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SPATIAL OCCUPANCY OF PASSERINES: RELATIVE TO OTHER INDIVIDUALS, RELATIVE TO WEATHER, AND RELATIVE TO CLIMATE CHANGE

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SPATIAL OCCUPANCY OF PASSERINES: RELATIVE TO OTHER INDIVIDUALS, RELATIVE TO WEATHER, AND RELATIVE TO CLIMATE CHANGE

A DISSERTATION APPROVED FOR THE
SCHOOL OF BIOLOGICAL SCIENCES

BY THE COMMITTEE CONSISTING OF

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I dedicate this dissertation to my husband, parents, and family, who supported and never gave up on me. Dissertation completion would not have been possible without their love and patience.

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Abstract

Behavioral changes are necessary for an individual to adjust to the environment to avoid fitness loss and death. Understanding how behaviors change based on environmental cues is important in their local management and supports conservation. Therefore, the dissertation has focused on how environmental conditions influence behavioral changes.

The first chapter investigated the flocking behaviors of a wintering passerine in Oklahoma. Birds often aggregate into more dense groupings during nonbreeding than breeding periods. This includes large flocks of wintering grassland birds, such as the Chestnut-collared Longspur (*Calcarius ornatus*). Understanding what drives flocking behavior in the nonbreeding period is essential for guiding their management. The spatial scale at which membership flocks remain consistent can inform the management of the winter habitats of these migrant birds. Therefore, the first chapter focused on the social behaviors of wintering Chestnut-collared Longspurs in Oklahoma. We captured and tracked individual longspurs during two winters between 2018 and 2020 and analyzed their social network structure. We found that this population consistently clustered into social communities rather than being associated with resource clustering alone. In the winter seasons we studied, 66.1% (2018-19) and 92.5% (2019-20) of individuals had associations solely within their community, while 33.3% (2018-19) and 7.5% (2019-20) of individuals had at least 60% of their associations within the community. The number of associations an individual experienced did not depend on sex or age. Since Chestnut-collared Longspurs occur in flocks in winter, managers should consider the spatial requirements of flocks, ranging from 38.3ha to 2468.4ha, rather than individual spatial requirements. Apparent thresholds for flock cohesion in the species differ across years and are likely driven by the availability of resources, such as seeds and surface water, rather than individual spatial requirements.

The second chapter investigated the activities of a wintering passerine around a standing livestock pond using automated telemetry, which monitored marked birds' presence in the vicinity of the pond. We used Chestnut-collared Longspur as the study species because they are often detected visiting open water sources in grasslands. We captured adult Chestnut-collared Longspurs (*Calcarius ornatus*) from January to March 2021 at Rita Blanca National Grasslands and attached solar-powered radio tags ("Life tags"). Node units installed around the pond detected radio-tagged birds. We analyzed their activity in the vicinity of the pond relative to weather conditions (e.g., Overnight minimum dewpoint temperature, dewpoint temperature at sunrise, wind speed, and day length). Our results imply that Chestnut-collared Longspurs adjust their daily activity in response to environmental conditions to balance their water needs with water accessibility. The timing of the first visit depended on the overnight minimum dewpoint temperature and dewpoint temperature at sunrise. The first detection of the bird in the vicinity of the pond occurred significantly earlier when the overnight minimum dewpoint temperature was below -15.86°C (cold and dry conditions). However, if dewpoint temperature at sunrise was below -7.2°C, the first visit was delayed until surface water is likely to be available. The number and duration of daily visits changed across the winter season. As birds approached migration, they increased the number of shorter visits to the pond, leading to an overall increase in total duration spent in the vicinity of the pond.

The third chapter focused on the distribution of Yellow-eared bulbul in Sri Lanka. Species' distributions may change in response to climate change as individuals seek to remain within preferred climatic niches. Migration options for island mountain species such as the Sri Lankan-endemic Yellow-eared bulbul (*Pycnonotus penicillatus*) may be limited. Considering the uncertain future this presents for the species, we used the correlative habitat suitability model *Maxent* to

parameterize Yellow-eared Bulbul's current climate niche and project its range shifts under three global climate change models (CNRM-C6, CNRM-ESM-2, and MIROC5), specifically scenario 'SSP126' every 20 years from 2030-2090. Our models fit each of two inter-monsoonal breeding seasons (area under curve > 0.95), with variation best explained by mean temperature of the driest quarter and minimum temperature of the coldest month. Relative to current distributions, our models predicted that the highly suitable Yellow-eared Bulbul niche area would increase by 10.1% by 2030 but decrease by 14.8% by 2070. This would coincide with a northward shift of suitable niche space, with severely reduced populations in the southwestern Sinharaja area. Although climatically suitable habitats in Sri Lanka are not projected to disappear by 2090, this does not guarantee Yellow-eared Bulbul's future. Its northward migration cannot continue indefinitely on this island nation, and areas of putatively suitable climates may not have necessary habitat characteristics (e.g., canopy height or species diversity). Therefore, although Yellow-eared Bulbul may not be immediately imperiled by climate change, it may have limited abilities to adapt and persist without pre-emptive habitat management.

Chapter 1: Spatial scale of social network structure of wintering Chestnut-collared Longspurs (*Calcarius ornatus*) in Oklahoma's grasslands

1.1 Introduction

Most grassland bird species have experienced dramatic population declines in the last 40 years due to modifying and degrading grassland habitats throughout the United States (Sauer et al. 2018; Rosenberg et al. 2019). Grassland habitats continue to degrade rapidly (Hoekstra et al. 2005), which has been attributed to climate change (Brookshire and Weaver 2015), agricultural expansion (Gage et al. 2016), oil development (Bernath-Plaisted and Koper 2016), or exotic plant introduction (Saalfeld et al. 2016). This situation has increased the call for targeted management for the conservation of grassland species (Brennan and Kuvlesky Jr 2005; Pool et al. 2014; Saalfeld et al. 2016), especially across the full life cycle of migratory birds (Marra et al. 2015).

Effective management of grassland birds requires understanding their breeding and non-breeding ecology (Rubenstein and Hobson 2004; Renfrew et al. 2013; Hostetler et al. 2015; Fretwell 2020). Yet, an information gap remains concerning the wintering ecology of grassland birds (Brennan and Kuvlesky Jr 2005; Monroe and O'Connell 2014; Pool et al. 2014; Somershoe 2018). Where this topic has been addressed, we are finding that the condition with which grassland birds emerge from the non-breeding period has important implications for the health of the species (Macías-Duarte and Panjabi 2013). We cannot ignore that perhaps two-thirds of the life cycle is considered the "non-breeding period" (Hostetler et al. 2015), and survivorship through this period is key to population vital rates (Pool et al. 2014). Likewise, we would benefit from a better understanding of how migratory grassland birds adopt winter-specific behaviors that can shape their needs for habitat and social interactions.

Most migratory bird species make behavioral changes to improve winter survival, such as adopting gregariousness and forming groups (Spencer 1982). Social groupings emerge when the benefits of such behaviors, including reduced predation risk and increased foraging success, exceed the cost of competition and disease transmission among clustered individuals (Krause and Ruxton 2002). Since the relative importance of these costs and benefits depends on the environment and the individual (Conradt and Roper 2000; Fortin et al. 2009), social groups have a spatiotemporal dynamic (Lehmann et al. 2007). Grassland birds of the southern Great Plains of North America have been observed to form loosely associated flocks (Grzybowski 1982; Grzybowski 1983a; Grzybowski 1983b; Cohen et al. 2020). For Chestnut-collared Longspurs (*Calcarius ornatus*), these associations appeared to depend on seed densities in grassland plots, with lower seed densities favoring solitary or small flock associations while higher seed densities appeared to spur large, gregarious flocks to form (Grzybowski 1983a). However, it was unclear whether the longspurs were overlapping simply because their home ranges overlapped or if individuals were non-randomly associating with flock mates as part of a functional social network.

Social networks are "any number of individuals interconnected via social ties (sexual, cooperative, etc.) between them" (Krause et al. 2015). This can include temporary aggregations of individuals in the same place simultaneously (Shizuka et al. 2014). We conduct Social Network Analysis (SNA) to quantify and test these associations based on spatially explicit occurrence data across space and time (Wey et al. 2008). Associations between individuals are determined in an SNA based on spatial and temporal proximities; therefore, social structures can reflect overlap of home ranges, temporal synchrony between individuals, or a combination of both (Pinter-Wollman et al. 2014). SNA can identify cohesive subgroups that are more connected with each other than with other members of the population. SNA can also distinguish the influence of spatial preference

from that of social preference (Best et al. 2014). With this in mind, we apply SNA to the Chestnut-collared Longspurs to determine if social interactions shape the species' wintering flocking behaviors or if they emerge simply because of home range dynamics.

Chestnut-collared Longspurs (hereafter CCLO) winter in small to large-sized flocks across the southern Great Plains of North America (Bleho et al. 2020; Muller and Ross 2022). They are often mixed with Thick-billed Longspurs (*Rhynchophanes mccownii*) and Smith Longspurs (*Calcarius pictus*) (Grzybowski 1982) and are often in higher densities in winter than during the breeding season (Somershoe 2018). To further study flocking behavior, we focused on the following questions: Do these wintering flocks present non-random associations consistent with a social network? If so, are those patterns driven simply by home range overlap, or is there evidence that individuals non-randomly associate with each other in time? We address these questions using an SNA of radio-tracked CCLO at a wintering location in southwest Oklahoma. We frame the results regarding local precipitation history and discuss the implications for managing non-breeding populations of migratory grassland birds.

1.2 Methods

1.2.1 Study area

Gambit-of-the-group is the most common type of social network data collection where individuals observed in the same group are assumed to be associated (Franks et al. 2010). Similarly, proximity-based social networks (PBSNs) assume that individuals in close proximity are associated (Spiegel et al. 2016). PBSNs rely on spatial location data collected using radiotelemetry, radio-frequency identification tags, and Global Positioning System (GPS) devices (Spiegel et al. 2016). To study the PBSN structure of CCLO, we captured and tracked longspurs at the Wichita Mountains Wildlife Refuge (WMWR) in Comanche County, southwestern

Oklahoma, during two consecutive winters, 2018-2019 and 2019-2020. The WMWR covers 59,029 acres and contains a variety of habitats, including short grass, tall grass prairies, and mixed-grass prairie with Post Oak (*Quercus stellata*) and Blackjack Oak (*Quercus marilandica*) (Buck 1964; Crockett 1964). Within the WMWR, hills and scrubland separate the grasslands, providing good quality habitat for CCLO in winter (Muller and Ross 2022). We captured birds alternating between three major grasslands in the refuge (separated by more than 5km) and maintained a similar capture rate in each site. We named these sites Meers Turnoff (MT), Visitor Center (VC), and Headquarters (HQ) (Figure 1.1). Wintering grassland birds are difficult to capture using traditional approaches (Martin 1969; Ralph et al. 2004), which forced us to use a novel capture technique that takes advantage of the longspurs' nocturnal roosting and flushing behaviors. Two people carried the spread-out mist net parallel to the ground, with one or more assistants walking behind the net, flushing flocks laterally into the net (Muller et al. 2021).

1.2.2 Data collection

We banded captured birds with numbered U.S. Geological Survey aluminum bands. We sexed and aged longspurs by plumage, looking at feather wear in the inner primary coverts and outer rectrices (Pyle 1997). We classified each bird's age as either first winter (FW) or after-first winter (AFW) (i.e., at least its second winter). VHF radios with an operating frequency range of 150-152MHz were attached to the birds with a fitted figure-8 leg loop harness (Rappole and Tipton 1991) made from degradable elastic thread. We used custom-manufactured radio transmitters from JDJC Corp. (Dewey, Illinois, USA) and Blackburn Telemetry (Nacogdoches, Texas, USA). Transmitters had an expected battery life of 45-60 days and weighed ~0.6g, which would be 2-3% of the typical body weight of a longspur. We focused our capture efforts during the middle of the wintering period from early December through end of January. Ellison et al. (2017) discovered

that longspurs reach their wintering locations by the first week of December; capturing during this period ensured that the birds were winter residents and not early or late migrants. We did not attach radios to birds after January 31, as we were uncertain when migration would begin and wanted to ensure each tagged bird provided data over a sufficient time period for the network analyses.

Using a handheld receiver [R2000 and R410 receivers and 3-element Yagi antennas (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA)], we attempted to triangulate the position of radio-tagged longspurs within a $100m^2$ area 3 times per day. To ensure the independence of our data points, our samples included flocks surveyed at least 30 minutes apart, as preliminary observations suggested that flock membership often changes within this time frame. This tracking occurred during mornings and afternoons in winter 2018-19 and winter 2019-20. During the second year, we also opportunistically located birds in the post-twilight (i.e., roosting) period. Tracking efforts stopped when any one of these conditions occurred: the end of the field season (~ March 8), the transmitter was detached and recovered, or the bird was known to be depredated. We located individuals by scanning at their last known location and at spots with good line of sight, as the WMWR is extremely hilly. At every location, we scanned for all potential radio-tagged birds in the same direction, walked toward the bird(s) until they flushed, and recorded GPS coordinates. If we were unsure which individual was the tagged bird when we flushed a flock, we recorded the GPS coordinates from the center of the flushed flock. We also surveyed short-term flocks by recording the total number of birds (tagged and non-tagged) flushed along with the radio-tagged individual(s).

Among the 55 and 61 CCLO captured in our 2018-19 and 2019-20 field seasons, we radio-tagged and attempted to track 44 and 46 individuals. We recorded a total of 1976 telemetry locations across two years (825 in 2018-2019 and 1151 in 2019-2020). Nine radios (11% of those

deployed) stopped working or fell off before we could relocate the bird. At least 4.9% of tagged longspurs were depredated across two years. We omitted transient individuals (observed fewer than five times) from the network analysis. We used 31 and 43 individuals for our final analysis in 2018-2019 and 2019-2020, respectively.

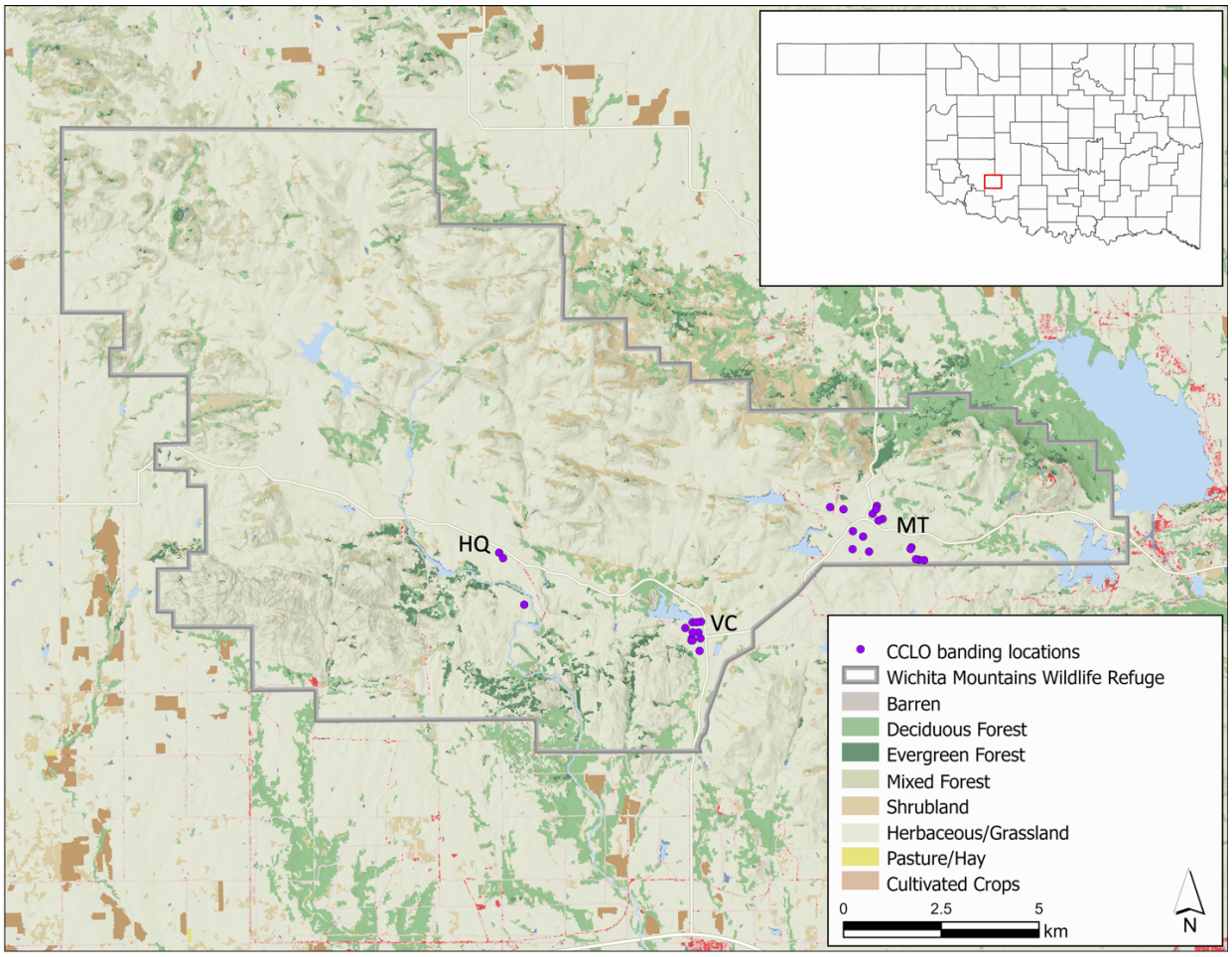

Figure 1.1: Chestnut-collared Longspur (*Calcarius ornatus*) banding locations in winter 2018-19 and 2019-20, MT: Meers Turnoff, VC: Visitor Center, HQ: Headquarters

1.3 Analyses

We calculated the Simple Ratio association Index (SRI) (Cairns and Schwager 1987) for each pair of radio-tagged individuals for each season, with values ranging from 0 to 1. A value of "0" indicates that the pair were never seen together in the same flock, while a value of "1"

represents pairs that were always detected together (Farine and Whitehead 2015). We then constructed social networks of flocks with each of the network's nodes representing individual birds, while edges connecting nodes representing the SRI (Cairns and Schwager 1987; Arnberg et al. 2015).

We used the Fast Greedy method, a modularity optimization community detection method, to detect social communities: groups of individuals tightly connected through a flock co-membership (Clauset et al. 2004). If a tagged bird had no interaction with other tagged birds, we did not consider those individuals as separate communities, even if they were observed in flocks with non-tagged individuals (Supplementary Table S1). We calculated modularity (Q), which is the weighted proportion of edges that fall within a pre-defined network minus the expected proportions of randomly placed edges in the network (Newman 2006). Division with high modularity is an effective way to detect communities; therefore, maximum modularity value (Q_{max}) is the decisive current method of community detection (Newman 2006), such that higher Q_{max} means birds are strongly associated within the community (Newman 2004). We then used bootstrapping to account for sampling errors in our observed networks (Lusseau et al. 2008).

Centrality measures an individual's structural importance in a group based on network position and detects which individuals are important connections between communities (Freeman 2002). Within the observed communities, we determined the centrality of individuals by calculating the individuals' participation coefficient (P) (Guimerà et al. 2005), using the igraph package (Csardi 2013). We classified individuals into two categories based on their participation coefficient: (1) ultraperipheral (individuals who have all their links within the community) and (2) peripheral (individuals who have at least 60% of their links within the community) (Guimerà and Nunes Amaral 2005). Since the sample sizes were small, we used Fisher's exact test to compare

the participation coefficients of individuals (Agresti 2012). Further, we used the unpaired Wilcoxon test to compare the mean number of associations between males and females as well as the mean number of associations between first-winter birds and after-first-winter birds (Divine et al. 2013).

Using two null models, we tested whether the observed social structure of longspur flock association patterns was random or driven purely by spatial clustering. The first null model (hereafter, the random flock model) assumes that flock associations are random and that any individual can join any flock at any time if the total number of flocks, number of individuals in each flock, and the number of flocks an individual joined match the empirical dataset. We conducted randomization using the 'Swap' algorithm using the "network permutation" function in the "asnipe" R package (Farine 2013).

We then applied the community detection methods described above to measure each network's modularity (Q_{max}) generated from a randomized flock matrix. Then, we repeated this process 10,000 times to produce a null distribution for comparing the empirically observed modularity measures. Our second null model, the Spatial Flock Model, included home ranges and assumed that birds flock randomly within their home range. First, we calculated kernel home range overlap using the "adehabitatHR" R package (Fieberg and Kochanny 2005). Then, we constructed flocks using the observed flock sizes and locations from the empirical data. We then used the flock membership matrix to construct the spatial flock model and calculate modularity as above. Finally, we compared the modularity values generated by the Random Flock and Spatial Flock models with the empirical modularity value via bootstrap confidence intervals.

Since these birds occur in flocks throughout the winter, it is necessary to understand the area used as a flock for local species management. Therefore, we calculated each community's

home range using minimum convex polygons. We used the centroid of the minimum convex polygon of each individual's home range to plot the spatial distribution of the communities.

1.4 Results

We observed flocks (including both tagged and untagged individuals) ranging from solitary individuals to >150 individuals. The average flock size was 21.7 in winter 2018-19 and 42.2 individuals in winter 2019-20. Radio-tagged individuals temporally overlapped during the study period (Figure 1.2). We observed three and four communities of CCLO in the winters of 2018-19 and 2019-20, respectively (Figure 1.3). The community structure was primarily driven by spatial segregation between the study areas (Figure 1.3). Most individuals in the W1-1 community left the area, except for one individual who joined the W1-2 community.

Participation coefficient results indicated that 66.7% and 92.5% of birds were ultraperipheral (meaning all of their associations were within their community) in winter 2018-19 and winter 2019-20, respectively. 33.3% and 7.5% of the tagged birds were peripheral (meaning at least 60% of the associations were within their community) in winter 2018-19 and 2019-20, respectively. Among the peripheral individuals in winter 2018-19, 60% were after-first-winter birds, while in winter 2019-20, 100% were after-first-winter (Supplementary Table S1). However, there was no significant difference between the age classes in the two winters (Fisher's test p-value = 0.528). Results from the Wilcoxon test (Table 1.1 and Table 1.2) suggest no difference in the number of associations between males and females (w = 496.5, p-value = 0.79) and no difference between first-winter birds and after-first-winter birds (w = 827, p-value = 0.19).

In each year, the modularity of the empirical flock was higher than the random flock model, suggesting that the observed network of the empirical flock is non-random (Figure 1.4). Also, the modularity of the empirical model is higher than that of the spatial null model, suggesting that

there was more discrete clustering of individuals in the social network than expected by patterns of home range overlap per se (Table 1.3).

Minimum convex polygon analysis reveals that during winter 2018-19, communities were distributed in 857 - 2594ha, whereas communities in winter 2019-20 were distributed in 38 - 632ha (Table 1.4).

