Spatial and seasonal variation in abundance within an insular grey parrot population

Simon Valle[1*], Nigel J. Collar[2], Edwin Harris[1] and Stuart J. Marsden[1]

[1] Division of Biology & Conservation Ecology, School of Science & the Environment, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, U.K.

[2] BirdLife International, Pembroke Street, Cambridge CB2 3QZ, UK

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[*] *Corresponding Author Email: S.Valle@mmu.ac.uk*

***Running title:** Habitat use variability in grey parrots*

Abstract

Populations of Psittacidae are endangered by habitat loss and the international pet market. The grey parrot (*Psittacus erithacus*) is among the most traded species, yet little is known about densities and their variability in time and space. The population of grey parrots on the island of Príncipe (Gulf of Guinea) was estimated with distance sampling, in both pre- and post-breeding seasons. Abundance was related to a range of habitat features using Generalized Additive Models. Densities averaged 48 ± 3 (SE) individuals km^{-2} in the pre-breeding and 59 ± 4 in the post-breeding season, both extremely high compared to elsewhere in Africa, or to other parrot species. Despite a population of 6,000–8,000 individuals over only 139 km^2, parrots were patchily distributed, being unrecorded in ~25% of surveyed areas. Abundance varied seasonally, with densities being significantly higher in secondary compared to primary forest in the post- but not in the pre-breeding season. Abundance was most tied to the presence of nest-tree species prior to breeding; and to feeding-tree species and lightly sloping ground after breeding. These results highlight the need to preserve a matrix of habitat types to provide resources for parrots across seasons, and ensure that surveys recognise seasonality in habitat use as a potential bias.

Introduction

Parrots (Psittacidae) are among the most endangered bird families in the world, with 37 % of all species listed as threatened or near threatened (BirdLife International, 2015). Excessive capture for the international pet trade coupled with habitat degradation and loss are considered the main

causes of worldwide parrot population declines (Snyder et al., 2000, Olah et al., 2016). However, despite their threatened status, little is known about the size of parrot populations in the wild (Marsden and Royle, 2015), their habitat requirements (Snyder et al., 2000), or the seasonality of these requirements (Renton, 2002). Parrot habitat is defined by a number of limiting factors, namely food (Saunders, 1990, Berg et al., 2007), nest sites (Beissinger and Bucher, 1992, Wiebe, 2011), roost sites (Chapman et al., 1989), and water and mineral licks (Lee et al., 2010). However, the availability of these resources can vary significantly in space and time, and over the annual cycle parrots may require a variety of habitats and forest types (Marsden and Pilgrim, 2003, Renton, 2002). Thus, understanding seasonal changes in habitat use by parrots is important for conservation monitoring, which can be particularly challenging owing to their flocking behaviour and low detectability (Marsden and Fielding, 1999, Lee and Marsden, 2012, Marsden et al., 2015).

The grey parrot (*Psittacus erithacus*) has recently been uplisted to IUCN Red List category 'Vulnerable' owing to a rapid and continuing population decline across its African range (BirdLife International, 2015). As with many other parrot species, the causes of this decline are thought to be a combination of habitat loss and harvest for the international pet trade (BirdLife International, 2016, Annorbah et al., 2016). Grey parrots have been recorded in a variety of habitats, namely forest edges, clearings, gallery forest, mangroves, wooded savanna, cultivated areas, and even gardens; but they typically inhabit dense forest (Juniper and Parr, 1998) Despite their ubiquity, information on the size and density of wild populations, local movements and habitat requirements is largely anecdotal and sparse (Martin et al., 2014, Amuno et al., 2007). However, despite a tradition of parrot trade, the relatively undisturbed island of Príncipe in the Gulf of Guinea has a stable, isolated population of grey parrots (Juste, 1996, Marsden et al.,

2015). Thus, Príncipe's population presents an opportunity to study grey parrot ecology without the bias of anthropogenic pressures present in mainland populations.

The aim of this study was to assess the habitat requirements of grey parrots on Príncipe and determine (1) if, and to what extent, these change seasonally, and (2) the implications that any changes may have for conservation management and survey design of the species elsewhere in its continental range.

Material and methods

Study area

The island of Príncipe (1°32'–1°43'N 7°20'–7°28'E; 139 km^2), part of the nation of São Tomé and Príncipe, lies 220 km off West Africa, in the Gulf of Guinea (Fig. 1). Príncipe is broadly divided in two geographically and climatically distinct regions: a low-lying basalt platform in the north, with hills below 180 m asl, and a mountainous region in the south (Jones and Tye, 2006). By the beginning of the twentieth century the forest in the north had been modified in many places by clear-felling, selective felling and the creation of cocoa, coffee and coconut plantations (Exell, 1973), while the south remains covered in pristine forest with much floral endemism (Figueiredo et al., 2011). The rainy season lasts from September to May and the dry season (*gravana*) from July to August, while a shorter dry season runs from December to early January, with the north being always drier than the south (Jones and Tye, 2006).

