus harwoodi*: recent observations on its status, distribution, habitat requirements, behaviour and threats. Bird. Conserv. Int. 7 (3), 275–282. https://doi.org/10.1017/S095927090000157X.

Saavedra, D., 2009. The Abune Yosef Massif: Birds and mammals of a hidden jewel of Ethiopia. Centre de Recursos de Biodiversitat Animal, Facultat de Biologia, 2. Universitat de Barcelona, Barcelona, p. 131. http://hdl.handle.net/2445/152578.

Saavedra, D., Such-Sanz, À., Díaz, G., Mariné, R., Regalado, Í., López, M., Dantart, L., 2009. The Mammals of the Abune Yosef. In: Saavedra, D. (Ed.), The Abune Yosef Massif: Birds and Mammals of a hidden jewel of Ethiopia, Publicacions del Centre de Recursos de Biodiversitat Animal. Universitat de Barcelona, pp. 26–70. http://hdl.handle.net/2445/152578.

Sewell, D., Beebee, T.J., Griffiths, R.A., 2010. Optimising biodiversity assessments by volunteers: the application of occupancy modelling to large-scale amphibian surveys. Biodivers. Conserv 143 (9), 2102–2110. https://doi.org/10.1016/j.biocon.2010.05.019.

Skagen, S.K., Adams, A.A.Y., 2012. Weather effects on avian breeding performance and implications of climate change. Ecol. Appl. 22 (4), 1131–1145. https://doi.org/10.1890/11-0291.1.

Smith, D.A.E., Smith, Y.C.E., Ramesh, T., Downs, C.T., 2017. Camera-trap data elucidate habitat requirements and conservation threats to an endangered forest specialist, the Spotted Ground Thrush (*Zoothera guttata*). Ecol. Manag 400, 523–530. https://doi.org/10.1016/j.foreco.2017.06.045.

Sutherland, W.J., 2006. Ecological Census Techniques: A Handbook. Cambridge university press.

Symonds, M.R., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65 (1), 13–21. https://doi.org/10.1007/s00265-010-1037-6.

Taylor, S.S., Cecco, G.D., Hurlbert, A.H., 2021. Using temporal occupancy to predict avian species distributions. Divers. Distrib. 27 (8), 1477–1488. https://doi.org/10.1111/ddi.13296.

Tekleab, S., Mohamed, Y., Uhlenbrook, S., 2013. Hydro-climatic trends in the Abay/upper Blue Nile basin, Ethiopia. Phys. Chem. Earth. Parts A/B/C. 61, 32–42. https://doi.org/10.1016/j.pce.2013.04.017.

Thapa, K., Kelly, M.J., 2017. Prey and tigers on the forgotten trail: high prey occupancy and tiger habitat use reveal the importance of the understudied Churia habitat of Nepal. Biodivers. Conserv. 26, 593–616. https://doi.org/10.1007/s10531-016-1260-1.

Tian, S., Xu, J., Li, J., Zhang, Z., Wang, Y., 2018. Research advances of Galliformes since 1990 and future prospects. Avian Res 9 (1), 1–13. https://doi.org/10.1186/s40657-018-0124-7.

Tilahun, S., Edwards, S., Gebregziabher, T. (Eds.), 1996. Important Bird Areas of Ethiopia: a first inventory.. Addis Ababa: Ethiopian Wildlife & Natural History Society.

Töpfer, T., Podsiadlowski, L., Gedeon, K., 2014. Rediscovery of the Black-fronted Francolin *Pternistis (castaneicollis) atrifrons* (Conover, 1930) (Aves: Galliformes: Phasianidae) with notes on biology, taxonomy and conservation. Vertebr. Zool. 64, 261–271. https://doi.org/10.3897/vz.64.e31494.

Tuanmu, M.N., Jetz, W., 2015. A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr.. 24 (11), 1329–1339. https://doi.org/10.1111/geb.12365.

Urban, E.K., Fry, C.H., Keith, S., 1986. The Birds of Africa, Volume 2. Academic Press, London.

van Niekerk, J.H., 2017. Orange River Francolins (*Scleroptila levaillantoides*) persist in fragmented Highveld farming landscapes, South Africa. Avian Res. 8 (1), 1–8. https://doi.org/10.1186/s40657-017-0069-2.

Wang, B., Xu, Y., Price, M., Yang, N., Liu, W., Zhu, B., Zhong, X., Ran, J., 2021. Niche partitioning among three montane ground-dwelling pheasant species along multiple ecological dimensions. Ibis 163 (1), 171–182. https://doi.org/10.1111/ibi.12842.

Worku, E.A., Bro-Jørgensen, J., Evangelista, P.H., Bekele, A., Atickem, A., Stenseth, N.C., 2023. Group size dynamics of the endangered mountain nyala (*Tragelaphus buxtoni*) in protected areas of the Arsi and Ahmar Mountains, Ethiopia. Glob. Ecol. Conserv 46, e02546. https://doi.org/10.1016/j.gecco.2023.e02546.

Wu, J., Li, H., Wan, H., Wang, Y., Sun, C., Zhou, H., 2021. Analyzing the relationship between animal diversity and the remote sensing vegetation parameters: the case of Xinjiang, China. Sustainability 13 (17), 9897. https://doi.org/10.3390/su13179897.

Zahoor, B., Liu, X., Songer, M., 2022. The impact of climate change on three indicator Galliformes species in the northern highlands of Pakistan. Environ. Sci. Pollut. Res. 29 (36), 54330–54347. https://doi.org/10.1007/s11356-022-19631-y.

Zamora-Marín, J.M., Zamora-López, A., Calvo, J.F., Oliva-Paterna, F.J., 2021. Comparing detectability patterns of bird species using multi-method occupancy modelling. Sci. Rep. 11 (1), 2558. https://doi.org/10.1038/s41598-021-81605-w.

Zwerts, J.A., Stephenson, P.J., Maisels, F., Rowcliffe, M., Astaras, C., Jansen, P.A., van Der Waarde, J., Sterck, L.E., Verweij, P.A., Bruce, T., Brittain, S., 2021. Methods for wildlife monitoring in tropical forests: comparing human observations, camera traps, and passive acoustic sensors. Conserv. Sci. Pract. 3 (12), e568 https://doi.org/10.1111/csp2.568.