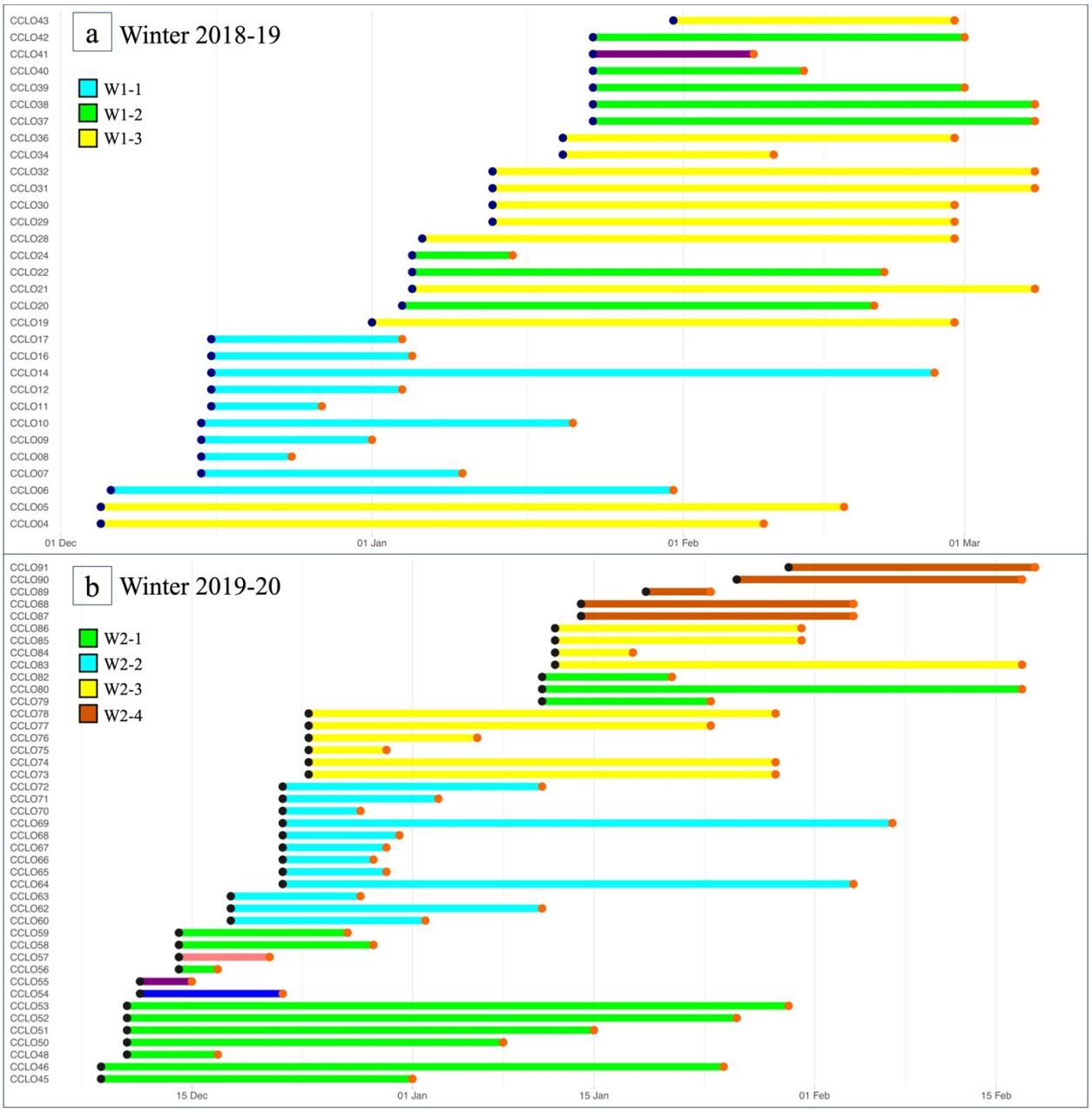

Figure 1.2: Duration of the detection of each radio-tagged Chestnut-collared Longspur (*Calcarius ornatus*) during the winter of 2018-19. Black circles represent the start date, and orange circles represent the end date of detection due to the departure or death of the bird or when it ran out of battery life. Different color horizontal bars represent different communities.

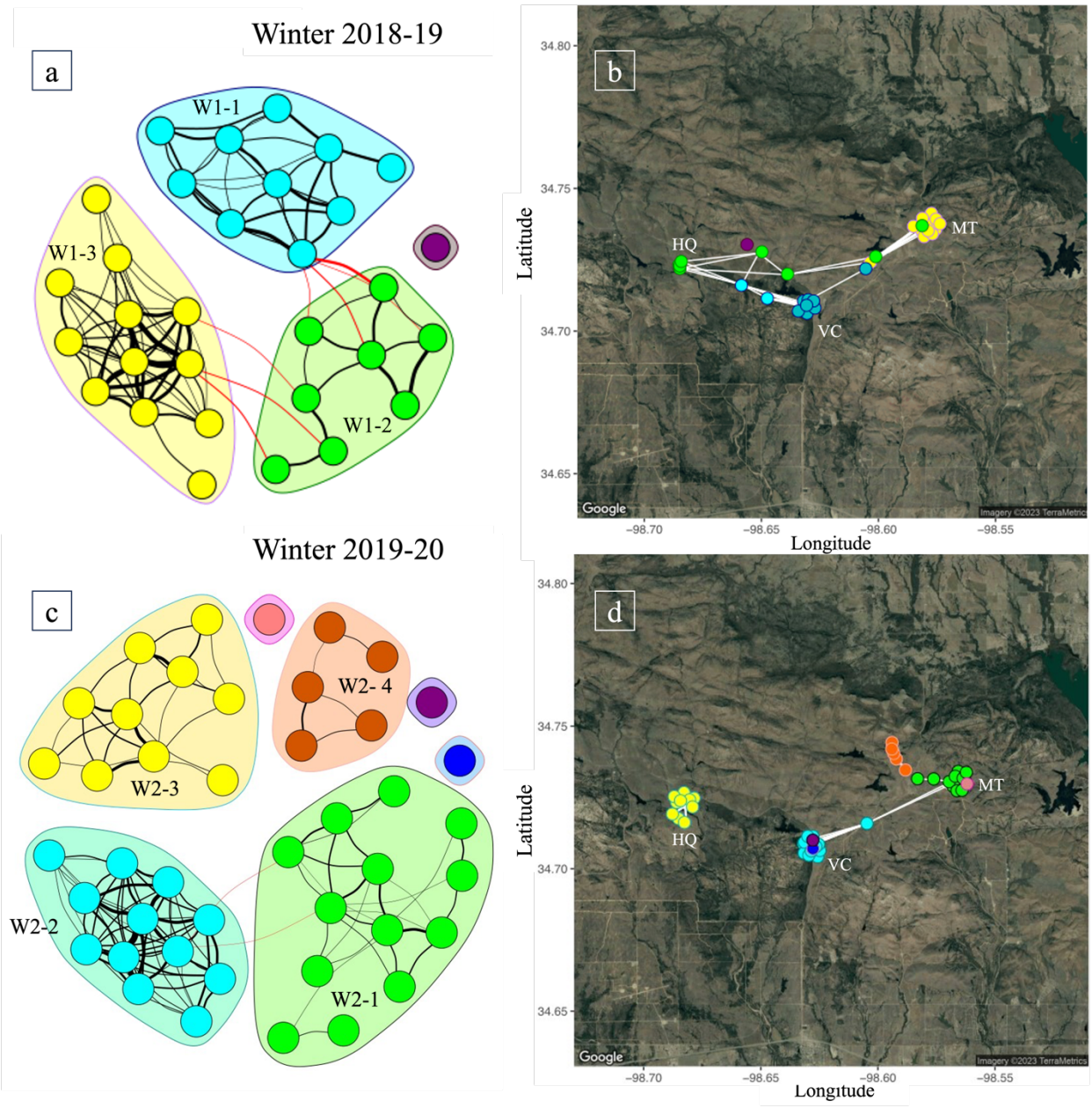

Figure 1.3: Observed social community structures and their spatial distribution in winter 2018-19 and 2019-20 in three grassland patches (MT: Meers Turnoff, VC: Visitor Center, HQ: Headquarters). a and c: Social networks of flock co-membership in each season. Each node represents an individual bird and is assigned to a social community denoted by a colored bubble. Edge widths are proportional to the association index. Edges connecting nodes in different communities are drawn in red. Node placement is determined by a force-directed algorithm from the igraph package, which tends to place strongly associated nodes close together. b and d: Spatial distribution of communities. Each node represents the centroid of an individual bird's home range.

Table 1.1: Summary metrics for the number of associations of Chestnut-collared Longspurs (MNA: Mean Number of Associations) between First-winter and After-first winter birds

Winter	Age	Count	MNA	SD
Winter 2018-19	FW	16	3.56	3.98
Winter 2018-19	AFW	20	5.9	3.11
Winter 2019-20	FW	12	5.67	3.7
Winter 2019-20	AFW	30	5.27	3.67

Table 1.2: Summary metrics for the number of associations of Chestnut-collared Longspurs (MNA: Mean Number of Associations) between males and females

Winter	Sex	Count	MNA	SD
Winter 2018-19	F	8	5.25	4.03
Winter 2018-19	M	28	4.75	3.63
Winter 2019-20	F	9	4.56	2.4
Winter 2019-20	M	33	5.61	3.9

Table 1.3: Descriptive statistics for social network structures of Chestnut-colored Longspurs

Winter	# Individuals radio tagged	# Individuals used in analysis	# Communities observed	Q_{max}
2018-19	44	36	3	0.539
2019-20	46	42	4	0.548

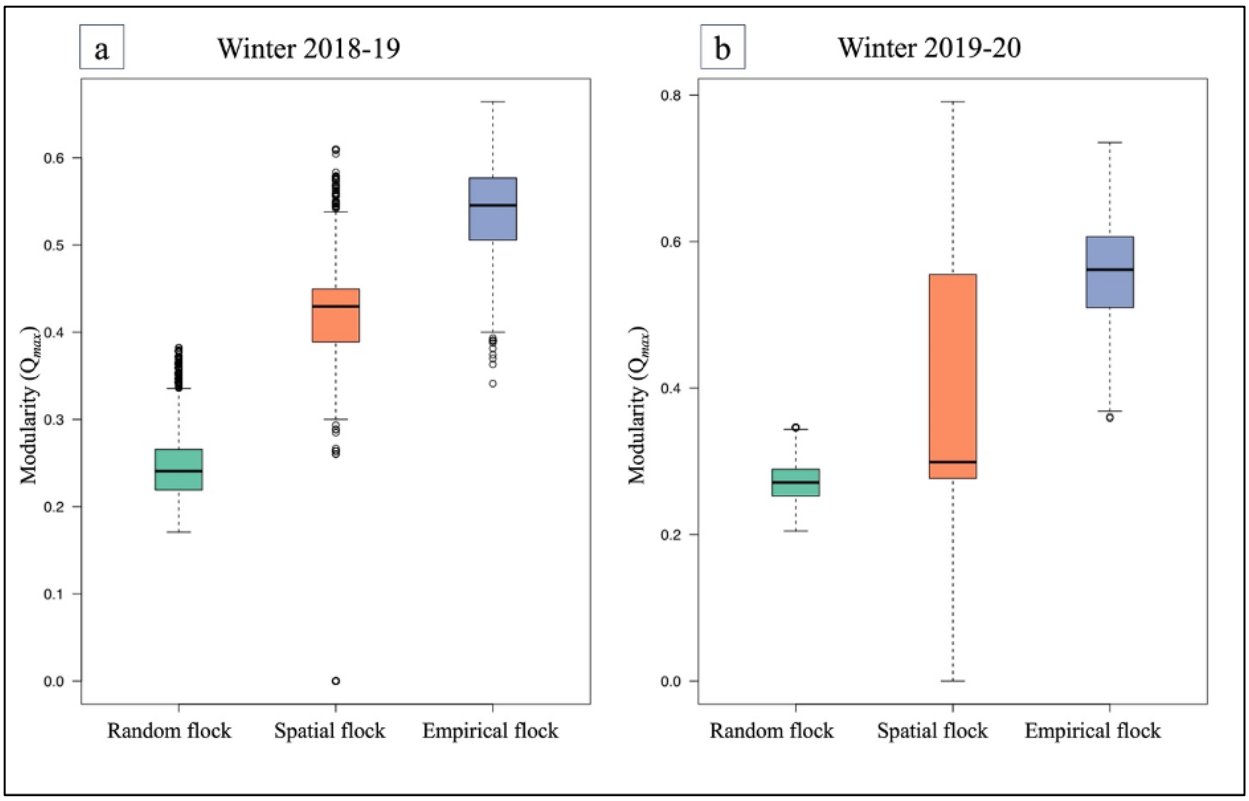

Figure 1.4: Comparison of empirical flock model with random flock model and spatial flock model for Chestnut-collared Longspurs. a - Winter 2018-19, b - Winter 2019-20. The empirical flock model has a greater community structure compared to null models. For each season, we calculated modularity for an ensemble of the Random Flock Null Model (Q_{max} = 0.24), Spatial Flock Null Model, and Empirical Bootstrap networks (Q_{max}=0.57). Box-and-whiskers plots are shown.

Table 1.4: Minimum convex polygons for each community (cluster of individuals) in winter 2018-19 and winter 2019-20

Community	# of tagged individuals	Area (ha)
W1 - 1	10	2468.4
W1 - 2	8	2594.2
W1 - 3	12	959.6
W2 - 1	13	160.3
W2 - 2	12	632.3
W2 - 3	10	242.8
W2 - 4	5	38.3

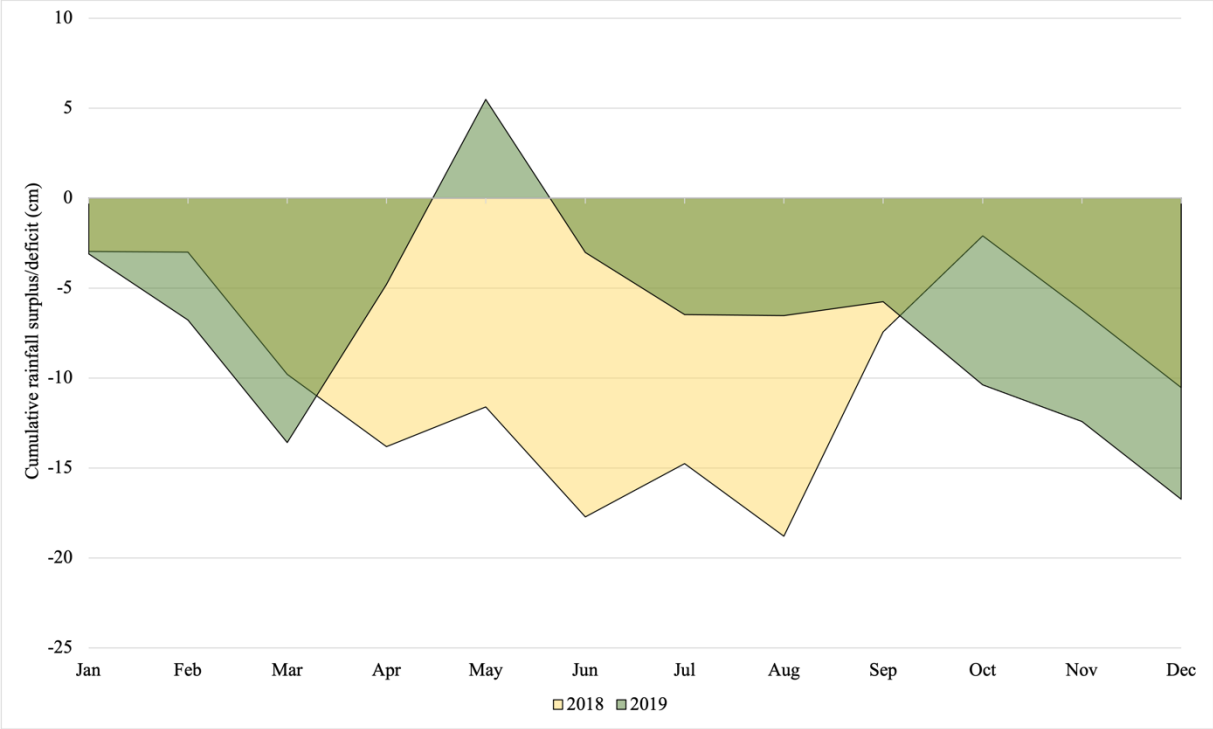

Figure 1.5: Monthly precipitation surplus/deficit in 2018 (yellow) and 2019 (green) at Wichita Mountains Wildlife Refuge collected from Oklahoma Mesonet.

1.5 Discussion

Our study supports the hypothesis that Chestnut-collared Longspurs are flocking during the winter in a way that individual occurrences overlap in both space and time beyond what would be expected if they were moving independently of conspecifics. Furthermore, the structure and interaction among social network communities appear to vary by year and may reflect the resource availability on the landscape. These findings are important for managing this declining grassland bird species because they shed new light on how CCLOs distribute themselves at their wintering grounds and because of the implications for estimating population sizes therein.

Our SNA revealed that CCLO communities co-occur not only because their members' home ranges overlap but also because they move about the area on a more synchronized schedule than expected by chance. Hence, some individuals' movements appear to influence other flock

members' movements. This aligns with our field observations that foraging CCLO would often vocalize when conspecifics flew overhead, causing those birds to descend nearby to join the foraging individuals immediately.

Yearly variation in social network characteristics

While birds captured on the same night at the same place were generally assigned to the same social community, the home range size of each community depended upon the year, with more individuals moving between sites when flocks were at lower densities. Most of the tagged birds in the Visitor Center community in the winter of 2018-19 appeared to dissolve relatively shortly after they were marked rather than mixing with other social communities. Yet some individuals, including one who joined another community, remained. However, birds marked at Meers turnoff and Headquarters were consistently located throughout the study period, suggesting that the pattern observed at the Visitor Center did not reflect radio failure *en masse*. We continued our efforts to locate departed birds at our sites throughout the study period to ensure that the birds had not returned to the area. This suggests the notion of resource depletion, causing an area to be insufficient to support the flock.

Winter 2019-20 had a higher flock density and communities with smaller home ranges when compared to winter 2018-19. Months leading up to winter 2019-20 (January-August) had a surplus of 4.83 cm of rain compared to the months leading up to winter 2018-19 (Figure 1.5). Precipitation differences could influence food availability because grasslands' biomass and composition rely on water availability (Knapp et al. 2002; Fry et al. 2014; Lenhart et al. 2015), and changes in precipitation can cause fluctuations in the abundance of grassland community (Carson and Pickett 1990; Collins et al. 2012). Muller and Ross (2022) discovered that CCLOs are associated with grass dominated by *Aristida spp.,* whose survival is highly dependent on rainfall

(Orr et al. 2011). Higher rainfall in 2019, relative to 2018, may have caused a high density of *Aristida spp*., increasing seed density, resulting in high individual density flocks with small home ranges. This reinforces the findings of Grzybowski (1983a) that a high density of birds is observed when seed density is high. However, grasslands at WMWR are isolated by wooded hills, and the home range size of communities could be skewed by habitat fragmentation, whether natural or anthropogenic. Thus, we encourage further investigation into factors driving the differences in flock home ranges and studies over more seasons for robust inferences, which will benefit effective management.

The nature of radiotelemetry (e.g., battery lifespan, line-of-sight detection, ground clutter, or detuning) plus the challenges of capturing non-territorial CCLO limited our ability to track potential long-distance movements, capture and mark all individuals at the same time, or fully quantify social networks within each year. To minimize this effect, we had capture days as frequently as the weather would allow, and we captured as many birds as possible on each capture day. Automated radio telemetry (e.g., Motus wildlife tracking) would allow us to better quantify the social networks over larger areas and longer periods.

WMWR has a relatively high CCLO density, averaging 371 birds/km^2, with an estimated population size of 20,000 longspurs (Muller et al. 2021). Yet only 55 birds were marked, representing less than 3% of the estimated population. Since we did not recapture any marked longspurs returning between years, it is possible that the returning birds were present but not captured. Therefore, more effort and an efficient capture method are needed to fully discern the site fidelity, inter-year population mortality, and survival on the wintering grounds.

Management implications

Even though the CCLO individual average home range is 29.87 ha (Muller et al. 2021), our study reveals that CCLO communities have home ranges between 38.2 ha and 2594.2 ha. Therefore, regarding CCLO management, we should consider the spatial requirements of flocks rather than individuals. Apparent thresholds for flock cohesion in the species differ across years and are likely to be driven by the availability of resources, such as seeds and surface water. Therefore, local habitat management for CCLO should integrate the home range used by flocks and precipitation before the winter.

Climate change models predict that western North American grasslands will move farther north within the coming decades (Wilsey et al. 2019); this means that sites such as the Wichita Mountains, which are currently along the northern edge of the species' winter distribution, may become a more valuable wintering area for the conservation of the species, if not crucial already. Our findings suggest that when CCLO flocks are small, their members are more likely to cover larger home ranges and join other flocks, especially as flock mates depart the area, perhaps due to resource exhaustion in that area. On the other hand, large flocks appear to remain largely independent of one another. The sum effect is that managers may be prone to overestimating the population size of CCLO when they are at low densities if they apply the same assumption of home range for the species across years. Therefore, managers should understand population densities at points throughout the winter.