Population and density estimation

The island was divided into 133 one-km^2 grid squares based on the Universal Transverse Mercator (UTM) geographic coordinate system. To account for habitat heterogeneity, these were then classified as primary or secondary forest, according to the latest vegetation surveys (Albuquerque et al., 2004) and visual ground-truthing. Fifty-nine squares (44%) were assigned to the primary forest habitat category. The remaining 74 squares (56%) fell into the secondary forest category, which included lowland forest (26%), as well as overgrown cocoa (*Theobroma cacao*) plantations (31%), coconut palm (*Cocus nocifera*) groves (29%), and oil palm (*Elaeis guineensis*) estates (11%). Forty-one squares (i.e. one in every five, cyclically) were selected systematically on a map (12 in primary and 29 in secondary forest). However, in most of these (63% of squares), owing to issues of accessibility logistics and safety, the nearest accessible square had to be visited instead (Fig. 1).

Parrots were surveyed using distance sampling (Buckland et al., 1993). This method is by far the most widely used method for estimating parrot populations (Marsden and Royle, 2015), by virtue of its perceived reliability over other methods (Casagrande and Beissinger, 1997, Marsden et al., 2015). Moreover, estimates derived from distance sampling are based on a snapshot of bird abundance at the moment of survey, so that the movement of birds around the island does not undermine the efficacy of the estimate, so long as they are random in respect to transect placement (Buckland et al., 1993). All assumptions required by the survey method were respected, i.e. (a) birds on the line were certain to be detected (many records in the study were of individuals perched overhead at distance = 0 from the transect); (b) birds were detected at their initial location; (c) distance measurements were exact (distances were first estimated and then measured with a range-finder wherever possible, in order to guide observer's estimates when the use of such device was not possible owing to dense vegetation); (d) for birds that occurred in

flocks, cluster sizes was recorded without error; and (e) the sampled strips were representative of the surveyed region square (Buckland et al., 2008). In each grid square, a transect (mean 1 km ± 0.4 SD, min – max = 0.3–1.9) was walked at a rate of 1 km ~~/~~h^{-1} regardless of terrain. Steep terrain and dense vegetation often prevented safe navigation, so only existing paths (width ≤ 0.5 m) and natural openings in the otherwise impenetrable vegetation were used. All grey parrots heard and seen perched along the transect route were counted, and their perpendicular distance from the transect line measured. A cut-off distance of 50 metres was established, since exploratory fieldwork showed that birds beyond this distance were very hard to detect and their contribution to the building of the detection function negligible (Buckland et al., 1993). All flying birds, since they were not detected at their initial location, were excluded from the counts unless they had been flushed, in which case their take-off point was recorded (Marsden, 1999). Transects were walked between 0700h and 1100h, when parrot activity is expected to be highest (Blake, 1992). All counts were conducted in calm dry conditions, by SV alone. Depending on terrain conditions and logistics, between one and four transects per day were surveyed, within a given area (i.e. some squares would be adjacent). Transects were initially walked once after the fledging period (March–April 2014; 'post-breeding') and again just before the following breeding season (August–September 2014; 'pre-breeding'). Distance sampling is most efficient when birds are spread relatively evenly through the survey region (Buckland et al., 2008). Thus, since nesting grey parrots movements are much more secretive and restricted during all phases of breeding (Valle, 2015), no surveys were conducted in this period to avoid sources of bias.

DISTANCE 6.0 (Thomas et al., 2010) software was used to estimate grey parrot density (individuals/km^2) in each of the surveyed grid squares using a shared detection function across squares. A measure of forest regeneration (see '*Habitat characterization*' below) was included as

a transect-specific covariate in the Multiple Covariates Distance Sampling (MCDS) engine, as it is believed to affect detectability (Marques et al., 2007). A multiple covariates distance sampling analysis was performed with multiple detection function models. A hazard-rate function and cosine adjustment term was selected as the optimal detection function based on the lowest Akaike's Information Criterion value (AIC; Akaike 1974). Parrot sightings were entered as clusters (i.e. number of birds seen or heard with certainty in a group) with exact measured distances rather than distance ranges. Variance was estimated by bootstrap resampling (999 resamples). Resulting densities were compared to all equivalent estimates (i.e. that used distance sampling) from elsewhere in the range.