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1.7 Supplementary materials

Table S1: Summary of tagged birds. W1: Winter 2018-19, W2: Winter 2019-20, Male, F: Female, AFW: After first winter,
FW: First winter, P: participation coefficient

Winter	Code Name	Home Range (ha)	Sex	Age	P	Community	Flock size
W1	CCLO41	854.227344	M	AFW	1	NA	29
W1	CCLO24	11.880487	F	AFW	0.5	W1-2	6
W1	CCLO14	949.129718	M	FW	0.48	W1-1	30.625
W1	CCLO22	404.013409	M	AFW	0.44444444	W1-2	37.8
W1	CCLO20	1883.50327	M	AFW	0.375	W1-2	23.4444444
W1	CCLO39	52.288761	M	FW	0.375	W1-2	34.4583333
W1	CCLO40	714.164395	M	FW	0.375	W1-2	28.9411765
W1	CCLO42	83.297867	M	AFW	0.375	W1-2	39.8
W1	CCLO21	92.899744	M	AFW	0.27777778	W1-3	38.2758621
W1	CCLO37	36.453397	M	AFW	0.27777778	W1-2	34.3103448
W1	CCLO19	557.530774	M	AFW	0.16528926	W1-3	33.5135135
W1	CCLO04	39.428496	M	AFW	0	W1-3	13.55
W1	CCLO05	49.072161	M	AFW	0	W1-3	20.5
W1	CCLO06	38.038212	F	AFW	0	W1-1	19.7674419
W1	CCLO07	201.493997	M	FW	0	W1-1	1
W1	CCLO08	1.038766	M	AFW	0	W1-1	1.88888889
W1	CCLO09	16.26062	M	AFW	0	W1-1	10.3076923
W1	CCLO10	191.263917	M	AFW	0	W1-1	6.30769231
W1	CCLO11	13.263929	M	FW	0	W1-1	4.25
W1	CCLO12	17.930658	F	FW	0	W1-1	1
W1	CCLO16	6.070674	M	AFW	0	W1-1	19.0769231
W1	CCLO17	15.2674	M	AFW	0	W1-1	9.71428571
W1	CCLO28	89.840572	F	AFW	0	W1-3	21.8636364
W1	CCLO29	84.286532	M	AFW	0	W1-3	27.2608696
W1	CCLO30	30.213702	M	FW	0	W1-3	29.8823529
W1	CCLO31	39.798174	M	AFW	0	W1-3	28.6206897
W1	CCLO32	38.773719	F	FW	0	W1-3	29
W1	CCLO34	14.608236	M	FW	0	W1-3	3.42857143
W1	CCLO36	18.970679	M	AFW	0	W1-3	33.8076923
W1	CCLO38	42.042936	M	FW	0	W1-2	24.0666667
W1	CCLO43	36.034658	F	FW	0	W1-3	33.4285714
W2	CCLO54	20.1335404	M	FW	1	NA	4.77777778
W2	CCLO55	4.3353617	M	AFW	1	NA	24
W2	CCLO57	14.4079096	M	FW	1	NA	39.6363636
W2	CCLO80	14.1855256	F	AFW	0.27777778	W2-1	17.3461539
W2	CCLO64	572.273811	M	AFW	0.26035503	W2-2	29.8684211
W2	CCLO53	26.4702426	F	AFW	0.19753086	W2-1	56.7538462
W2	CCLO45	62.721073	F	AFW	0	W2-1	39.6666667

W2	CCLO46	5.4657238	M	AFW	0	W2-1	9.33962264
W2	CCLO48	17.83239	F	AFW	0	W2-1	26.0714286
W2	CCLO50	26.8303596	M	FW	0	W2-1	34.875
W2	CCLO51	24.9942195	M	FW	0	W2-1	36.3
W2	CCLO52	41.6921186	F	FW	0	W2-1	41.171875
W2	CCLO56	0.382857	M	FW	0	W2-1	70.6
W2	CCLO58	10.6150842	M	AFW	0	W2-1	39.9375
W2	CCLO59	12.9130781	M	AFW	0	W2-1	31.44
W2	CCLO60	14.6720482	M	FW	0	W2-2	63.6428571
W2	CCLO62	18.2607992	M	AFW	0	W2-2	36.36
W2	CCLO63	21.0452477	M	AFW	0	W2-2	45.3157895
W2	CCLO65	18.3723561	M	FW	0	W2-2	34.9
W2	CCLO66	21.7760508	M	FW	0	W2-2	73.8
W2	CCLO67	22.7879395	M	AFW	0	W2-2	50
W2	CCLO68	29.5002014	M	AFW	0	W2-2	45.8235294
W2	CCLO69	22.4765555	M	AFW	0	W2-2	27.6136364
W2	CCLO70	37.8058299	M	AFW	0	W2-2	66.5454546
W2	CCLO71	20.8664844	M	AFW	0	W2-2	30.4615385
W2	CCLO72	24.2360117	M	AFW	0	W2-2	50.3571429
W2	CCLO73	85.2906918	M	AFW	0	W2-3	67.9354839
W2	CCLO74	101.893106	F	AFW	0	W2-3	85.7674419
W2	CCLO75	6.7039518	F	FW	0	W2-3	85.875
W2	CCLO76	46.788698	M	AFW	0	W2-3	67.1818182
W2	CCLO77	144.836469	M	FW	0	W2-3	85.1428571
W2	CCLO78	93.536059	M	FW	0	W2-3	45.7179487
W2	CCLO79	0.9844529	F	AFW	0	W2-1	57.2
W2	CCLO82	5.9508965	M	AFW	0	W2-1	52.4285714
W2	CCLO83	18.5650709	M	AFW	0	W2-3	8.63636364
W2	CCLO84	96.3460326	M	AFW	0	W2-3	30
W2	CCLO85	5.8147193	M	AFW	0	W2-3	24.5
W2	CCLO86	38.6993443	M	AFW	0	W2-3	48
W2	CCLO87	5.4509258	M	AFW	0	W2-4	20.6296296
W2	CCLO88	17.2537531	F	AFW	0	W2-4	36.3611111
W2	CCLO89	3.3950842	M	AFW	0	W2-4	18.4444444
W2	CCLO90	12.8344109	M	AFW	0	W2-4	26.2432432

Chapter 2: Environmental conditions lead to shifts in wintering passerines' activity around a standing-water pond

2.1 Introduction

The Southern Great Plains provide diverse overwintering or stopover habitats for grassland birds (Atuo and O'Connell 2017). Yet the non-breeding ecology of migratory grassland birds here is poorly understood, despite some species that winter here, such as longspurs (family Calcariidae), drawing increased conservation concerns after decades of population decline (Sauer et al. 2018). To conserve and manage these rapidly declining migratory grassland species, there is a need for a full-life-cycle conservation (Hostetler et al. 2015; Marra et al. 2015). Factors on wintering grounds have been suggested as a potential cause for the population declines of many migratory species (Rappole 1995; Macías-Duarte and Panjabi 2013; Morrison et al. 2013). To sustain a species, wintering grounds must provide resources (food, fresh water, shelter from weather and predators) necessary to survive during winter (Burt 1943; Studds and Marra 2005) and to fuel spring migration (Briedis et al. 2018; Akresh et al. 2019). Studies have focused on how food availability influences daily activity (Orell 1989; Nilsson et al. 2020; Stanley et al. 2021). However, water availability can also be a limiting factor influencing birds' daily activity schedules.

Water is a critical resource for animals that can be replenished by metabolic processes (Hinds et al. 1993) or from the environment (MacMillen 1990; MacMillen and Baudinette 1993). When the evaporation loss due to breathing cold and dry air exceeds water replenishment by metabolic processes, birds must actively seek water resources, leading to shifts in their daily schedules (MacMillen 1990). The most common source of drinking water in the environment is surface water, including dew and snow (Hendricks 1996). However, water accessibility depends on local environmental conditions. For example, in arid environments, birds seek water at

increasingly distant sources as internal water stress increases, despite this also amplifying travel costs and predation risks (Cade 1965; Fisher et al. 1972; Engel et al. 2006). In these dry areas, the net result is that open-canopy ponds increase bird species abundance and richness (Phillips et al. 2019). The question remains: do birds adjust their water-seeking behaviors in response to cues about surface water accessibility?

During wintering periods in temperate ecosystems, water accessibility can vary throughout the day depending on the temperature (whether above or below 0°C). For grassland bird species of the southern Great Plains, such conditions can be commonplace, especially in the northern reaches of the region. Species of Calcariidae that winter in the region are routinely observed drinking from open water sources, such as cattle stock ponds or puddles left after precipitation events (Bleho et al. 2020). Chestnut-collared Longspur (*Calcarius ornatus;* hereafter CCLO), for one, are so often detected visiting surface water sources that these ponds seem to be important drivers of the species' occupancy of a site (Bleho et al. 2020). CCLO winter across grasslands of the southwestern United States and Northern Mexico, yet their wintering ecology has primarily been studied in the southern or middle portion of their non-breeding range, such as Chihuahuan Desert grasslands (Desmond 2004; Kelly et al. 2006; Macías-Duarte and Panjabi 2013; Pool et al. 2014) or mixed-grass prairies (Grzybowski 1982; Grzybowski 1983a; Grzybowski 1983b; Muller et al. 2021). At the northern reach of CCLO's winter range, only habitat associations have been examined (Muller and Ross 2022), and the visitation behavior of CCLO to winter water sources has not been scientifically evaluated in the non-breeding grounds.

By better understanding when, how often, and how long CCLOs come to surface water sources in winter, we gain critical insights into how climate change might disrupt the relationship between this rapidly declining species and open water sources, including managed ponds. With

this in mind, we have used automated radio-telemetry to track and analyze the visitation schedule of CCLO at a focal pond in the northern portion of the species' wintering range, where open water accessibility can vary with environmental conditions. We focus on how daily weather and seasonal progressions alter the species' visitation behaviors and test if (1) the timing of daily first visits varies due to overnight and local weather conditions at sunrise and if (2) daily pond visits shift in frequency and duration as the wintering season progresses.

2.2 Methods

2.2.1 Automated radio telemetry

Rita Blanca National Grassland (RBNG) in Dallam County, northwestern Texas, is in the northern part of the CCLOs' wintering range. RBNG has a semiarid climate with a dry steppe dominated by shortgrass and forbs (Hazlett et al. 2009). Heavily grazed areas are dominant with purple three-awn (*Aristida longiseta*) (Hazlett et al. 2009), providing a suitable habitat for CCLO (Muller and Ross 2022). Within RBNG, we deployed an automated radio-telemetry system, Motus Towers, for autonomous data collection and spatial tracking of tagged birds in winter 2020/21. The Motus wildlife tracking system (motus.org) is an internationally collaborative automated radio telemetry network. Each data collection station had an automated radio-telemetry receiver (Sensor Station) connected to four antennas. Each station was powered by a 100W solar array connected through a charge controller to a 12-V deep cycle marine battery, and data was automatically uploaded every hour to a server via a cellular network connection. The Sensor Station continuously "listened" for nearby tags and recorded the tag identity code, date, time, signal strength, and bearing of detections of uniquely coded transmitters whenever a tagged longspur came within detection range.

In January 2021, we installed an array of nodes within the Motus system around a livestock pond (Latitude: 36.490, Longitude: -102.649, approximate surface area: 120.41m^2), which was also used as the banding location. We used the fence lines to set up 20 nodes, with five nodes generally aligned to each cardinal direction (east, west, north, and south) (Figure 2.1). Each node (CTT node v.2, manufactured by Cellular Tracking Technologies, Rio Grande, New Jersey, USA) consists of a small radio receiver with an integrated solar panel and an omnidirectional whip antenna (Figure 2.2A). Nodes continuously scan for uniquely coded IDs emitting from radio transmitters at 434 MHz frequency and log tag ID, signal strength (RSS; range −30 to −120), and a time stamp that is regularly calibrated to GPS satellite time. Nodes periodically transmit the logged information to base stations (CTT Sensor Stations, v.2, Cellular Tracking Technologies, Rio Grande, New Jersey, USA) dispersed throughout the node network. Since these nodes have a detection range of 150-200m, node units were spaced at distances ranging from 65.83m-156.36m.

2.2.2 Longspur trapping and marking

We captured 87 adult CCLOs in winter 2020-21 (December 2020 - March 2021) using mistnets at frequently used livestock ponds in RBNG. Due to the availability of tags, we attached only 38 coded solar-powered radio transmitters (‘LifeTags’) manufactured by Cellular Tracking Technologies (CTT) (Figure 2.2B). All LifeTags were attached using a leg-loop harness (Rappole and Tipton 1991) made of 0.7mm Stretch Magic elastic thread. Each tag emitted a unique identification code in ‘beeps’ produced every 5 seconds, which enabled us to monitor all tagged individuals on the common 434MHz frequency. The primary advantage of using solar-powered tags is that they have an unlimited lifespan, although this limits beep detections to the daylight period.

We also surveyed 25 surrounding waterholes using a handheld receiver to track if radio-tagged birds showed up at surrounding ponds and to monitor flock sizes throughout the season. We conducted one-hour surveys at each waterhole throughout the wintering season. We observed only 4-5 waterholes daily and rotated the survey order weekly to avoid time-of-day bias. Using binoculars, flocks at waterholes were monitored until the flock was out of sight. We recorded the maximum number of individuals observed in each flock as the flock size.

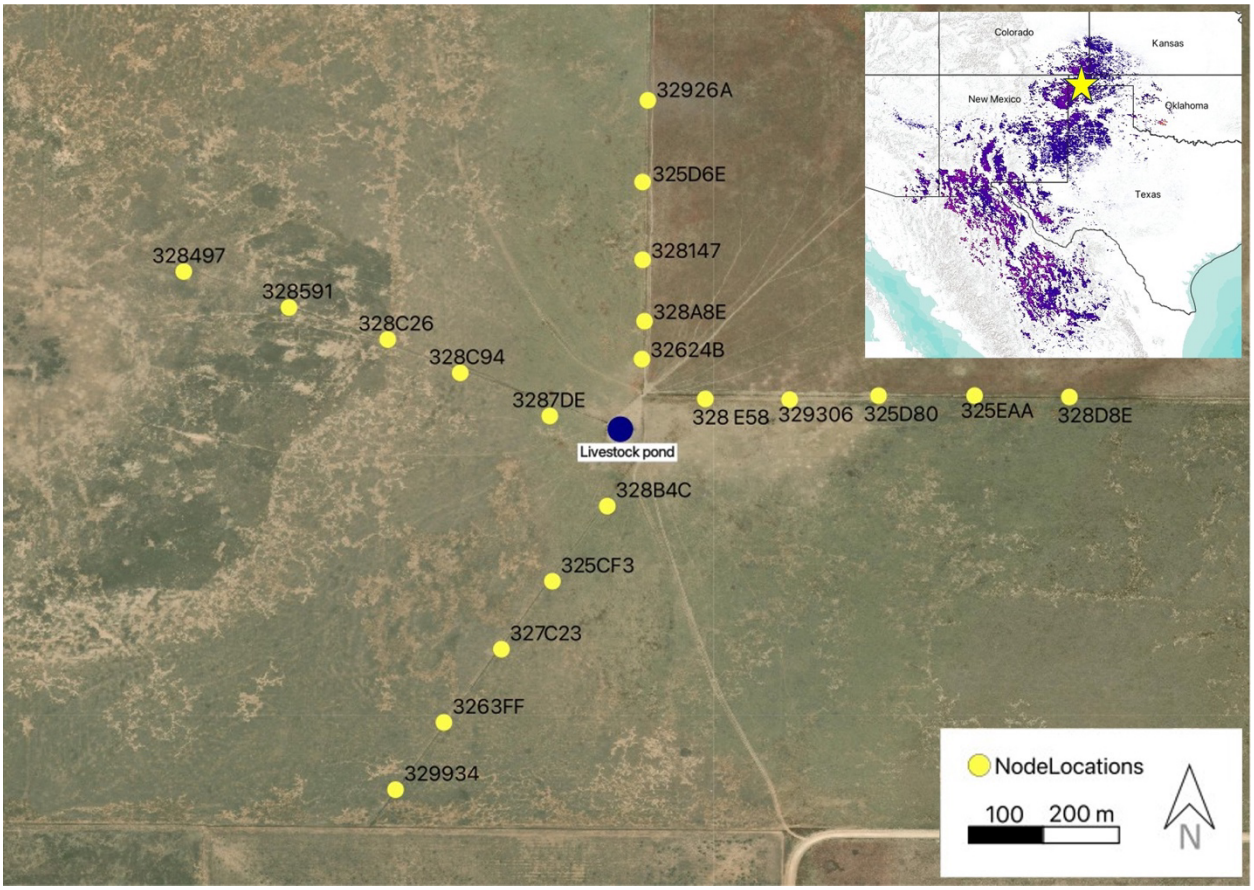

Figure 2.1: Node locations (indicated by yellow circles) around a livestock pond (blue circle) at Rita Blanca National Grasslands. Inset panel shows the relative winter abundance of Chestnut-collared Longspurs (*Calcarius ornatus*) (purple-to-blue) modeled using eBird data (Fink et al. 2022) and the study pond location (yellow star).

Figure 2.2: A: Cellular Tracking Technology node unit attached to an existing fence post, B: Solar-powered LifeTag attached to a Chestnut-collared Longspur (*Calcarius ornatus*).

2.2.3 Weather data

Daily temperature, relative humidity, wind speed, sunrise time, sunset time, and day length data for RBNG were obtained from Oklahoma Mesonet, Boise City station via the "OKmesonet" R package (Allred et al. 2014). The Boise City station (Latitude: 36.69, Longitude: -102.49, elevation = 1267m AMSL) is located 26.1 km from the livestock pond.

Since air temperature and relative humidity at sunrise were correlated (cor = -0.24, p-value = < 0.001) and minimum overnight temperature and minimum relative humidity were correlated (cor = -0.21, p-value = < 0.001), we used dew point temperature and minimum overnight dewpoint temperature in our analysis. We calculated the daily dewpoint temperature at sunrise and the daily overnight minimum dewpoint temperature using relative humidity and temperature data. Both dew

point temperature at sunrise and overnight minimum dew point temperature data were plotted as time series data to visualize variation over the study period (Figure 2.3).

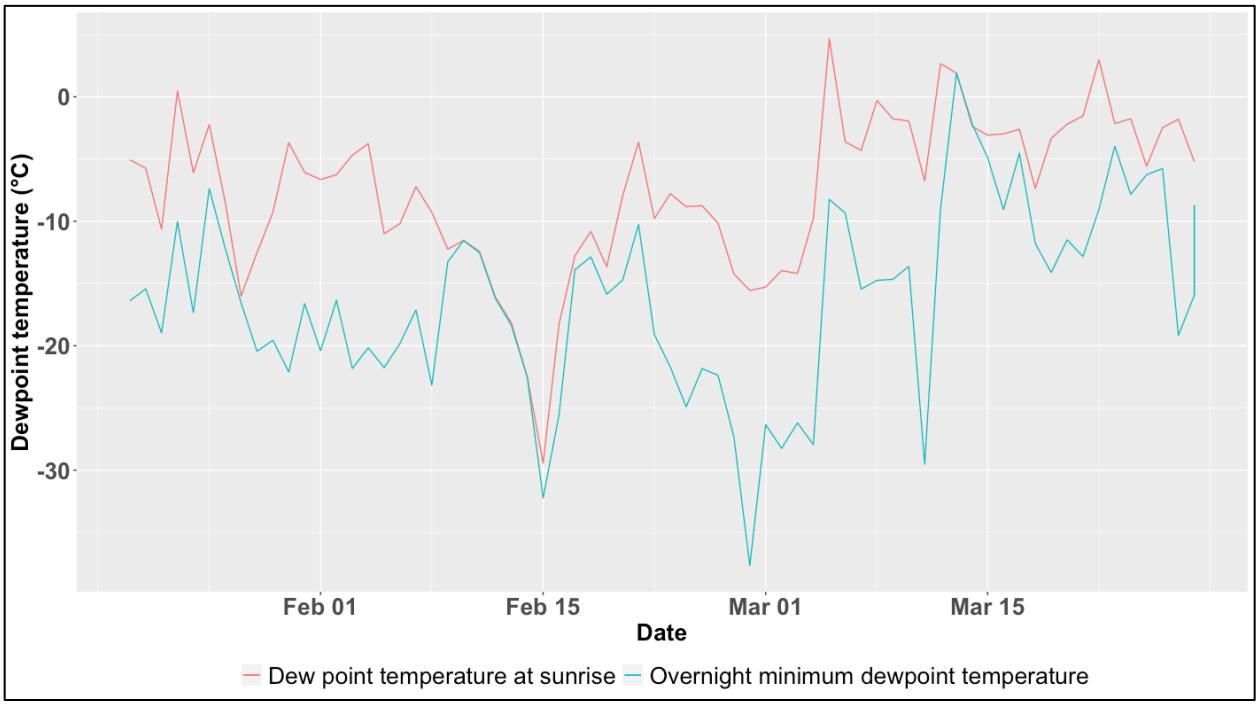

Figure 2.3: Daily dew point temperatures recorded at Boise city mesonet weather station during the study period. The pink solid line represents the dew point temperature at sunrise and the blue solid line represents the overnight minimum dew point temperature.

2.3 Statistical analysis

For our final analysis, we used all data gathered by the nodes while deployed at the study site (January 22-March 28, 2021). Birds with less than 55 beeps were excluded from our analysis. If birds were detected by multiple nodes, we selected the beeps with the strongest signal to avoid duplication. All data processing and analyses were completed using the R statistical environment (RStudio Team 2022). To examine the effects of environmental variables (overnight minimum temperature, overnight minimum relative humidity, overnight minimum dewpoint temperature, temperature at sunrise, relative humidity at sunrise, dewpoint temperature at sunrise, and wind speed at sunrise) on the presence/absence of CCLO in the vicinity of the pond, we constructed

regression trees (Roff and Roff 2003; Breiman 2017) using no more than one absence date adjacent to the presence date to avoid zero inflation. Trees were constructed using the R package 'rpart' (Therneau and Atkinson 2019), with the complexity parameter (cp) set to 0.015, ensuring fine resolution and a response variable of present (1) or absent (0). Results were visualized with the R package 'rpart.plot' (Milborrow and Milborrow 2022).

We used a threshold of at least 9 minutes of absence between visits ("absence timespan") to delineate detections into independent visits to the pond area. If a detection occurred within 9 minutes of the previous detection, it was considered a continuance of the same visit. Preliminary analysis indicated that if we delineated using absence timespans of less than 6 minutes, there was an overabundance of short-duration visits with short absence timespans. This suggested that the birds remained in the area but were not detected for short periods (e.g., flying or landing for short times just beyond the range of the nodes). With at least a 9-minute threshold, there was a lower imbalance between the duration of visits and absence timespans. This generally aligned with our field observations of CCLO, wherein birds would often leave and return to ponds after short reprieves.

During the study period, we examined the effects of environmental variables on the arrival time of the first daily visit of CCLO at the pond by constructing a conditional inference tree using 'ctree' function (Hothorn et al. 2015) in the "partykit" package (Hothorn et al. 2023) in R program. Classification trees are nonparametric tests that simultaneously allow powerful categorical and continuous data comparisons (De'ath and Fabricius 2000). Classification trees can avoid overfitting data and produce easily interpretable graphs. The classification tree used a Bonferroni-adjusted p-value to determine the splits, which is implemented in the R package "party" (Loh

2014). We used time since sunrise, day length, overnight minimum dewpoint temperature, wind speed, and dewpoint temperature at sunrise as environmental variables in the classification tree.

We then developed a Generalized additive mixed model (GAMM) to analyze how environmental conditions (day length, overnight minimum dewpoint temperature, wind speed, and dewpoint temperature at sunrise) would affect the number of pond visits, mean duration of a pond visit, and total duration of visits per day. In the negative binomial GAMM analysis, the random effect was the individual ID, and the dependent variables were the number of visits per day, the mean duration of a visit, and the total duration of the daily visits. We used the Kruskal-Wallis nonparametric ANOVA to compare the mean number of visits per day and the mean total duration of daily visits among individuals (Ostertagova et al. 2014).

2.4 Results

2.4.1 Bird detection by nodes and Flock observations at waterholes

Node units detected beeps when marked birds were in the immediate proximity of the pond (<1km). For a given bird, beeps were counted every minute. We found that Nodes detected beeps from the solar-powered LifeTags from an earliest of 0.161 hours after sunrise to a latest of 0.48 hours before sunset. Out of the 38 CCLOs we tagged, only 13 birds were detected by node units during the three-month period. We observed flocks ranging from 2 - 105 individuals at waterholes. Results from t-test using Least-Square method suggest that the observed flock size declines across the season (slope = -0.1183/day; $t = -5.690$, d.f. = 764, $p < 0.0001$).

2.4.2 Environmental conditions during the study period

The day length increased from 10.07 to 12.45 hours over the study period, with a mean day length of 11.13 hours (SD = 0.7). Overnight minimum temperature ranged from -29.2°C to 10°C, and overnight relative humidity ranged from 8%-100%. Overnight minimum dewpoint temperature

ranged from 1.9°C to -37.7°C, and dewpoint temperature at sunrise ranged from 1.9°C to -29.4°C. Of 68 days, 29 had a minimum overnight dewpoint temperature below -16°C. During the study period, birds were present 67% of the time and were absent 33% of the time. The regression tree using dewpoint temperatures and wind speeds revealed that 51% of CCLO visits were detected on days when the overnight minimum dewpoint temperature was below -16°C and dewpoint temperature at sunrise was above -18°C (Figure 2.4A). Results from regression tree that included overnight minimum relative humidity and overnight minimum temperature revealed that, 53% of CCLO visits were detected when the minimum dewpoint temperature was below -16°C, but the overnight minimum temperature was above –22°C. Only 2% was detected when the overnight minimum temperature was below –22°C. 38% of the CCLO presence data was recorded when the overnight minimum dewpoint temperature was above –16°C and overnight minimum relative humidity was less than 87% (Figure 2.4B).