Habitat characterization

Every 500 m along each transect, the following habitat measures were taken within a 20 m radius sample plot: geographic coordinates and altitude (GPS); slope (clinometer); aspect (compass); maximum canopy height (clinometer and range finder); canopy closure in five equidistant points (type-A spherical densitometer); number of woody stems at 1 m height (counted by swinging a 1-m-long stick through 360° at 1 m height, and hereafter referred to as 'regeneration'); diameter at breast height (DBH) of the three largest-girthed trees (tape measure); and estimated percentage of ground covered by understorey, estimated by eye (hereafter 'ground flora'). Measurements were then averaged across sample plots to give a single value per variable per grid square. In each vegetation plot, presence or absence was recorded for all tree species which, from according to the available literature on the species's habitat use and local knowledge, grey parrots were known to feed on or nest in (Table S1). Also recorded were 12 widespread introduced/cultivated tree species as an indicator of anthropogenic disturbance (Lee and Marsden, 2008). For each

square, the proportion of vegetation sample plots holding each of the above tree species was calculated, and this was then averaged for three categories, namely ‘food-tree species’, ‘nest-tree species’ and ‘introduced/cultivated species’. In two grid squares the length of the transect was <500 m and, thus, no vegetation sampling was carried out. These squares were excluded from any further habitat association analysis. Habitat variables were sampled in a total of 99 plots across the island, i.e. 2.5 per square.

Seasonality in parrot-habitat associations

Differences in density between primary and secondary forest within and between survey periods were tested using a Mann-Whitney U test, and variation in density estimates within squares between the two seasons examined with Spearman's Rank correlation analysis. Random Forests, a decision-tree modelling technique (henceforth ‘RF’), was used to rank habitat variables as predictors of density for each season (Cutler et al., 2007). RF models of 100,000 classification trees were built, and variables were identified as important if their importance scores (i.e. mean decrease in accuracy, MDA, in predicting parrot density after each tree permutation) were above the absolute value of the lowest negative-scoring variable (Strobl et al., 2008). These selected (candidate) variables were then used as independent variables in two Generalized Additive Models (GAMs; one for each season) to explore how more exactly they were linked to parrot density. GAMs were preferred to other multivariate modelling options in order to detect any relationship, whether this was linear or non-linear. All statistical analysis were performed in R software, with RF models and GAMs built using ‘party’ and ‘mgcv’ packages, respectively (R Core Team, 2014).

Results

Population size and density estimate

The total population was estimated at 6,517 ± 361 (mean ± SE) grey parrots in the pre-breeding season, and at 7,996 ± 568 in the post-breeding season, with mean densities of 47.9 ± 2.7 and 58.78 ± 4.2 parrots/ km^{-2} respectively (Table S2). The total number of detections did not vary greatly between the two seasons (125 and 139 in pre- and post-breeding season respectively), and in each of them parrots were detected in the majority of the surveyed squares (58% in each season), with no particular inclination for either type of forest ($\chi^2 = 2.98$, df = 1, $P = 0.08$). In both seasons, 17 grid squares (5 in primary and 12 in secondary forest in pre-breeding season; 8 and 9 in post-breeding season) had no records, and thus had an estimated zero density. There was no systematic difference (i.e. increase or decrease) in abundance within the 41 grid squares ($W = 260$, $P = 0.36$), between pre- and post-breeding season. However, there was considerable variability in densities across squares between the two seasons (Fig. 2). In the pre- and post-breeding seasons, three and four grid squares respectively had a density between 100 and 200 parrots/ km^{-2} (max ± SE = 154.06 ± 8.24; Fig. 3a,b). In the latter season, three grid squares had a density ≥ 200 parrots/ km^{-2} (max ± SE = 336 ± 24; Fig. 3b). Parrot density was significantly lower in primary than in secondary forest in the post-breeding season ($W = 64$, $P < 0.01$), but there was no significant difference between forest types in the pre-breeding season ($W = 139$, $P = 0.85$).

Seasonality of parrot-habitat associations

RF analyses indicated that the presence of nest-tree species was the best predictor of local parrot density in the pre-breeding season, while slope and presence of food-trees were the strongest predictors in the post-breeding season (Fig. 4). GAM shows a near-significant nonlinear relationship between local parrot density and nest-tree species ($F = 2.99$, $P = 0.07$; Fig. 5). In the post-breeding season, local density was related to slope in a nonlinear way, with gently sloping terrain (0–20°) associated with high densities ($F = 8.04$, $P < 0.01$, Fig. 6a), and linearly with presence of feeding trees ($F = 8.04$, $P < 0.01$, Fig. 6b). There was no correlation between terrain slope and the presence of food-tree species ($r_s = +0.08$, $P = 0.63$, $N = 39$).