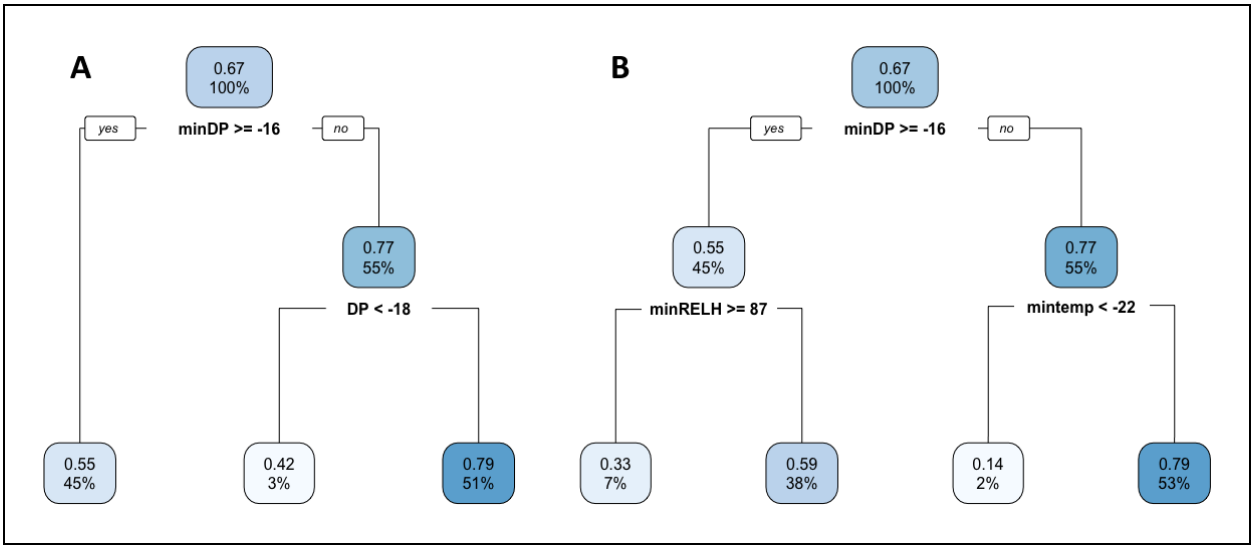

Figure 2.4: The panels show the Presence of Chestnut-collared Longspurs (CCLO) around the livestock pond at Rita Blanca National Grassland, Texas, USA, from January to March 2021. A: Presence (%) of CCLO based on Overnight minimum dewpoint temperature and Dewpoint temperature at sunrise. B: Presence of CCLO (%) based on Overnight minimum temperature, overnight minimum relative humidity, temperature at sunrise, and relative humidity at sunrise.

According to the conditional inference tree results, the first daily detections of each tagged bird at the pond occurred significantly earlier (< 4.5 hours after sunrise) if the minimum overnight dewpoint temperature ranged from -15.86°C to -29.52°C, relative to overnight conditions with either higher or lower dewpoints. Furthermore, among the early-arriving CCLO, if the dewpoint had risen above -7.2°C by sunrise, birds arrived even earlier (3 hours after sunrise) than if the conditions remained cold & dry (i.e., dewpoints <-7.2°C; Figure 2.5).

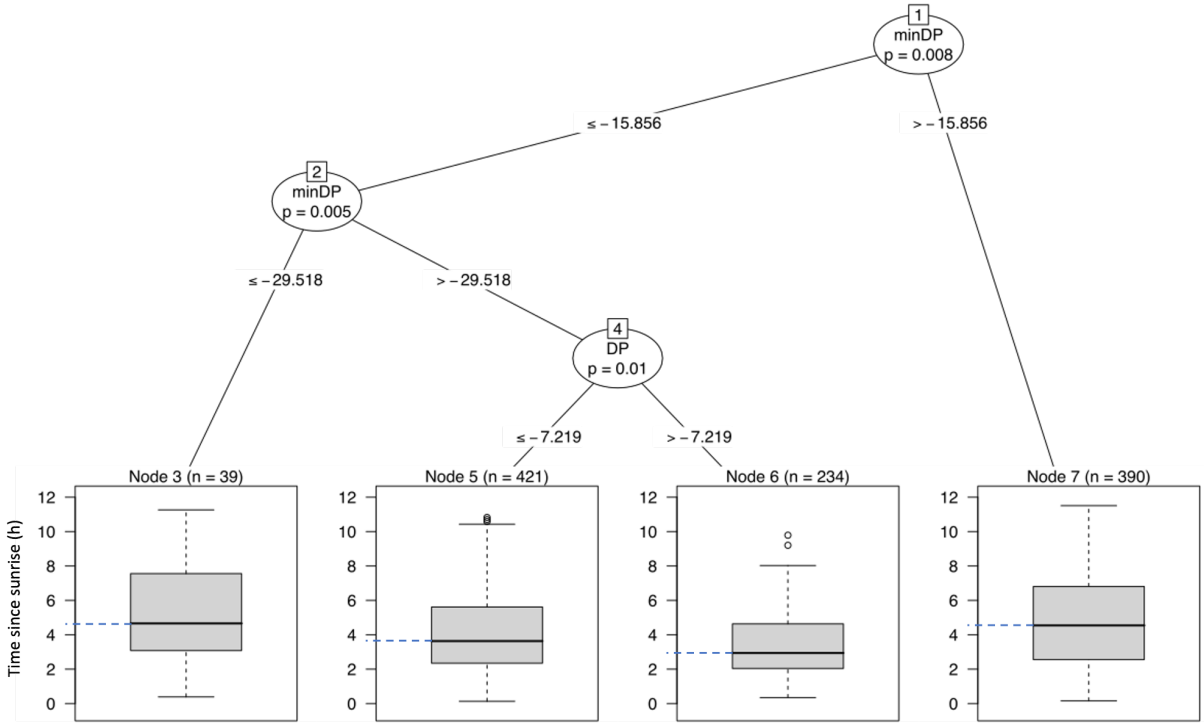

Figure 2.5: Conditional inference tree used for the arrival time of the first visit of Chestnut-collared Longspurs at livestock pond. minDP = minimum overnight dew point temperature, DP = dew point temperature at sunrise.

2.4.3 Number and duration of visits at the livestock pond

The number of CCLO daily visits to the pond varied across the season, ranging from 0-15 visits. When birds visited the pond, the mean number of visits per day was 2.99 (SD= 2.35) with a median of 2 visits per day. Birds increased the number of daily visitations closer to their

migration (Figure 2.6A). Kruskal-Wallis test results suggested that individuals' mean number of daily visits was significantly different among individuals (Kruskal-Wallis H = 57.7, df = 12, p-value = 5.9e-06) (Supplementary materials: Figure S2.1). The mean duration of pond visits varied across the season, ranging from 0-33 minutes per visit, with an average of 3.77 minutes (SD = 3.87) and a median of 3 minutes per visit. The mean duration of the birds' visits decreased over the season (Figure 2.6B). Kruskal-Wallis test results suggest that the mean duration of a visit of individuals was significantly different (Kruskal-Wallis H = 57.66, df = 12, p-value= 5.9e-08) (Supplementary materials: Figure S2.2). The total duration of daily pond visits varied across the season, ranging from 0-84 minutes per day. The average of total duration of daily visits was 14.12 minutes (SD = 31.13), with a median of 6 minutes per day. The total duration of daily visits increased over the season (Figure 2.6C). A Kruskal-Wallis test results suggest that individuals' total duration of visits was significantly different (Kruskal-Wallis H = 70.459, df = 12, p-value = 2.63e-10) (Supplementary materials: Figure S2.3).

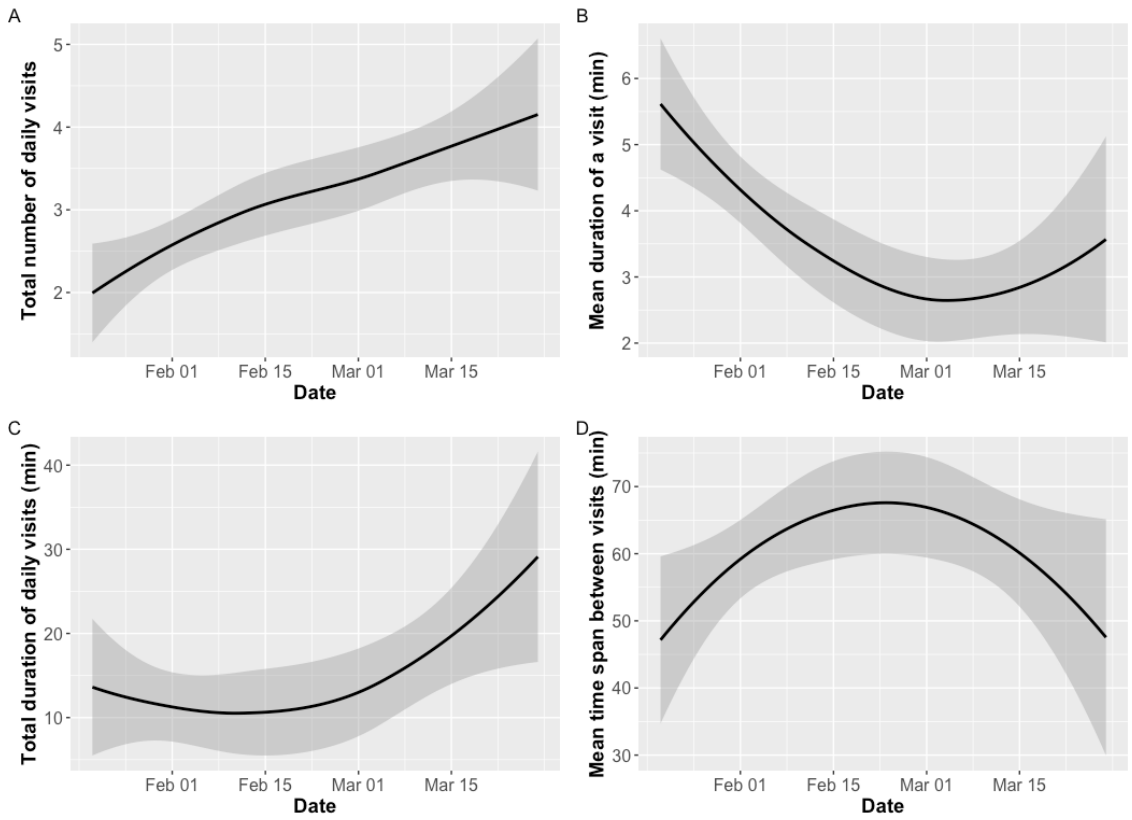

Figure 2.6: Activity of Chestnut-collared Longspur population around the livestock pond at Rita Blanca National Grasslands across the winter season. A: Total number of daily visits, B: Mean duration of a visit (min), C: Total duration of daily visits (min), D: Mean Time span between visits (min). Solid lines are loess regression fitting (span = 0.95), implemented with R function geom_smooth from ggplot2).

2.4.4 Effects of environmental variables on the number of daily pond visits

The GAMM model output of each environmental variable is provided in Table 2.2. The effective degree of freedom reflects the degree of non-linearity of a curve (Wood 2006). EDF>2 implies a quadratic relationship. Results suggest that the number of visits has a significant linear relationship with day length. The number of visits showed a negative, linear, but non-significant relationship with overnight minimum dewpoint temperature, while wind speed had a positive, linear, non-significant relationship. Dewpoint temperature at sunrise had neither a linear nor significant relationship (Figure 2.7).

Table 2.1: Generalized Additive Mixed Model (GAMM) output summaries for the number of visits at the vicinity of the standing pond of Chestnut-collared Longspurs at Rita Blanca National Grassland, relative to predictor variable (Edf: effective degree of freedom). Significant p-values are highlighted in **bold.**

Predictor variables for number of visits	Approximate significance of smooth terms		p-value
	Edf	F	
Day Length	1.00	29.459	**<2.54e-07**
Overnight minimum dewpoint temperature	1.00	3.055	0.0814
Wind Speed	1.00	2.919	0.0885
Dew point temperature at sunrise	2.049	2.203	0.0705

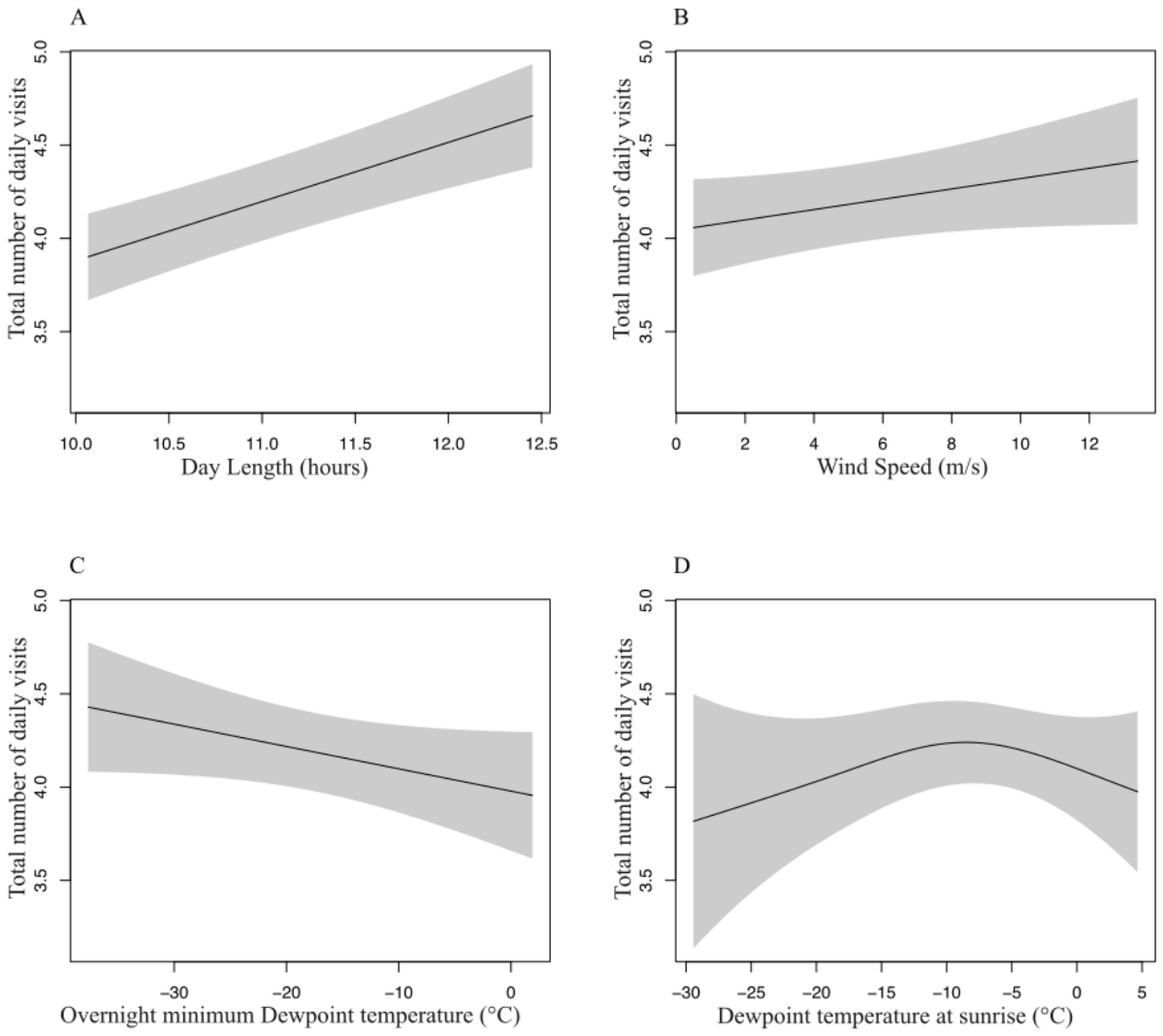

Figure 2.7: Number of visits of Chestnut-collared Longspurs at a livestock pond from January 2021 to March 2021 at Rita Blanca National Grasslands relative to predictor variables. A: Day length (hours), B: Wind speed (m/s), C: Overnight minimum dew point temperature (°C), D: Dew point temperature at sunrise (°C). The shaded area represents the confidence interval.

2.4.5 Effects of environmental variables on the mean duration of pond visits

The model output for each environmental variable is provided in Table 2.3. Results suggest that the mean duration of visits has a significant non-linear relationship with day length, wind speed at sunrise, and overnight minimum dewpoint temperature. However, dewpoint temperature

at sunrise did not have a significant relationship with the mean duration of the daily visits (Figure 2.8).

Table 2.2: Generalized Additive Mixed Model (GAMM) output summaries for the mean duration of daily visits at the vicinity of the standing pond of Chestnut-collared Longspurs at Rita Blanca National Grassland, relative to predictor variable (Edf: effective degree of freedom). Significant p-values are highlighted in **bold.**

Predictor variable for mean duration of visits	Approximate significance of smooth terms		p-value
	Edf	F	
Day Length	3.213	13.794	**<2e-16**
Overnight minimum dewpoint temperature	1.787	13.318	**1.97e-04**
Wind Speed	3.219	2.685	**0.0267**
Dew point temperature at sunrise	1.000	0.028	0.867

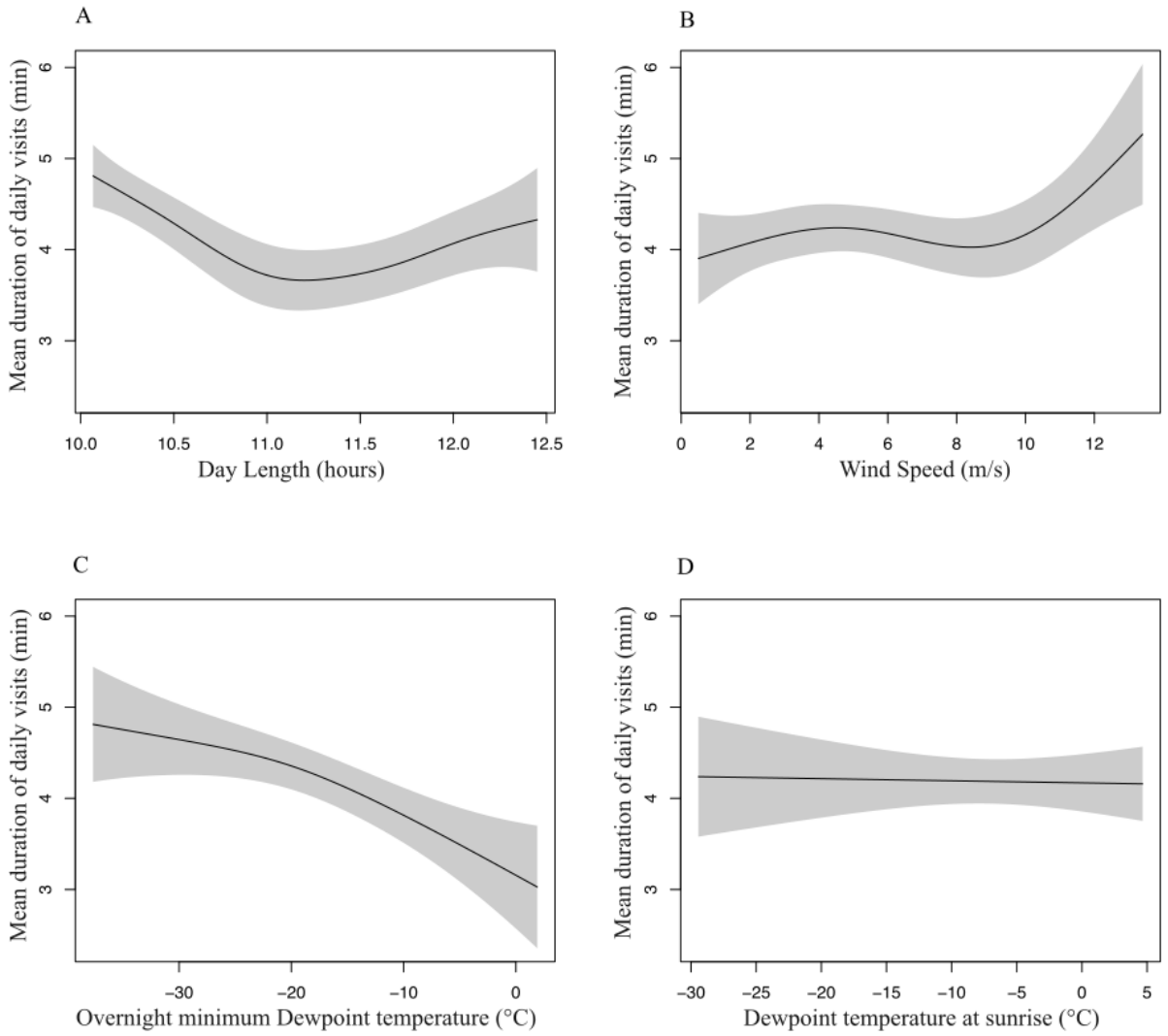

Figure 2.8: Mean duration of daily visits of Chestnut-collared Longspurs at a livestock pond from January 2021 to March 2021 at Rita Blanca National Grasslands relative to predictor variables. A: Day length (hours), B: Wind speed (m/s), C: Overnight minimum dew point temperature (°C), D: Dew point temperature at sunrise (°C). The shaded area represents the confidence interval.

2.4.6 Effects of environmental variables on the total duration of pond visits

The GAMM model output for each environmental variable is provided in Table 2.4. Results suggest that the total duration of daily visits has a significant linear relationship with overnight minimum dewpoint temperature, while day length has a significant quadratic relationship. Wind

speed had a significant non-linear relationship with the total duration of the daily visits (Figure 2.9).

Table 2.3: Generalized Additive Mixed Model (GAMM) output summaries for the total duration of daily visits at the vicinity of the standing pond of Chestnut-collared Longspurs at Rita Blanca National Grassland, relative to predictor variable (Edf: effective degree of freedom). Significant p-values are highlighted in **bold.**

Predictor variables for total duration of visits	Approximate significance of smooth terms		p-value
	Edf	F	
Day Length	2.522	0.17	**0.037**
Overnight minimum dewpoint temperature	1	11.302	**0.001**
Wind Speed	3.049	3.828	**0.008**
Dew point temperature at sunrise	1.992	1.955	0.133

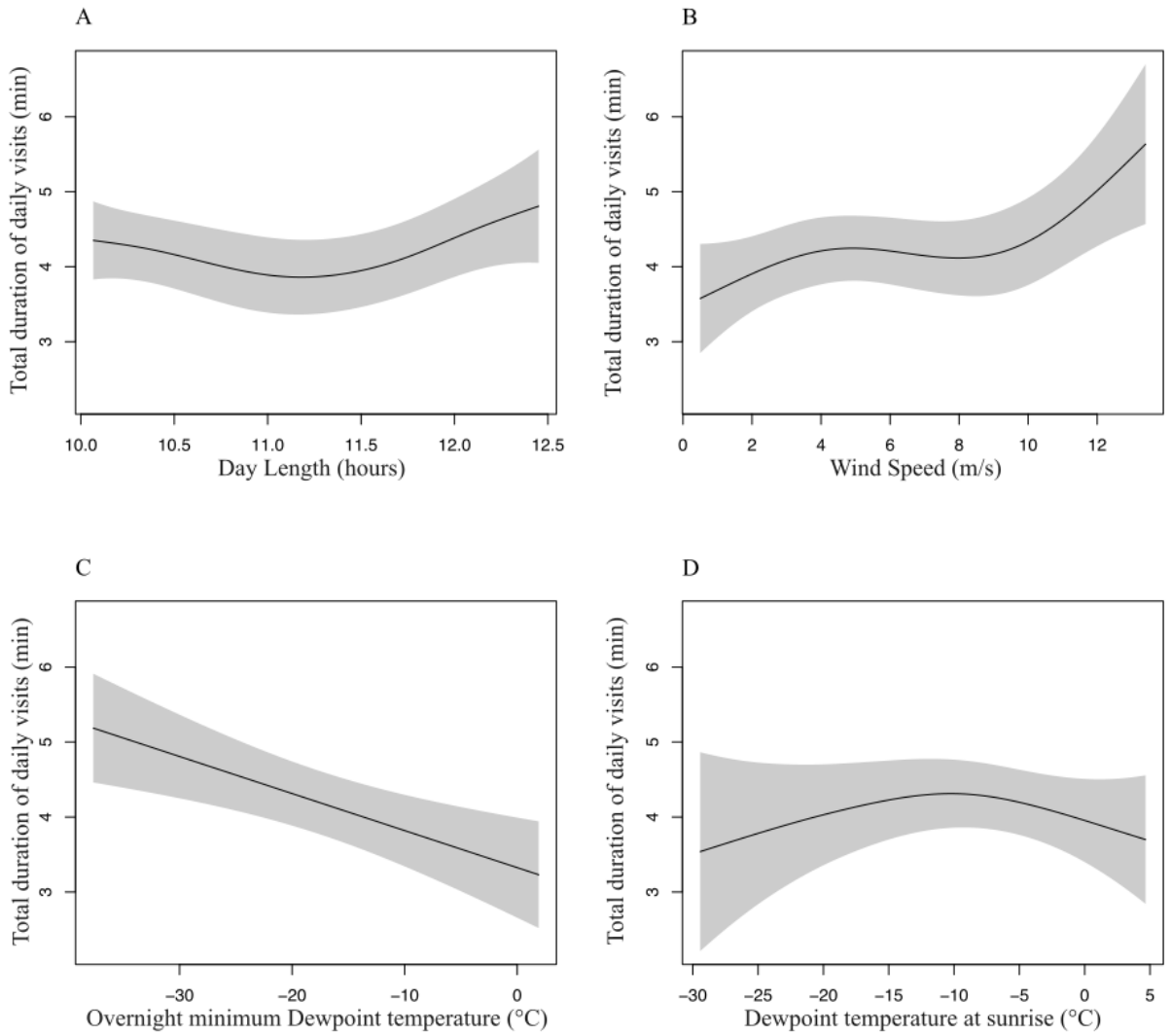

Figure 2.9: Total duration of daily visits of Chestnut-collared Longspurs at a livestock pond from January 2021 to March 2021 at Rita Blanca National Grasslands relative to predictor variables. A: Day length (hours), B: Wind speed (m/s), C: Overnight minimum dew point temperature (°C), D: Dew point temperature at sunrise (°C). The shaded area represents the confidence interval.

2.5 Discussion

Chestnut-collared Longspurs appear to be present in the vicinity of the pond in a range of environmental conditions, except in extremely cold and dry overnight conditions. Further, CCLOs adjust their daily movements to and from a livestock pond to balance their water needs with water accessibility. Following dry and/or cold (i.e., low dewpoint) overnight conditions, which can drain

body moisture more readily, radio-tracked individuals arrived earlier in the subsequent mornings when compared to overnight conditions with higher dewpoint temperatures. Furthermore, as the day length grew across the season, individuals were in the vicinity of the pond more frequently, with decreased mean duration. Birds visited and remained close to the pond for greater proportions of the day when wind speeds were elevated and when overnight dewpoint temperatures were low. Collectively, these data support the hypothesis that CCLOs adjust their activity in the vicinity of ponds in response to environmental conditions, especially those associated with greater body water loss.

Even though homeotherms generate water as a by-product of energy metabolism by oxidizing organic compounds containing hydrogen (i.e., proteins and fat) (Bartholomew and Cade 1963; Jenni and Jenni-Eiermann 1998) in the absence of ingestible water, fat catabolism is greatly increased to produce metabolic water (Rutkowska et al. 2016). Since fat catabolism is accompanied by heat production, it leads to additional costs related to heat dissipation and constraining physiological performance (Speakman and Król 2010). Further, when birds are under cold stress, dehydration may occur via the lungs (Klaassen 1996). Inhaled cold, dry air is brought to body temperature and saturated with water. The air cools down during exhalation, causing water vapor condensation, which leads to partial recovery of water lost during respiration (Berger et al. 1971). However, the exhaled air temperature is still above the inhaled air temperature, and the inhaled air is rarely saturated with water, in contrast to the exhaled air, resulting in a net water loss (Berger et al. 1971). Therefore, birds need to spend sufficient time not just foraging but also replenishing water storage in winter.

In the winter, birds must actively find water resources to replenish their water needs. When the temperature drops below freezing, surface water resources are frozen. Even though CCLO

visited the pond earlier in the day when conditions were relatively cold and dry, these visits were delayed until the conditions improved to the point where there was likely to be liquid water available, possibly due to warming conditions upon sunrise. Longspurs delayed their first visit when overnight temperatures were below -15.86°C and dew point temperature at sunrise was below -7.2°C. Personal observations supported this finding, as CCLO began visiting the frozen pond when liquid water became available at the fringes of the pond.

Over the study period, a shift in CCLO activity in the vicinity of the pond to shorter but more frequent visits resulted in an increase in the total duration of daily pond visits. Though the absence timespan (time between visits) displayed a slight increase from February 15 through March 1, the mean absence timespan between visits remained relatively equal throughout the study period (Figure 2.6D). These results suggest that CCLO were in the vicinity of the pond at regular intervals, though the duration of those visits decreased over time. This combination results in a higher number of daily visits, which is compounded by the increasing day length.

Birds are known to increase their body mass and energy intake to accumulate fat tissues before migration to be used as fuel during migration (Biebach et al. 1986). Therefore, this shift toward a higher number of shorter visits to water sources may reflect a shift toward more active behavior with more foraging in the taller grasses away from the pond, avoidance of predator attraction sites, or a combination of both. Our observation that CCLO flock sizes significantly decreased over the late winter supports the assertion that the species shifts away from forming large flocks that presumably getting ready for spring migration. CCLO arrives at breeding grounds singly or in groups of 2 -3 birds (Harris 1944).

Our study provides a foundation on how CCLO use standing water during winter and how environmental variables affect both the frequency and duration of their pond visits. Identifying the

number of ponds birds visit within their home range might further clarify their water requirement in winter. This could potentially inform management practices, if providing supplemental water resources could enhance their winter survival. Further analyses across species' home ranges are needed to gain insights into how CCLO use standing water in response to environmental changes.

2.6 Reference

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2.7 Supplementary material

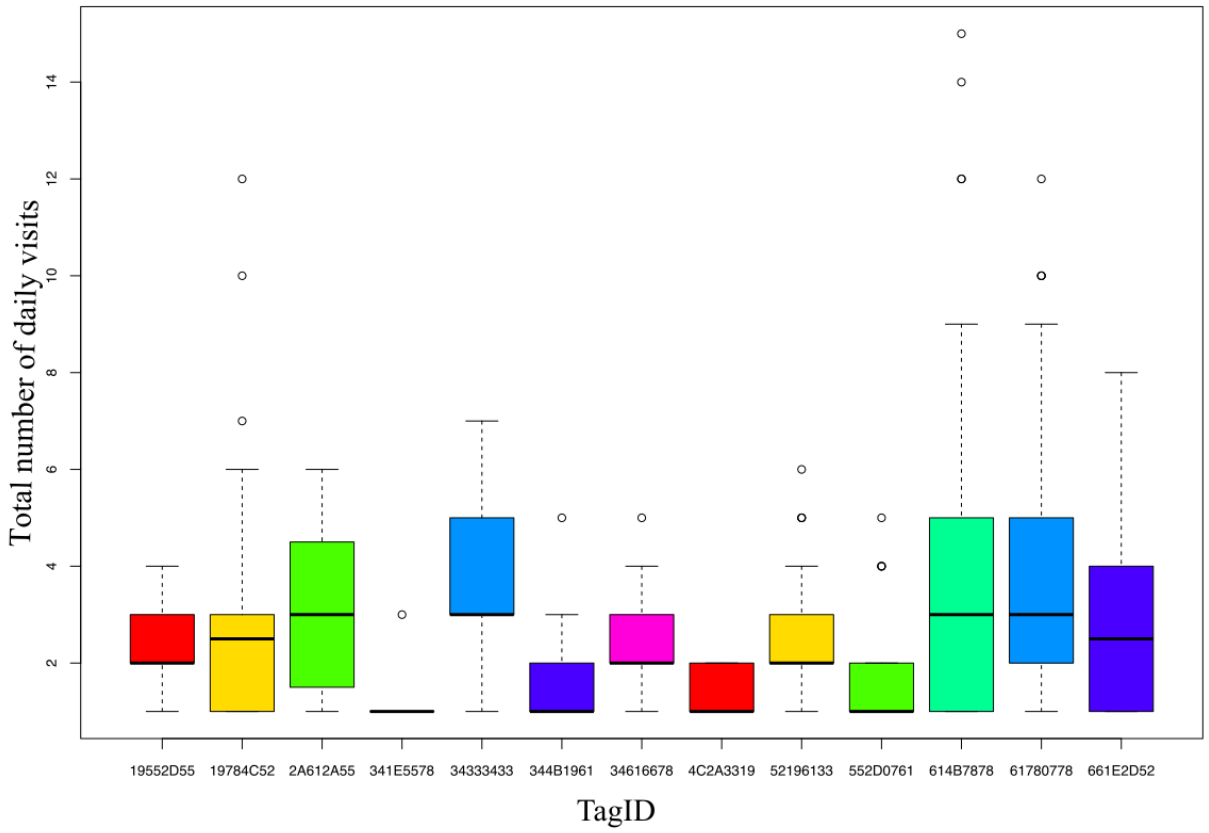

Figure S2.1: Variation of the total number of daily visits among tagged Chestnut-collared Longspurs (Kruskal-Wallis $H = 57.7$, df = 12, p-value = 5.9e-06).

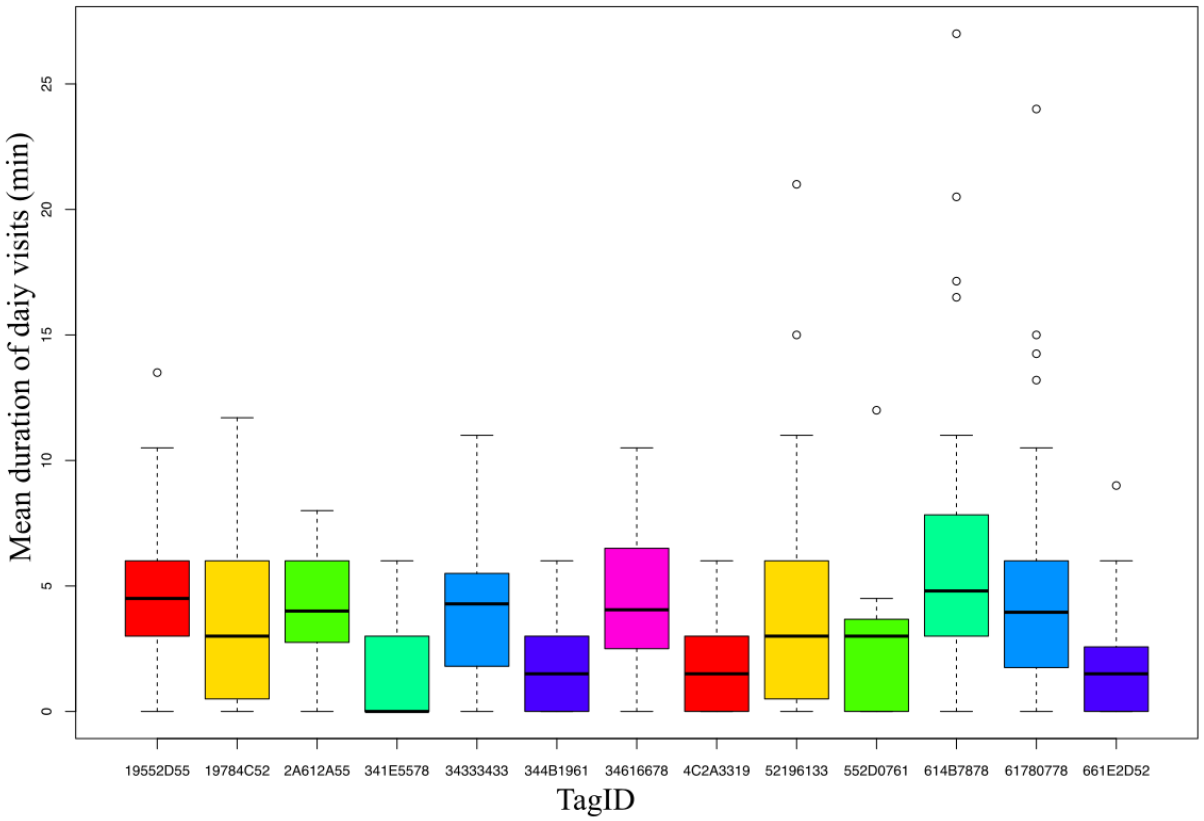

Figure S2.2: Variation of the mean duration of visits (min) among tagged Chestnut-collared Longspurs (Kruskal-Wallis $H = 57.66$, df = 12, p-value= 5.9e-08).

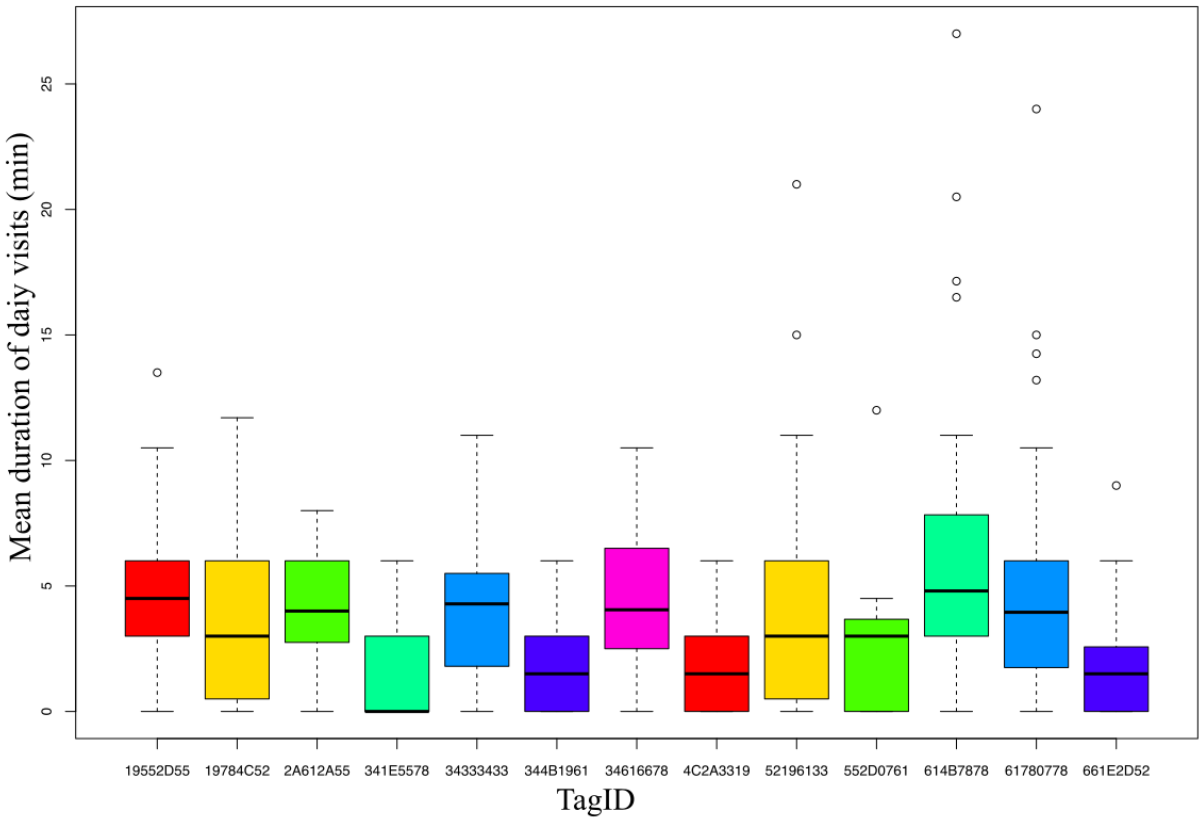

Figure S2.2: Variation of the total duration of visits (min) among tagged Chestnut-collared Longspurs (Kruskal-Wallis $H = 70.459$, df = 12, p-value = 2.63e-10).

Chapter 3: Modeling niche suitability of Yellow-eared Bulbul (*Pycnonotus penicillatus*) in Sri Lanka

3.1 Introduction

Climate plays a major role in shaping species' geographical ranges (Schweiger et al. 2008; Ockendon et al. 2014; Hill and Preston 2015). The global climate has been anthropogenically altered since at least the mid-19th century, with drastic shifts since the 1950s and 1960s (IPCC 2023), forcing species to persist by shifting range with their climatic niches (Kelly and Goulden 2008; Chen et al. 2009; Freeman and Class Freeman 2014). Species that cannot move or adapt may suffer local or complete extinction (Maggini et al. 2011), with reverberating effects on local biological diversity (Santhakumar et al. 2018; Rai et al. 2020). In this respect, range-restricted species such as island endemics may be particularly vulnerable to shifts in climatic niches, as they likely have limited opportunities to colonize new areas (Patten and Patten 2011; Lenoir and Svenning 2015).

Birds respond to climate changes at scales ranging from global (e.g., temperature increases) (Parmesan and Yohe 2003; Chen et al. 2011; Gottfried et al. 2012), to regional (e.g., migrations in latitude or elevation) (Chen et al. 2011; Chhetri et al. 2018), and local (e.g., habitat shifts in tropical systems) (Sekercioglu et al. 2008). While birds are generally thought to be sensitive to climate change (La Sorte and Jetz 2010; Sodhi et al. 2010; Harris et al. 2011; Wormworth and Sekercioglu 2011), those particularly at risk from climate change include geographically isolated, year-round resident endemic species of tropical mountains (Janzen 1967; Sekercioglu et al. 2008) and species inhabiting lowlands without access to higher elevations (Loarie et al. 2009). Emerging evidence also suggests that tropical bird species are actually highly vulnerable to climate change (Sekercioglu et al. 2008). In the absence of information about current extents and predicted

changes of climatic niches for tropical bird species, we will be hindered in choosing appropriate conservation practices, such as guided management of existing habitats or expansion of protected area networks. In this study, we focus on climatic shifts in the highland areas of Sri Lanka that may affect species adapted to this area's unique tropical climatology.

Sri Lanka is a relatively small island in the Indian Ocean (65,525 km^2) but boasts a rich avifaunal diversity of 237 breeding residents, 33 of which are island endemics (Warakagoda et al. 2020). Despite being tropical, there are stark temperature variations across the island, primarily due to the high-elevation topography at its center (Naveendrakumar et al. 2018). Sri Lanka receives most of its precipitation during two monsoon seasons: the southwest 'Yala' monsoon (May to September) and the northeast 'Maha' monsoon (December to February; (Malmgren et al. 2003; Naveendrakumar et al. 2018). Rain predominantly falls in the southwest during the Yala monsoon, leaving the northeastern mountain slopes and the rest of the country drier. In contrast, rain from the Maha monsoon approaches mostly from the northeast, effectively flipping the precipitation map for both the island and its mountain slopes. Because of this, the central mountain range creates a split ecosystem (Premathilake and Risberg 2003). This unique system provides a suitable habitat for several plants and animals endemic to the highlands, including the Yellow-eared Bulbul (*Pycnonotus penicillatus*; Pycnonotidae).

The Yellow-eared Bulbul (hereafter YEBU) inhabits the wet zone highlands of Sri Lanka at elevations above 850m. These bulbuls are a charismatic species with bright yellow auricular "ear" tufts, which gives it high cultural value, exemplified by its image being featured on Sri Lankan currency notes. Their mountain habitats receive an annual average of 132.4 mm of precipitation across 165.5 rainy days (45.3% of the time). YEBU breed in two post-monsoonal seasons (Fishpool and Tobias 2020); the first breeding season occurs from February to May (i.e.,

"post-Maha"), and the second breeding season takes place from August to October (i.e., "post-Yala"). Although YEBU breeding ecology has been studied extensively at a core population in the Horton Plains National Park (Chandrasiri and Mahaupatha 2016 Oct; Chandrasiri and Mahaulpatha 2017; Chandrasiri and Mahaulpatha 2019), no studies have examined the current distribution of the species' climatic niche or how it might shift under climate change.

YEBU was categorized as "Near Threatened" on IUCN Red List assessments from 1998-2016, but in 2020 was downlisted to "Least Concern" (BirdLife International 2023 Oct 14). Even though the YEBU population size has not been quantified, the population trend was assumed to have stabilized because forest cover loss across its range has fallen to below 2% losses over three bulbul generations or 10.9 years (BirdLife International 2023 Oct 14). Yet, forest losses had already been severe, with the central area of Sri Lanka losing 232 ha of tree cover from 2001 to 2022 alone, equivalent to an 8.1% decrease in the central area (Hansen et al. 2013). Despite the assertion that the species' future is apparently secure, the distribution of its current populations and future habitat suitability projections remains poorly understood or entirely unstudied. Since suitable habitat is strongly associated with suitable climatic conditions (Araújo et al. 2006), our study aims to model YEBU's current and future climatic niches to help determine how the range of suitable habitat for this tropical highland resident may be affected by climate change.

The YEBUs' hypothesized stability could be jeopardized if either reproductive season was disrupted by declines or shifts in its preferred climatic niche. Furthermore, the YEBU breeds across three distinct highland regions of Sri Lanka, which may be functionally isolated enough to warrant independent management. With all this in mind, we have centered this study on two interrelated questions: (1) Are there different suitable habitats associated with the two different breeding seasons and the non-breeding season, and if so, how does the distribution vary? (2) Based on these

models, how will the distribution of suitable climatic niches for YEBUs' breeding seasons shift as a result of climate change?" A significant shift from the current climatic niche would have strong implications for this evolutionarily unique species' conservation status and long-term management.

3.2 Methods

3.2.1 Maxent Model

Habitat suitability models use confirmed presence data of species and relevant environmental variables to build the model according to a machine-learning algorithm. These models can forecast geographic shifts (Abdelaal et al., 2019) in species' habitat range in response to environmental changes, whether the range is expanding (Nameer, 2020) or contracting (Bolitho & Newell, 2022). Different modeling techniques are used depending on the format of the biological information recorded at sample sites: (1) presence-only data (which relies solely on presence records) and (2) presence/absence data (each sample site is carefully monitored and the species is documented as present or absent) (Hirzel et al. 2006). The presence-only method assumes that sampling is either random or representative throughout a landscape, and detection probability is constant across sites, which could be a drawback if the model does not meet these assumptions. However, among the available suitability-predicting methods, the presence-only approach is the simplest to model habitat suitability (Peterson et al. 2011). Among the machine-learning modeling methods, the Maximum Entropy (Maxent) method (Phillips et al. 2006) has become one of the most popular modeling techniques because it requires a relatively smaller presence-only sample (Phillips et al. 2006). Maxent has also shown a strong predictive accuracy (Elith* et al. 2006; Graham et al. 2008) with great flexibility and a friendly interface in model construction, allowing the user to alter the model to specific requirements and available information (Merow et al. 2013; Muscarella et al. 2014). Therefore, it has become a popular

predictive tool (Phillips et al. 2006; Kaky and Gilbert 2019; Tang et al. 2021; Valavi et al. 2022; Rodríguez-Pérez et al. 2023). The Maxent model has been widely used in the field of species distribution research, such as the potential distribution of tea (*Camellia sinensis* (L.) O. Kuntze) in Sri Lanka in response to current and future climate change scenarios (Jayasinghe and Kumar 2019), modeling habitat suitability of a range-restricted vulnerable western tragopan (*Tragopan melanocephalus*) of the Himalayan region in response to climate change (Singh et al. 2020), and potential distribution of underutilized fruit species in Sri Lanka (Ratnayake et al. 2020).

We used Maxent to model the current habitat suitability for YEBU (using presence data and environmental variables) and to project future habitat suitability. We used permutation importance and jackknife validation to determine which environmental variables are the most influential in the distribution. Permutation importance indicates which environmental variables are significant in Maxent's final model. Jackknife validation evaluates the relative impact of each variable on the final model by generating additional models with each variable in isolation and with each variable excluded. The results of these additional models are compared to the final model to determine the relative impact of each variable. We used 75% of occurrence points as a training data set, and the remaining 25% was used as a test data set, with auto features for YEBU Maxent modeling. The Maxent output was evaluated by the Area Under the Curve (AUC) from the receiver operating characteristics (ROC).

3.2.2 Collection and preparation of occurrence points

Occurrence data of YEBU were downloaded from the Global Biodiversity Information Facility (GBIF) and eBird. GBIF is a portal that gathers data from museums, surveys, and other data sources, and eBird is a citizen-based bird observation network. We only used complete checklists on eBird. The occurrence points for YEBU from 1970-2022 during breeding season 1

(hereafter B1), breeding season 2 (B2), and the non-breeding season (NB) were organized and cleaned to remove duplicate coordinates to avoid model overfitting and bias. We incorporated 197 occurrence points for breeding season 1, 61 occurrence points for breeding season 2, and 225 occurrence points for the non-breeding season in the final analysis and plotting of the distribution map (Figure 3.1).

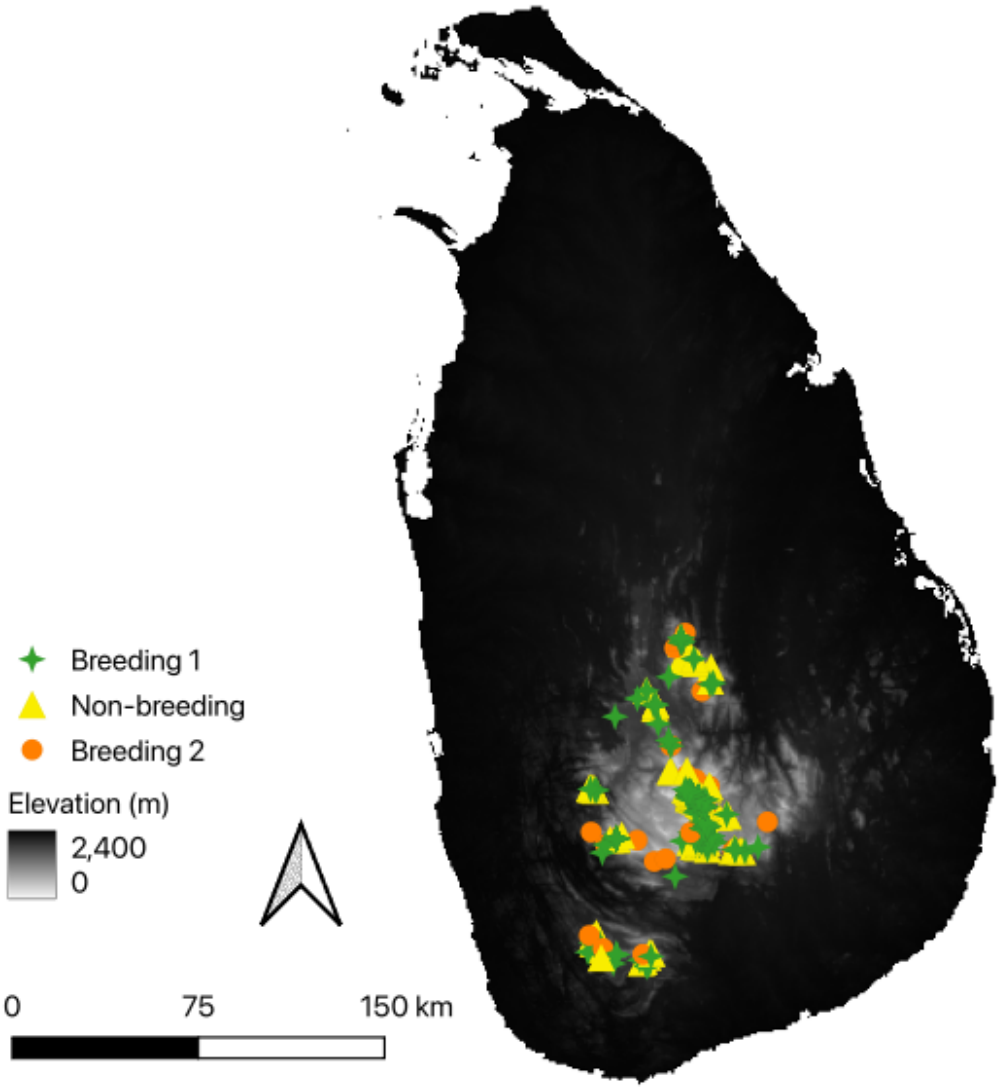

Figure 3.1: Occurrence points for Yellow-eared Bulbul (*Pycnonotus penicillatus*) during breeding season 1 (green star), breeding season 2 (orange circles), and non-breeding season (yellow triangles) in Sri Lanka.

3.2.3 Environmental variables

Temperature, rainfall, geographical barriers, and other environmental factors such as geological formations influence species distribution (Kaeslin et al. 2012; Gao et al. 2022). To determine which environmental factors influence YEBU distribution during the breeding seasons and the non-breeding season, 19 bioclimatic variables, one biophysical variable (elevation), and one ground cover factor (forest cover) were included in our model (Table 3.1). Current bioclimatic factors and elevation data from 1970–2000 were used to predict current distribution. All environmental variables and elevation data were downloaded from the World Climate Database WorldClim2.1 (https://www.worldclim.org/) at 30s (about 1 km × 1 km) coordinate system (WGS1984). The ground cover type and vegetation coverage data with a resolution of 1 km were obtained from the Global Forest change (Hansen et al. 2013). The above data were converted into ".asc" files required by Maxent modeling using the ArcGIS software.

By default, Maxent outputs a 'cloglog' estimate of the probability of occurrence between 0 and 1. We classified these suitability estimates into four classes: unsuitable (values $\leq$ 0.25), marginal (values 0.25 - $\leq$ 0.5) suitability, moderate suitability (values 0.5 - $\leq$ 0.75), and most suitable (values 0.75 $\leq$ 1). To determine if the present distribution of moderate and most suitable habitats for the bulbul were non-randomly distributed with respect to slope and aspect, we conducted a chi-squared distribution test of the 1km^2 pixels within the rasters for suitability relative to each of these topographic categories. For slope, we classified the landscape as either hillside (>10% slope) or flat ($\leq$ 10% slope), while aspect we classified according to whether the slopes faced either the southwest or northeast monsoon (202.5-247.5° or 22.5-67.5°) or were off-axis relative to either monsoon.

3.2.4 Future breeding climatic niche suitability

We used three atmosphere-ocean General Circulation Models (GCMs): MIROC6 (Tatebe et al. 2019), CNRM-ESM2-1 (Séférian et al. 2019), and CNRM-CM6-1 (Voldoire et al. 2019) models to predict future climatic suitability for YEBU distribution. Out of four emission scenarios driven by different Shared Socio-economic Pathways (SSPs), only SSP1-2.6 (the most optimistic scenario) was used in our analysis. Because our goal was to predict climatically suitable habitats for YEBU in the future, we did not include either elevation or tree cover in future projections.

Table 3.1: List of environmental and bioclimatic variables used to predict the current and future habitat suitability for Yellow-eared bulbul (*Pycnonotus penicillatus*)

Code	Environmental/ bioclimatic variables	Unit
Bio1	Annual Mean Temperature	°C
Bio2	Mean Diurnal Range (Mean of monthly (max temp–min temp))	°C
Bio3	Isothermality (Bio2/Bio7) (×100)	–
Bio4	Temperature Seasonality (standard deviation × 100)	C of V
Bio5	Max Temperature of Warmest Month	°C
Bio6	Min Temperature of Coldest Month	°C
Bio7	Temperature Annual Range (Bio5–Bio6)	°C
Bio8	Mean Temperature of Wettest Quarter	°C
Bio9	Mean Temperature of Driest Quarter	°C
Bio10	Mean Temperature of Warmest Quarter	°C
Bio11	Mean Temperature of Coldest Quarter	°C
Bio12	Annual Precipitation	mm
Bio13	Precipitation of Wettest Month	mm
Bio14	Precipitation of Driest Month	mm
Bio15	Precipitation Seasonality (Coefficient of Variation)	
Bio16	Precipitation of Wettest Quarter	mm
Bio17	Precipitation of Driest Quarter	mm
Bio18	Precipitation of Warmest Quarter	mm
Bio19	Precipitation of Coldest Quarter	mm
ELE	Elevation	m

3.3 Results

YEBU were distributed differently during the B1, B2, and NB seasons (Supplementary materials: Figure S3.1). The MaxEnt cloglog output estimating current habitat suitability fit the YEBU occurrence data well. Maxent's Area Under the Curve (AUC) scores for the test data (random test percentage = 25%) for B1, B2, and NB were 0.98 (SD = 0.007), 0.99 (SD 0.004), and 0.98 (SD 0.008), respectively. The AUC score for the test data for the combined breeding seasons (both B1 and B2) was 0.97 (SD 0.007) (Supplementary material: Figure S3.2). AUC scores for training data for B1, B2, and NB were 0.98, 0.99, and 0.99 respectively. The AUC score training data for the combined breeding seasons was 0.98, indicating a high level of accuracy in the model fit (Wiley et al. 2003).

3.3.1 Current Habitat Suitability for B1

Permutation importance results indicated that among the environmental variables used, the minimum temperature of coldest month (bio6) showed the greatest impact (39.9%), followed by the mean diurnal range (bio2) (15%) and the mean temperature of the wettest quarter (bio8) (10.8%) (Supplementary material: Table S 3.1). Jackknife validation indicated that the environmental variables that were most useful in estimating the distribution of YEBU (relatively high gain) were Annual Mean Temperature (bio1), Mean Temperature of the Warmest Quarter (bio10), Mean Temperature of the Coldest Quarter (bio11), Max Temperature of the Warmest Month (bio5), Min Temperature of Coldest Month (bio6), Mean Temperature of Wettest Quarter (bio8), Mean Temperature of Driest Quarter (bio9), and Elevation. The highest gain variable was the mean temperature of the driest quarter (bio9) (Supplementary materials: Figure S3.3A).

The dependence of predicted suitability on the environmental variables was determined through response curves, as shown in Figure 3.2. According to the response curves, high

probabilities of presence were predicted when the minimum temperature of the driest month (bio6) was low, and suitability decreased with increased temperature. However, YEBU prefer a diurnal range (bio2) between 6-8°C. The response curve for the mean temperature of the wettest quarter (bio8) follows a similar pattern as the response curve for the minimum temperature of the driest month.

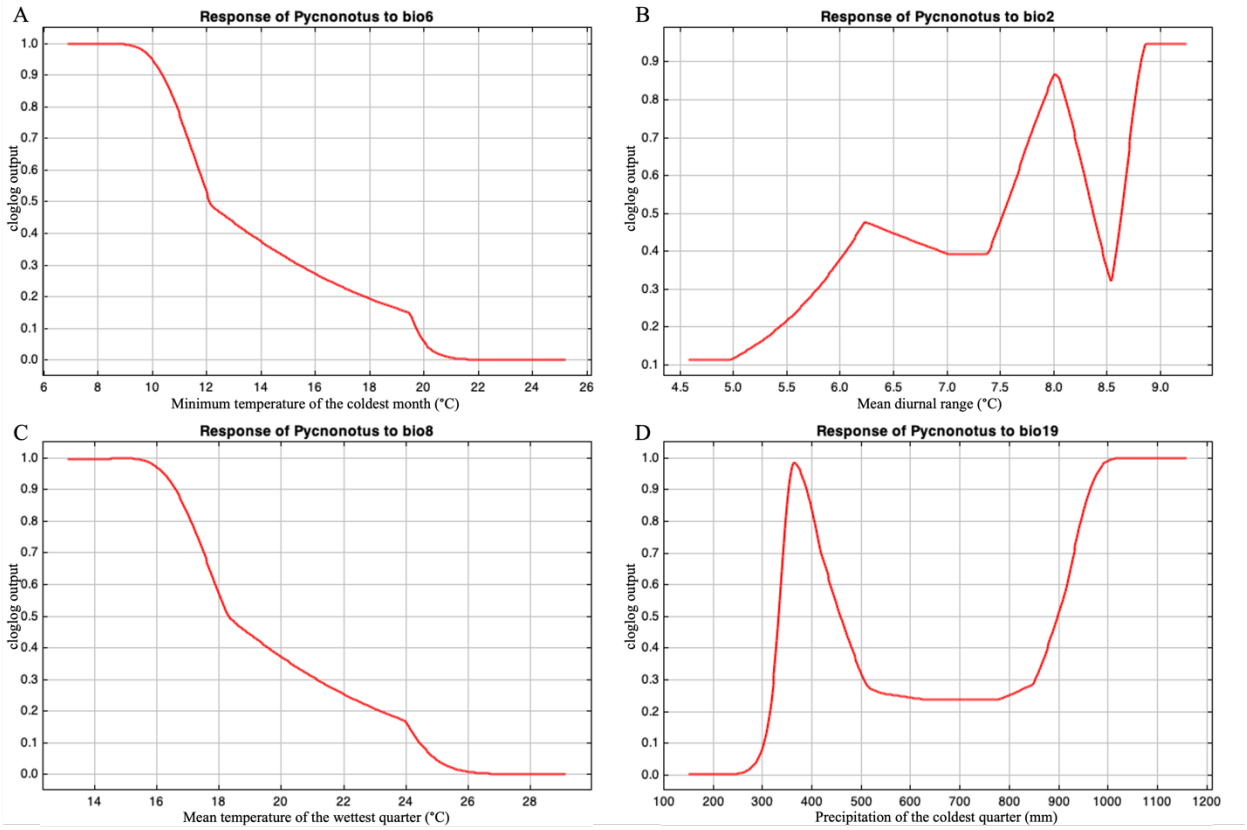

Figure 3.2: Response curves for the major predictors of habitat suitability of Yellow-eared Bulbul (*Pycnonotus penicillatus*) during breeding season 1, based on the Maxent model using only bioclimatic variables: A – minimum temperature of the coldest month (bio 6) (°C), B –mean diurnal range (bio 2) (°C), C- mean temperature of the wettest quarter (bio 8) (°C), D- precipitation of coldest quarter (bio 19) (mm).

3.3.2 Current Habitat Suitability for B2

Permutation importance results indicated that among the environmental variables used, the mean temperature of the driest quarter (bio9) showed the greatest impact (93.7%), followed by precipitation of the coldest quarter (bio19) (1.6%) and mean diurnal range (bio2) (1.3%)

(Supplementary material: Table S3.1). The Jackknife validation indicated that the mean temperature of the driest quarter (bio9) was the most important predictor of YEBU distribution during their second breeding season (Supplementary material: Figure S3.3B).

The response curves showing the effect of individual variables for model prediction are presented in Figure 3.3. According to the response curves, high probabilities of presence were predicted when the mean temperature of the driest quarter (bio9) is below 18°C. The response curve for the precipitation of the coldest month (bio19) shows that bulbuls prefer rainfall of 375mm. As the precipitation increases, habitat suitability for YEBU decreases.

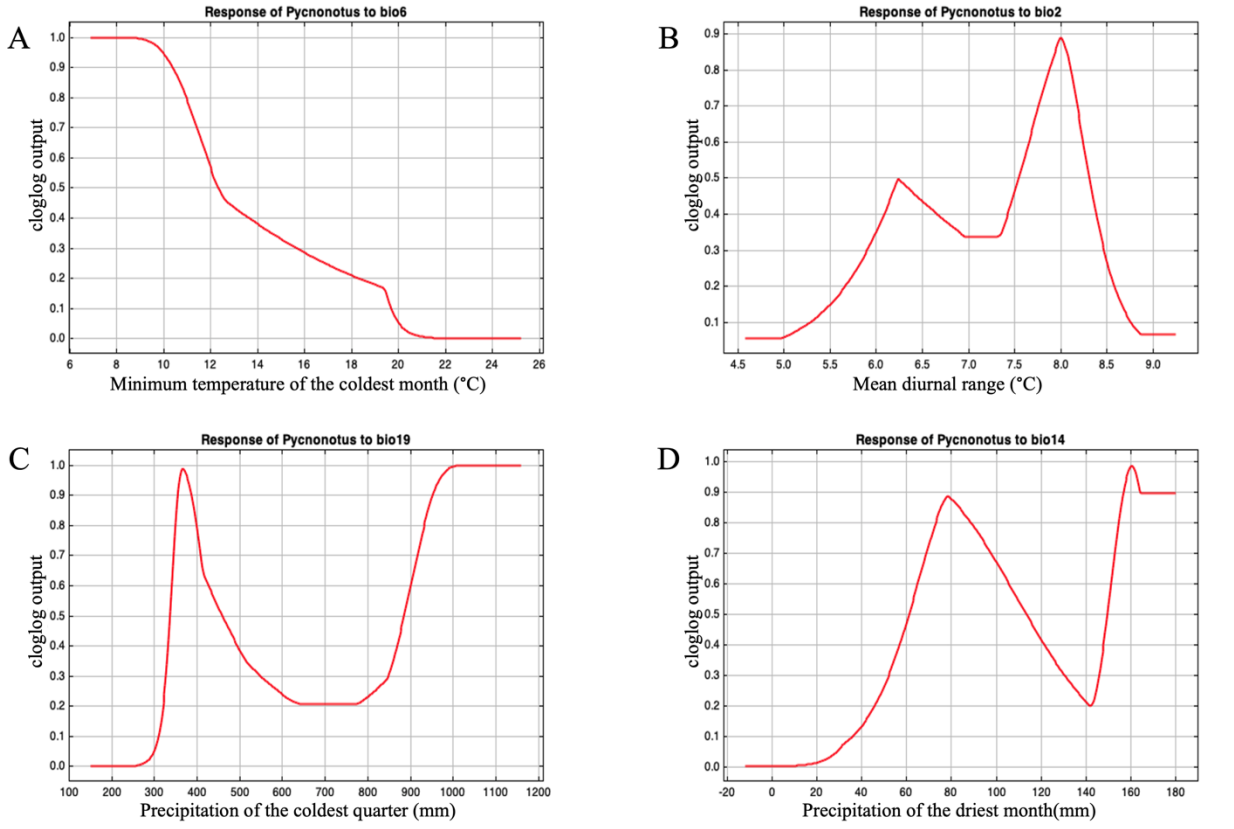

Figure 3.3: Response curves for the major predictors of habitat suitability of Yellow-eared Bulbul (*Pycnonotus penicillatus*) during breeding season 2, based on the Maxent model: A –mean temperature of the driest quarter (bio 9) (°C), B –precipitation of the coldest quarter (bio 19) (mm), C- mean diurnal range (bio 2) (°C), D- precipitation of the wettest quarter (bio 16) (mm).

3.3.3 Current habitat suitability for the non-breeding season

Permutation importance results indicated that among the environmental variables used, the mean temperature of the wettest quarter (bio8) was the most influential and contributed to modeling the non-breeding distribution (42.5%). The mean temperature of the driest quarter (bio9) (34%) was the next most influential variable, followed by annual precipitation (bio12) (7%). Jackknife validation indicated that the environmental variables that were most useful in estimating the distribution of YEBU (relatively high gain) were the mean temperature of the driest quarter (bio9), annual mean temperature (bio1), and mean temperature of the warmest quarter (bio10). (Supplementary material: Table S3.1) was the most important predictor of YEBU distribution during their second breeding season (Supplementary material: Figure S 3.3C).

According to the response curves (Figure 3.4), YEBU habitat suitability decreases with an increased mean temperature of the wettest quarter (bio8) (Figure 3.4A) and mean temperature of the driest quarter (bio9) (Figure 3.4B). Bulbuls also prefer annual precipitation (bio12) of 2000mm during their non-breeding season.

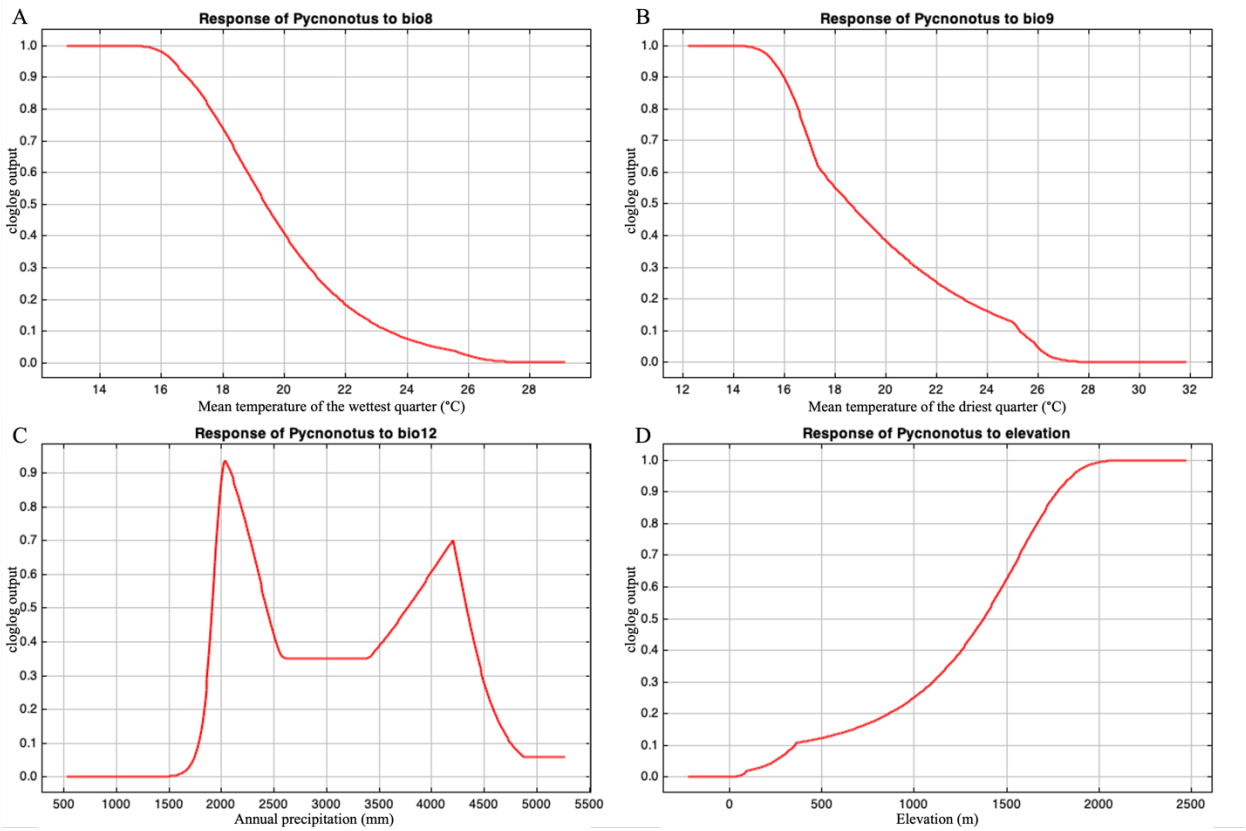

Figure 3.4: Response curves for the major predictors of habitat suitability of Yellow-eared Bulbul (*Pycnonotus penicillatus*) during the non-breeding season, based on the Maxent model: A –mean temperature of the wettest quarter (bio 8) (°C), B - mean temperature of the driest quarter (bio 9) (°C), C - annual precipitation (bio 12) (mm), D – elevation (m).

3.3.4 Current climate suitability for B1 and B2

Only the bioclimatic variables were used in the model predicting current climate suitability for YEBU breeding seasons (elevation and tree cover were excluded). Among the bioclimatic variables used, the minimum temperature of the coldest month (bio6) was the most influential and contributed most to the model (73.3%). The mean diurnal range (bio2) (9.9%) was the next most influential variable, followed by precipitation of the coldest quarter (bio19) (5.6%) and precipitation of the driest month (bio14) (2.8%) (Supplementary materials: Table S 3.1). Maxent's jackknife validation indicated that the bioclimatic variable with the highest gain was the mean temperature of the driest quarter (bio9) (Supplementary material: Figure S 3.3D).

According to the response curves (Figure 3.5), YEBU habitat suitability decreased with an increased minimum temperature of the coldest month (bio6) (Figure 3.5A), with a diurnal range (bio2) between 6-8°C. YEBU also prefer precipitation of 375mm during the coldest quarter (bio19) and precipitation of 80mm during the driest month (bio14) for their breeding seasons.

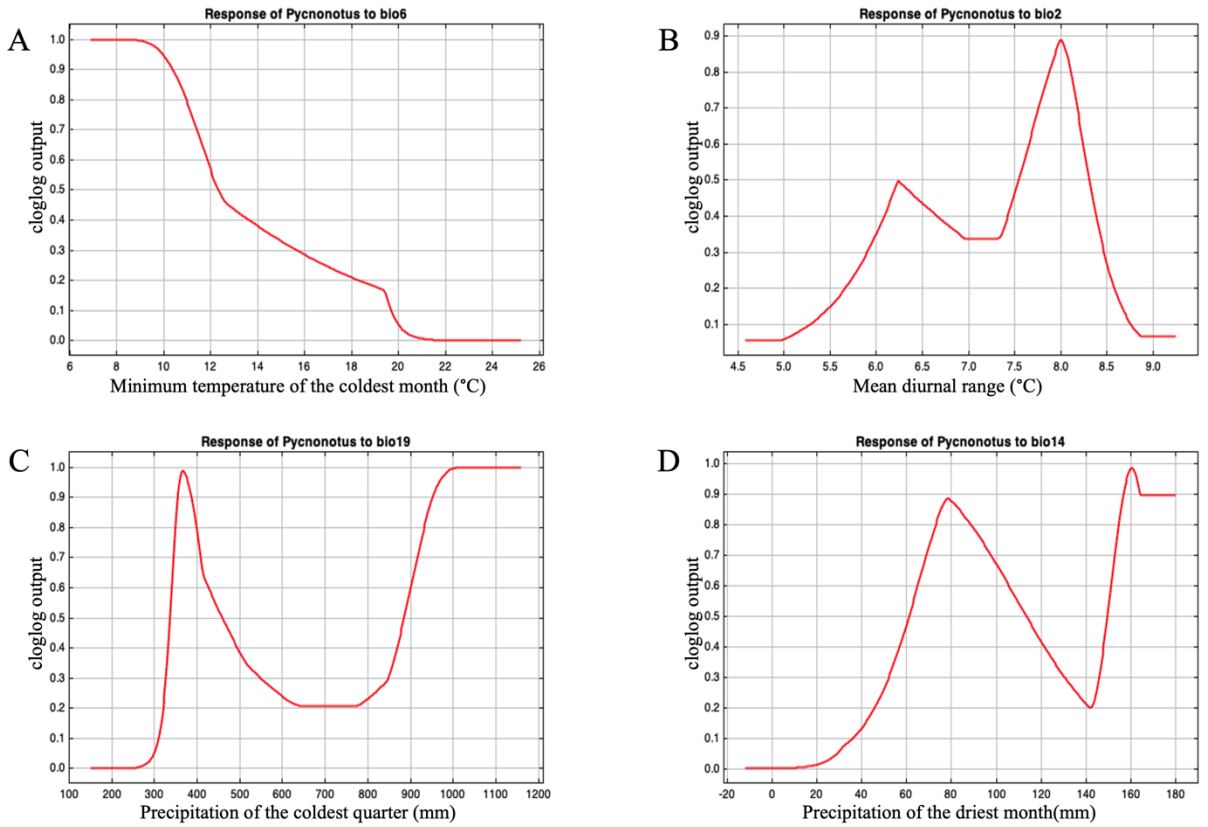

Figure 3.5: Response curves for the major predictors of habitat suitability of Yellow-eared Bulbul (*Pycnonotus penicillatus*) during breeding seasons (1 and 2), based on the Maxent model: A – minimum temperature of the coldest month (bio 6) (°C), B - mean diurnal range (bio 2) (°C), C – precipitation of the coldest quarter (bio 19) (mm), D – precipitation of the driest month (bio 14) (mm).

3.3.5 Current and future projections

YEBU are distributed mainly in three sub-regions in Sri Lanka: The Knuckles region, the central highlands, and the Sinharaja area (Figure 3.6). We considered only bioclimatic variables for climate suitability in the future. Climate suitability is categorized as unsuitable, marginal, moderate, and optimal. The model shows that the suitable habitats of YEBU will change under GCMs of MIROC6, CNRM-CM6, and CNRM-ESM-2 under SSP126 by 2030, 2050, 2070, and 2090 compared to current climate distribution (Figure 3.7).

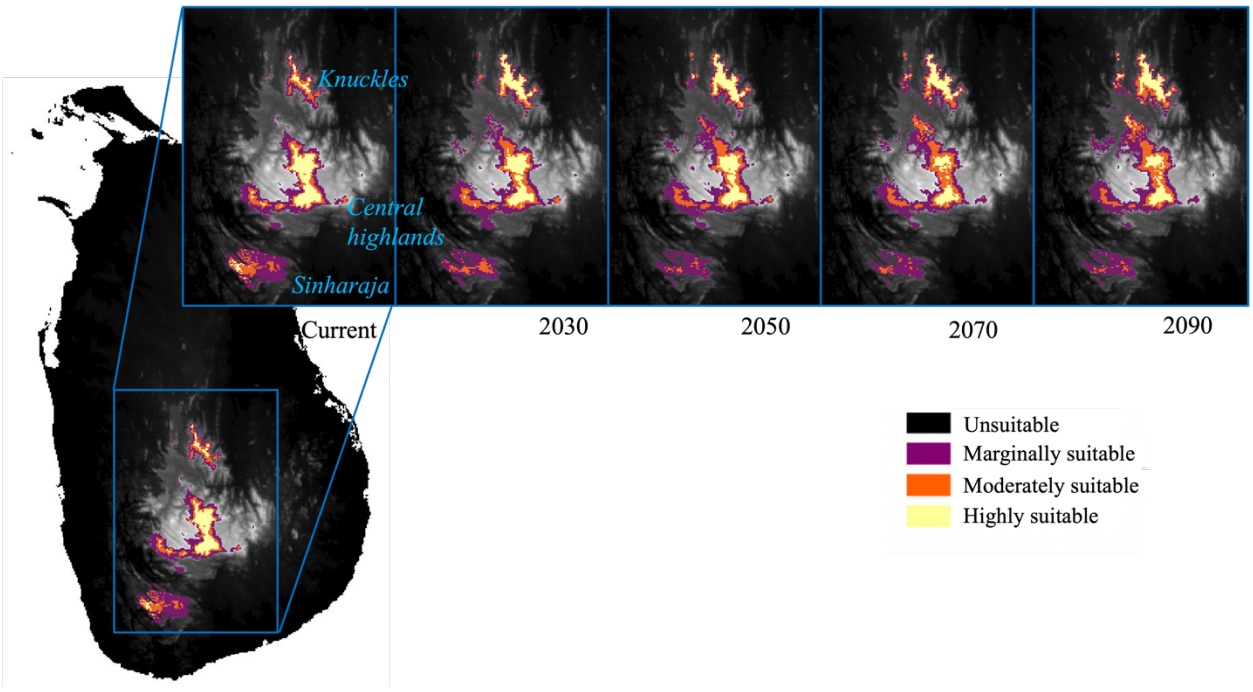

Figure 3.6: Changes in climatic niche suitability for the Yellow-eared Bulbul (*Pycnonotus penicillatus*) based on ensemble climate change model projections at 20-year intervals, starting with the current distribution model over the digital elevation model (greyscale; from black < 1000m to white > 2000m).

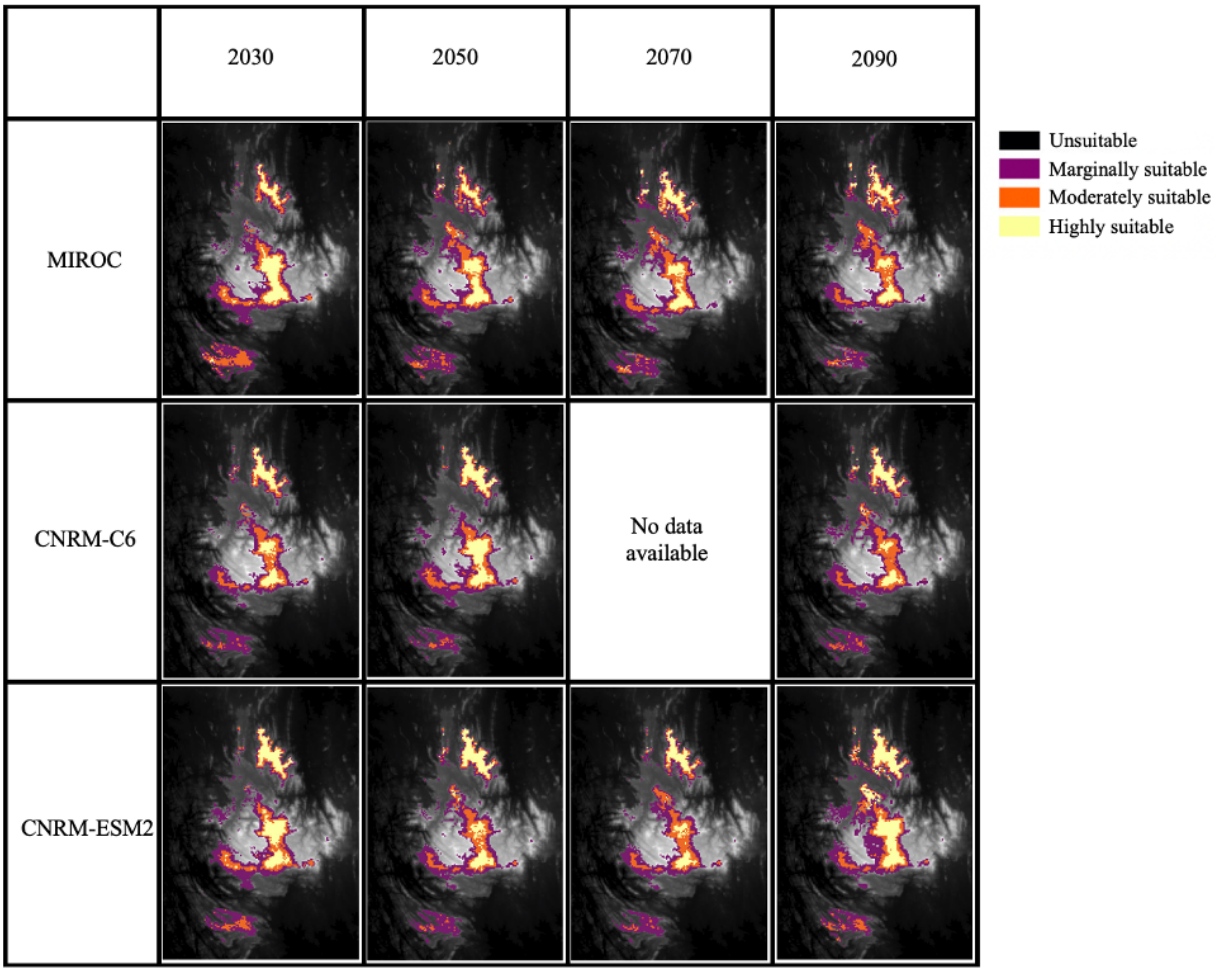

Figure 3.7: Projected climate suitability of Yellow-eared Bulbul (*Pycnonotus penicillatus*) under MIROC, CNRM-C6, and CNRM-ESM models in 2030, 3050, 2070 and 2090.

According to the current climate suitability, an area of 412.6 km^2 in Sri Lanka has optimal suitable climatic conditions for YEBU, representing 0.6% of the island's total area. It has 1170.6 km^2 (1.8%) of marginal suitability and 513.0 km^2 (0.8%) moderate suitability. An area of 63806.8 km^2 (97.3%) is unsuitable for YEBU distribution.

Relative to slope and aspect, we found that moderate to most suitable YEBU habitats are non-randomly associated with hillside slopes and monsoonal aspects. For slope, we expected 32 square-kilometer pixels to be randomly categorized as "hillside" and moderate/most suitable if slope and suitability were randomly distributed with respect to each other. Instead, we observed

that 301 km^2 of moderate/most suitable habitat occurred on hillsides, a significantly non-random association ($x^2 = 2632.32$, d.f. = 1, $p < 0.0001$). For aspect, we found that moderate/most suitable habitat pixels coincided with Southwest or Northeast monsoon-facing aspects more extensively (347 km^2) than expected by chance (289 km^2; $x^2 = 16.27$, d.f. = p = 0.00005).

The Maxent projections of future climatic suitability for YEBU under different GCMs showed that the changing climatic conditions alter the distribution of future suitable habitats. Each model predicted YEBU distribution differently. MIROC6 model suggests that the most suitable habitat for YEBU will be decreased by 15.9% while moderately suitable habitat will increase by 18.9% in 2090. In contrast, the CNRM-ESM model suggests that optimally suitable habitat increases by 73.8% and moderately suitable will increase by 18% in 2090 (Table 3.2). Therefore, we looked at the ensemble of three different models, using the "cell statistics average" feature in ArcGIS pro. The ensemble climatic suitability map for YEBU shows an increase of 10.1% and 10.9% in the highly suitable habitat category in 2030 and 2050 but a decrease of 14.8% and 2.7% in 2070 and 2090 respectively (Table 3.3).

Table 3.2: Habitat suitability classes of Yellow-eared Bulbul (*Pycnonotus penicillatus*) under different global climate models in 2030, 2050, 2070, and 2090. Habitat loss is highlighted in grey; habitat gain is highlighted in yellow.

Model	Unsuitable (km^2)	Marginally suitable (km^2)	Moderately suitable (km^2)	Highly suitable (km)
Current	63806.8	1170.6	513.0	412.6
MIROC2030	63463.1 -0.5	1307.5 11.7	664.4 -29.5	467.9 -13.4
MIROC2050	63462.3 -0.5	1413.9 20.8	644.0 25.5	382.8 -7.2
MIROC2070	63475.0 -0.5	1368.8 16.9	620.2 20.9	439.0 6.4
MIROC2090	63728.6 -0.1	1217.4 4.0	610.0 18.9	347.1 -15.9
CNRM_CM6_2030	63895.3 0.1	1127.2 -3.7	514.7 0.3	365.8 -11.3
CNRM_CM6_2050	63692.0	1157.8	497.7	555.5

	-0.2	-1.1	-3.0	34.6
CNRM_CM6_2070	No data available	No data available	No data available	No data available
CNRM_CM6_2090	63685.2 -0.2	1318.6 12.6	549.6 7.1	347.1 -15.9
CNRM_ESM_2030	63561.0 -0.4	1221.6 4.4	566.6 10.4	553.8 34.2
CNRM_ESM_2050	63714.1 -0.1	1227.6 4.9	504.5 -1.7	456.8 10.7
CNRM_ESM_2070	63846.0 0.1	1174.0 0.3	550.4 7.3	330.1 -20.0
CNRM_ESM_2090	63111.8 -1.1	1459.8 24.7	605.7 18.1	717.1 73.8

Table 3.3: Habitat suitability classes of Yellow-eared Bulbul (*Pycnonotus penicillatus*) based on ensemble climate change model projections at 20-year intervals starting in 2030. Habitat loss is highlighted in grey; habitat gain is highlighted in yellow.

Model	Unsuitable (km^2)	Marginally suitable (km^2)	Moderately suitable (km^2)	Highly suitable (km^2)
mean 2030	63619.7 -0.3	1252.2 7.0	576.8 12.4	454.3 10.1
mean 2050	63576.3 -0.4	1347.5 15.1	521.5 1.7	457.7 10.9
mean 2070	63639.2 -0.3	1309.2 11.8	603.1 17.6	351.3 -14.8
mean 2090	63475.0 -0.5	1393.4 19.0	632.9 23.4	401.5 -2.7

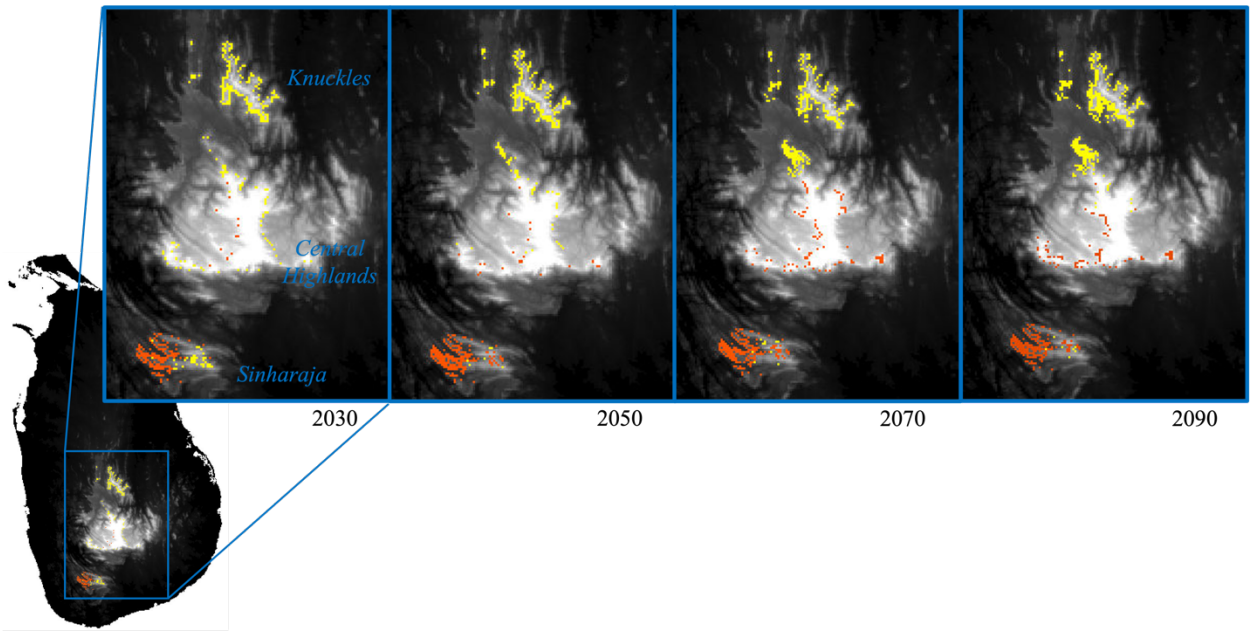

Figure 3.8: Changes in climatic niche suitability for the Yellow-eared Bulbul (*Pycnonotus penicillatus*) based on ensemble climate change model projections at 20-year intervals starting in 2030. Highlighted over the digital elevation model (greyscale; from black < 1000m to white > 2000m) are projected habitat losses in orange and habitat gains in yellow. The three focal mountain ranges are indicated on the 2030 panel.

Table 3.4: Area gain and loss in ha in three regions in the most suitable and suitable categories for Yellow-eared Bulbuls (*Pycnonotus penicillatus*)

	2030		2050		2070		2090	
	gain	loss	gain	loss	gain	loss	gain	loss
Sinharaja	44.0	113.0	14.8	140.4	15.8	141.3	22.8	136.4
	25.7%	66.0%	8.7%	82.0%	9.3%	82.5%	13.3%	79.7%
Central Highlands	64.2	63.7	82.5	32.8	86.5	75.4	131.3	91.6
	10.6%	10.5%	13.7%	5.4%	14.3%	12.5%	21.7%	15.2%
Knuckles	137.0	0.0	108.8	0.0	140.4	0.0	265.7	0.0
	87.4%	0.0%	69.4%	0.0%	89.6%	0.0%	169.6%	0.0%

Even though the size of the optimally suitable habitat is not predicted to change substantially over the next 70 years, there is a shift in the optimally suitable area. The most suitable areas in Sinharaja are declining whereas the Knuckles region gets more climatically suitable (Table 3.4 and Figure 3.8).

3.4 Discussion

Model output implies that <3% of Sri Lanka has a suitable habitat for the endemic Yellow-eared Bulbul, and <1% of the island was modeled to have a "highly suitable" habitat. The mean temperature of the coldest month (bio6) was found to be the most influential variable during the breeding seasons (February–May and August–October). YEBU breeding season 1 coincides with a relatively dry period of the year. YEBU preferred when the mean temperature of the driest quarter was <18°C in breeding seasons. The climatic requirements indicate its affinity to the cool and dry habitats during the breeding seasons. Heavy rainfall, high humidity, and low temperatures during the wet season in the mountains often prevent birds from breeding. Maxent modeled current and future distributions of the YEBU area mapped in three separate areas that coincided with the documented distribution of YEBU in Sri Lanka, which is restricted to the central highlands. Based on the future model predictions, climatically most suitable areas for YEBU show changes (declines and expansions) at low elevations of the mountains, with a net increase of 10.9% of the most suitable area. However, the most suitable areas will be shifted north, while the geographic range in the Sinharaja forest reserve in the south will shrink. The geographic range expansion was mostly seen in the low elevations of the Knuckles region (Figure 3.8) and may not overlap with monsoon-facing aspects that the species currently appears to favor.

The climate is significant in defining a species' distribution and evaluating the interactions between abiotic and biotic factors (Morelle et al. 2015). Tropical birds are renowned as the most

vulnerable species to climate change (La Sorte and Jetz 2010; Wormworth and Sekercioglu 2011) and their geographical ranges are expected to change with climatic changes (Huntley et al. 2008). Some of the consequences of climate change could have advantageous effects, whereas others are expected to be disadvantageous. Studies showed that the cloud cover in mountains can affect the temperature. Clouds affect both shortwave and longwave radiation and insolation and longwave radiation at the surface (Rangwala and Miller 2012). Moreover, fog and stratus clouds elevate temperature at lower elevations (Beniston and Rebetez 1996; Beniston 2003), and variation in precipitation is lower in high-elevation areas than in the mid- and low-elevation areas in Sri Lanka (Wickramagamage 2010). More changes are therefore seen in low elevations compared to higher elevations. The standardized precipitation index (SPI) also suggests that areas at low elevations will be more affected by drought than areas at high- or mid-elevation (Eriyagama et al. 2009), indicating that hilly areas will have a more favorable climate for YEBU. Even so, montane systems are inherently difficult to understand owing to their complex topography, leading to a high spatial and temporal variability in their climatic responses.

Three GCMs we used in our study projected that the Sinharaja area would be climatically unsuitable for bulbuls while the Knuckles and Central Highland regions would be more suitable. Even though the ensemble model predicts an increase in climatically suitable habitat for YEBU in the Knuckles region, this model may be overly optimistic because the suitable habitats in the projections include regions outside their current distribution. Some of these new regions might be unsuitable for reasons unrelated to climate. Habitat availability may depend on human activities and land use, which the models do not account for. For example, some new regions of projected suitable habitat in the Central Highlands region overlap with human occupancy. Furthermore, the species' ability to expand into areas that have recently become climatically suitable depends on

the dispersal rate and the habitat availability for the species to colonize (Lovejoy and Hannah 2004). Furthermore, even if bulbuls can disperse to new areas, they will use up energy they could otherwise use for reproduction. It could be argued, then, that a "stay-at-home" scenario (Lovejoy and Hannah 2004) most benefits the target species and the land managers tasked with the species' conservation. Dispersal distance in the YEBU is unknown, but it is short in congeners, such as a maximum of 267 m for *P. xanthopygos* (Green et al. 2009) or 735 m for *P. jocosus* (Ramaswami et al. 2016). The average nearest neighbor distance (the average distance between neighbors in a hypothetical random distribution) for YEBU is 744m. Yet, the Sinharaja area is 18km from the central highlands, and the Knuckles region is 7km from the central highlands (Supplementary material: Figure S3.4). So, limited dispersal capacity may mean that the northern (Knuckles) area forecast to be suitable cannot be colonized. Further studies on YEBU dispersal across valleys are required, as are studies on vegetation characteristics of suitable or occupied versus unsuitable habitats, to determine if landscape connectivity could facilitate movement. Connectivity could indicate a functional "neighborhood mover" scenario (Lovejoy and Hannah 2004).

Despite the possibility of finding potentially suitable areas in the future, the ongoing conversion of the forest areas into agricultural lands (Wickramagamage 2010) and infrastructure in Sri Lanka are worrisome, particularly for frugivorous birds. Given that forest frugivorous birds depend on forest cover (Morante-Filho et al. 2021), it is essential to concentrate efforts on keeping the few forest remnants across Sri Lanka. Improving the conservation status of forest remnants across the whole area will be of utmost importance, including strategies to connect isolated fragments, allowing species to pursue their suitable habitat. Because forest frugivorous birds are critical to seed dispersal for most tropical trees (Howe and Smallwood 1982), deprivation of forest-dependent bird communities may have cascading effects on seed dispersal (Galetti et al. 2013),

thus limiting plant recruitment and leading to biodiversity depletion within this hotspot in the future (Mota et al. 2022).

CMIP6 models project that annual mean temperature and precipitation are predicted to increase in South Asian countries under all SSP climate scenarios. Under the SSP585 scenario, precipitation projections predict that Sri Lanka will have a 25.1% increase by the end of the 21st century (Almazroui et al. 2020). Models also forecast large variability in seasons in the future, suggesting that Sri Lanka will experience warmer climates and more intense precipitation. Many tropical bird species will likely shift their breeding periods in response to changes in temperature and rainfall regimes (Sekercioglu et al. 2008). If climate change results in a mismatch between a critical reproductive cue such as the photoperiod (Wikelski et al. 2000), and the optimal temperature and rainfall regime for reproductive success, it may result in population decline. Changes in the frequency and severity of tropical storms also have important consequences for the ecology and conservation of tropical birds (Boyle et al. 2010). Previous studies also reported that 3.5°C surface warming can result in the extinction of 600-900 land bird species. Among the predicted extinctions, 89% may occur in the tropics (Sekercioglu et al. 2008). Yet, these models might not adequately capture what occurs in this dual-monsoon system. When the country gets intense precipitation, the wettest and driest quarter could change depending on the year and location on the island, which could throw off Maxent projections, which necessarily assume some sort of within-year temporal stability. Monsoon dynamics may be much harder to model for Sri Lanka, because it is a relatively small landmass and the Southwest monsoon depends on how much India impacts the airflow (Turner and Annamalai 2012; Clemens et al. 2021; Katzenberger et al. 2021; Wang et al. 2022). These climate models might not adequately capture what is driving YEBU reproduction and, hence, population stability. Our findings nevertheless can be treated as

hypotheses for future field study (e.g., equate localized reproductive effort and success to actual climatic conditions before, during, and after the breeding period at various locations across the species' range). After all, the fact that YEBU has two breeding seasons per year may not imply that all individuals retain their reproductive capacity for both seasons. It is possible that individual pairs are out of synchrony with other pairs, which gives the (false) impression of double breeding on the individual level (Miller 1965; Wingfield et al. 1997). It is therefore imperative to document individual breeding behaviors throughout the year.

This study provides insight into potential shifts in YEBU suitable habitats due to climate change. Many physiological, ecological, and biogeographical characteristics that make certain bird species more vulnerable to climate change are also present in non-avian groups. Ongoing measures and management strategies to reduce climate change threats to bird communities could also help species in other groups. We may be forced to assume, purely for expediency, that shifts in bird ranges and habitat suitability may mirror shifts in habitat suitability for other species. Protected areas are important and effective in current conservation strategies (Bruner et al. 2001), and they will continue to be fundamental in conservation strategies designed for climate change (Lovejoy and Hannah 2004). However, areas that once protected a species might become obsolete if that habit is no longer suitable for the species. If the species' range shifts and the protected areas do not shift accordingly, the species will be at risk.

3.5 Conclusion

Yellow-eared Bulbuls are distributed in less than 3% of land area in Sri Lanka, with less than 1% of land being highly suitable. Different bioclimatic variables impact the two breeding seasons and the non-breeding season. The suitable climate niche of YEBU will change under global climate models in the future compared to the current climate niche, with a 10.1% and 10.9% increase in

the highly suitable category in 2030 and 2050, but a decrease of 14.8% and 2.7% in 2070 and 2090. Even though the size of the highly suitable climatic niche is not predicted to change substantially, there is a shift in the climate niche. The most suitable areas in Sinharaja are declining, whereas the Knuckles region gets more suitable. Since species' dispersal ability across valleys has not been studied yet, further studies on species' dispersal ability and associated vegetation are required.

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3.7 Supplementary material

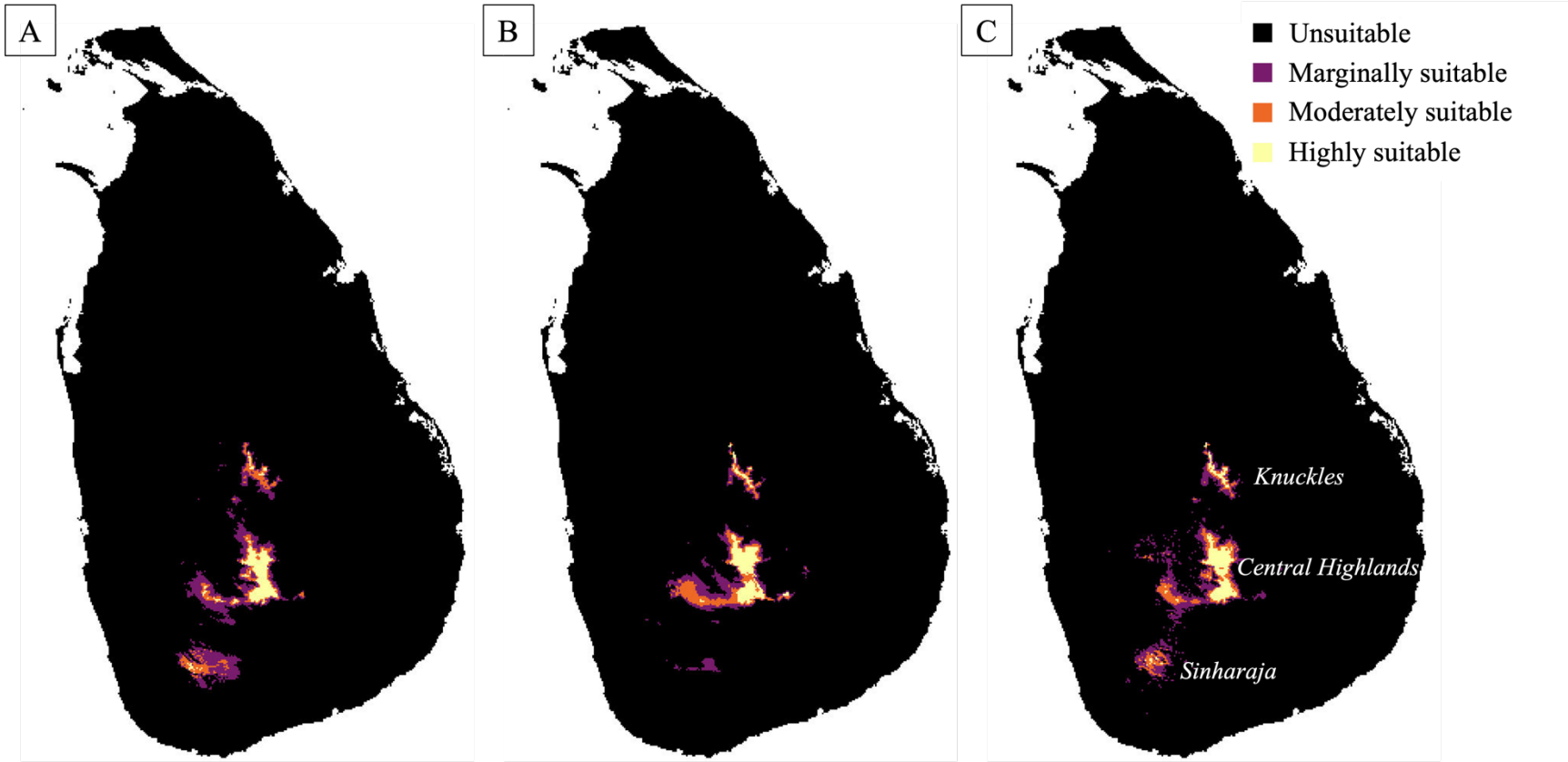


Figure S3.1: Current habitat suitability for Yellow-eared Bulbuls (*Pycnonotus penicillatus*) in Sri Lanka. A: Habitat suitability during breeding season 1, B: Habitat suitability during breeding season 2, C: Habitat suitability during non-breeding season

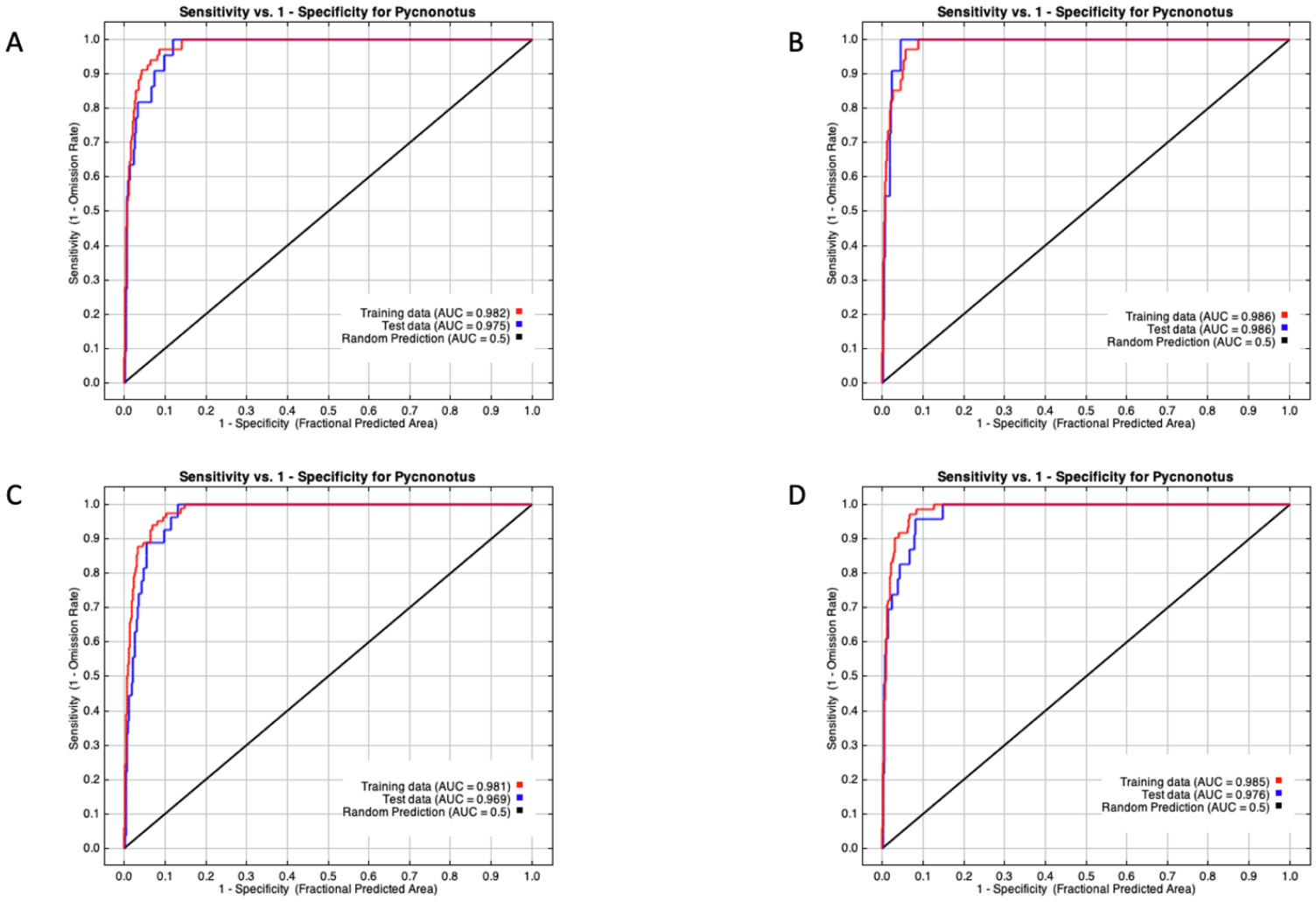


Figure S3.2: ROC curve for MaxEnt model of *Pycnonotus penicillatus*. A: breeding season 1, B: breeding season 2, C: breeding seasons 1 and 2, D: non-breeding season

Table S1: Percent contribution and Permutation importance of the predictor variables to Maxent models. B1 - Breeding season 1, B2 - Breeding season 2, B1 and B2 - Breeding seasons, non-breeding - non-breeding season

B1			B2			B1 and B2			non-breeding		
Variable	% contribution	Permutation importance	Variable	% contribution	Permutation importance	Variable	% contribution	Permutation importance	Variable	% contribution	Permutation importance
bio6	1.1	39.9	bio9	3.6	93.7	bio6	3.1	75.7	bio9	48.6	34
bio2	0.5	15	bio19	1.8	1.6	bio19	3.5	4.5	bio11	15.5	0.1
bio8	0.3	10.8	bio2	0.3	1.3	bio3	0.5	4.5	elevation	12.8	5
bio19	2.1	10.5	bio16	0.1	1.1	bio2	0.3	4.4	bio6	6.3	1.6
bio14	3.7	8.3	bio4	0.2	0.8	bio8	2.9	3.3	bio8	4.7	42.5
bio3	0.2	4.5	bio17	0.4	0.5	bio9	21.7	2.4	bio19	2	1.1
bio9	33.1	2.1	bio15	0.9	0.4	bio17	0.5	1.4	bio4	1.8	3.3
tree cover	0.3	1.9	bio8	10.4	0.3	elevation	41.8	1	bio17	1.5	0.2
bio4	0.2	1.8	bio7	0.4	0.2	bio18	0.5	0.9	bio10	1.4	0
bio15	2.5	1.5	bio12	0.6	0.1	bio4	0.2	0.8	bio12	1.1	7
bio18	0.2	1.4	tree cover	0.9	0.1	bio14	5.8	0.6	bio1	0.9	0
bio16	0	0.9	bio1	12.5	0	bio15	0.6	0.2	bio18	0.8	0
elevation	47.9	0.9	bio10	0	0	tree cover	0.2	0.2	bio14	0.6	0.6
bio12	0.1	0.3	bio11	7.1	0	bio11	9.6	0	bio15	0.5	0.6
bio11	0.2	0.2	bio13	0.1	0	bio12	3.1	0	bio3	0.4	1.2
bio1	0	0	bio14	0.5	0	bio7	2.4	0	tree cover	0.4	0.5
bio10	5.5	0	bio18	0.1	0	bio10	1.4	0	bio2	0.2	1.2
bio13	0	0	bio3	0.7	0	bio1	1.3	0	bio16	0.2	0.8
bio17	1.7	0	bio5	4	0	bio13	0.3	0	bio7	0.2	0.1
bio5	0	0	bio6	1	0	bio5	0.3	0	bio5	0.1	0.1
bio7	0.2	0	elevation	54.5	0	bio16	0	0	bio13	0	0

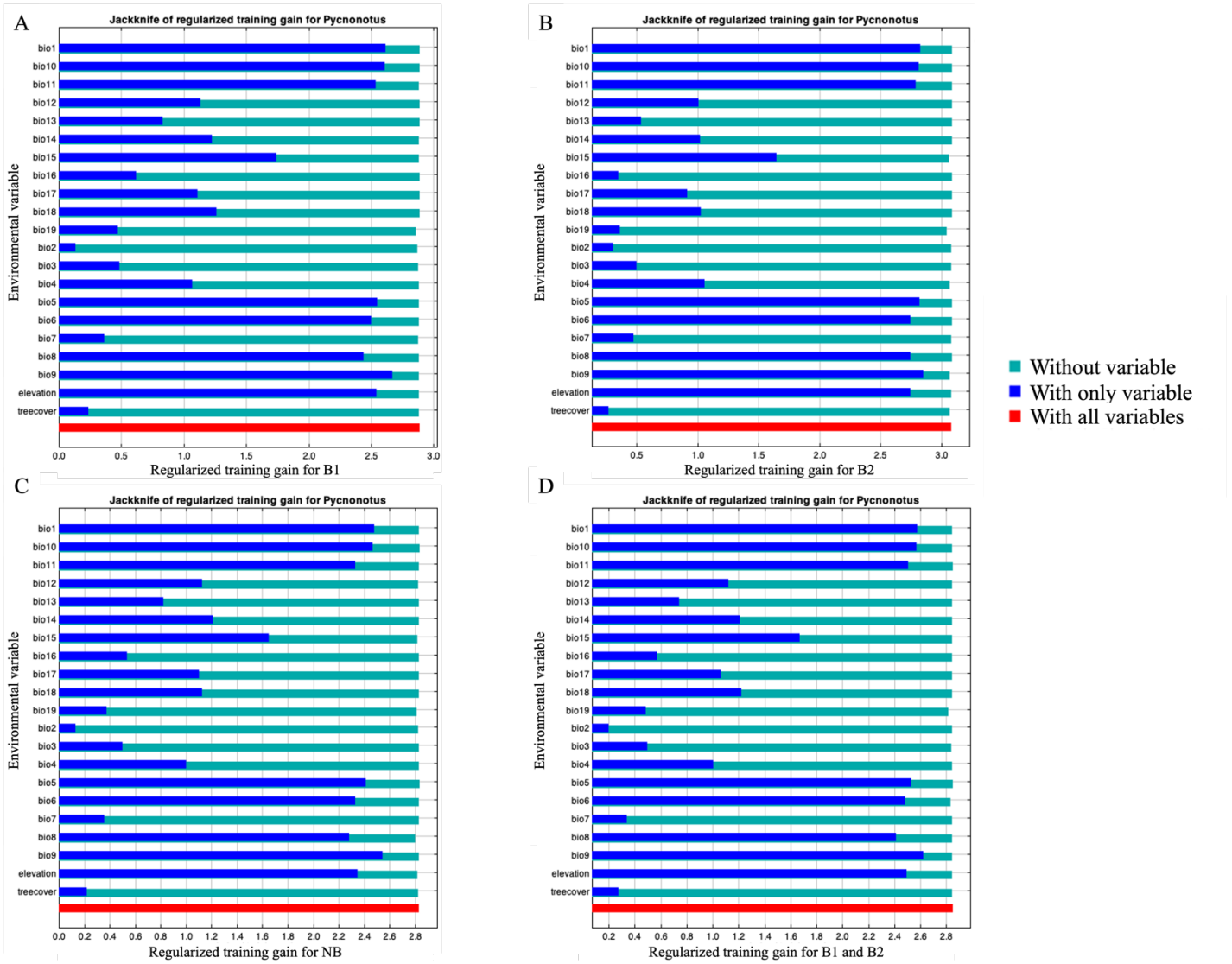
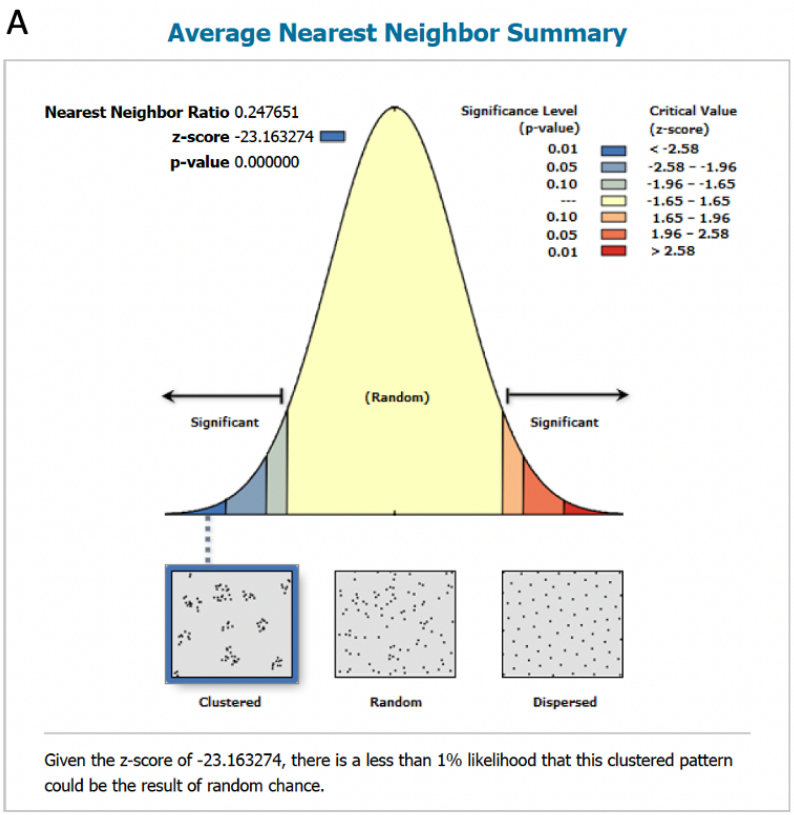


Figure S3.3: Jackknife test for variable importance of *Pycnonotus penicillatus* niche suitability. A: Breeding season 1, B: Breeding season 2, C: Non-breeding season, D: Breeding seasons 1 and 2

A



Average Nearest Neighbor Summary

Observed Mean Distance	744.1789 Meters
Expected Mean Distance	3004.9467 Meters
Nearest Neighbor Ratio	0.247651
z-score	-23.163274
p-value	0.000000

B

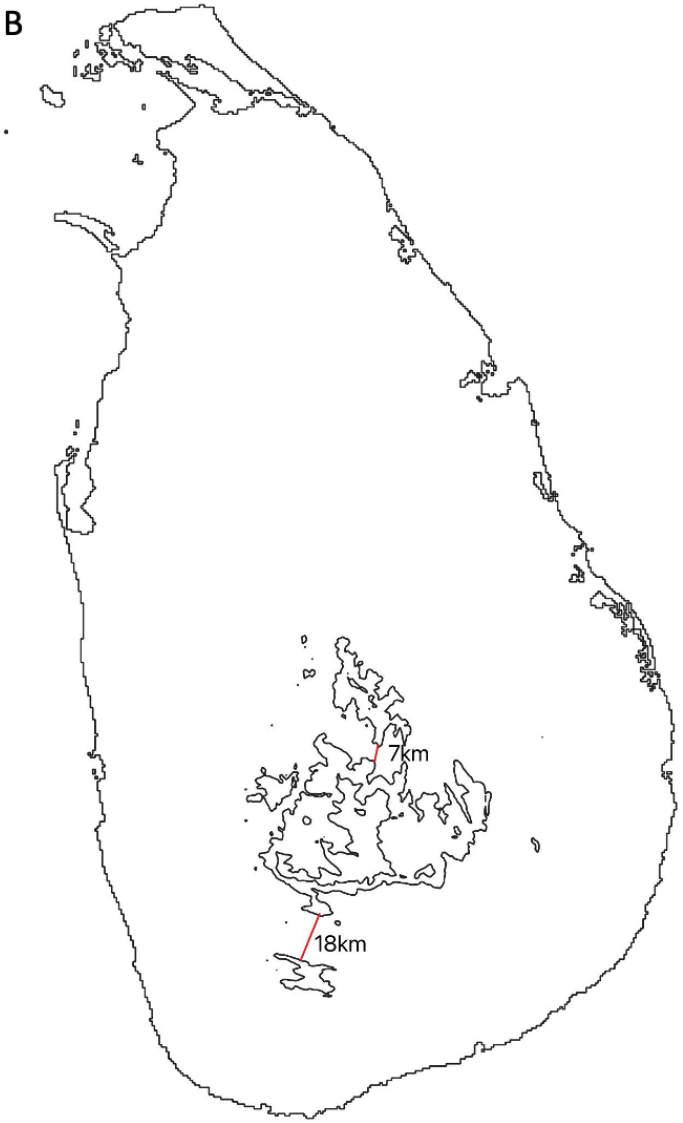


Figure S3.4: A: Summary of the average nearest neighbor of *Pycnonotus penicillatus*, 3B: The shortest distance between Sinharaja and central highlands (18km), the distance between central highlands and Knuckles region (7km)