Discussion

On Príncipe, grey parrots show both geographical and seasonal preferences in their use of available habitat. Densities were estimated to be in the range of 48–59 individuals ~~/~~km^{-2} on the island, which is the highest ever recorded for the species previous maxima being 29 and 10.7 birds ~~/~~km^{-2} estimated in Lobeke and Campo Ma'an National Parks, Cameroon, respectively (Marsden et al., 2015). These densities are also relatively high compared to other psittacines. Out of 90 parrot species for which at least one density estimate is available, only 17 have densities higher than 50 birds~~/~~ km^{-2}, and all but two of these (Red-faced Parrot *Hapalopsittaca pyrrhops* and White-crowned Parrot *Pionus senilis* in Ecuador) are island populations (Marsden and Royle, 2015). This pattern may be the consequence of a combination of Príncipe's particular environmental conditions, but is also is consistent with the phenomenon known as 'density compensation', where the summed high population densities of the few species on islands is similar to the summed lower densities found on the species-rich mainland (MacArthur et al.,

1972). Whatever the cause, such high densities may have important conservation implications for the species. Príncipe is clearly serving as a small stronghold for the otherwise declining global population, as other islands are for other parrot species, for example the Bolama-Bijagós Archipelago for the Timneh Parrot (*Psittacus timneh*) (Clemmons, 2003).

Parrot abundance varied greatly across the island, to the point where it was entirely absent from some areas in both seasons (26% of surveyed grid squares). This suggests that some areas may be permanently unattractive to the species despite the small size of the island, the large population present, and the well-known mobility of grey parrots (Collar, 1997, Juniper and Parr, 1998). By contrast, in the post-breeding season, there were three grid squares in secondary forest which had very high densities (i.e. ≥ 200 parrots/km^{-2}). Owing to their environmental characteristics, these areas are likely to host periodically high concentrations of important resources, as indicated by the positive relationship we found between parrot density and food-tree species. Such large densities could also be attributable solely to the influx of newly fledged juveniles, or to some more complex post-breeding behaviour, as some parrot species are known to establish crèches as an anti-predator behaviour or for flight training (Rowley, 1980, Wanker et al., 1996, Taylor and Perrin, 2006). Both densities and total population estimates were consistent with results from a similar survey carried out in 2012 and with what is known about the species's nest densities and reproductive output on the island (Valle, 2015).

Local abundance also has a clear temporal variation, with primary and secondary forest being used more in pre- and post-breeding season respectively. In the pre-breeding season, there is a movement of birds towards areas with high numbers of nest trees. Like most parrots, grey parrots nest in natural tree cavities (Collar, 1997), and the availability of nest sites, which are likely to occur in older trees such as are found in primary forest (Cockle et al., 2012), is a crucial factor in

parrot breeding success (Beissinger and Bucher, 1992). Thus it is likely that parrots, which typically form long-term-pair bonds (Collar, 1997), may be seeking to secure a nesting site long before the start of laying. In the post-breeding season, by contrast, Príncipe's grey parrots preferred areas with intermediate levels of slope and good availability of food resources. The direct influence of slope on animal diversity has seldom been examined, although there is a known relationship between slope and plant diversity (*e.g.* Maurer *et al*. 2006). The selection of areas rich in food-trees in the post-breeding season is presumably linked to the developmental needs of the newly fledged juveniles, the first 3–4 months of which are characterised by low survivorship (Young et al., 2012), and high parental dependency (Benson et al., 1988). Results from post-breeding surveys would certainly be inflated by the newly recruited juveniles (mean estimated recruitment ± SD = 8 ± 3%/year^{1}: Valle, 2015), which cannot be told apart from adults in the field. Thus, the pre-breeding season would be the most appropriate time for estimating the effective population size. Estimates may also differ between seasons owing to behavioural traits, e.g. an increase in detectability owing to the presence of juveniles in the post-breeding season, or a decrease owing to pairs occupying nest-sites in the pre-breeding season.

Mainland grey parrots are anecdotally known to undergo seasonal shifts in distribution (Benson et al., 1988), and our findings on Príncipe reinforce this evidence, consistent with the insight that parrot distribution in general varies seasonally with the availability of preferred foods (Galetti, 1997). One general observation and two key conclusions arise from this. First, while seasonal changes in parrot habitat use probably correlate with degree of overall regional seasonality, even in less seasonal regions habitat use may be complex. Parrot species in Papua New Guinea, for example, use selectively logged forest for feeding and primary forest for nesting within the same season (Marsden and Pilgrim, 2003). Second, parrot management plans

need to allow for multiple habitat requirements and to target a matrix of habitats (Marsden and Pilgrim, 2003), including known and potential roost- and nest-sites, salt licks, and different foraging resources (Lewis et al., 2001). Third, an understanding of variations in habitat use is crucial to the already arduous task of surveying parrot populations (Marsden et al., 2015). The accuracy of density estimates depends on the appropriate choice of time and location in any population or monitoring survey (Buckland et al., 1993). Thus, surveys of parrots need to ensure that sampling strategy is representative of both spatial and temporal variation in the presence and abundance of the target species.

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Figure legends

FIGURE 1. Orographic map of Príncipe and its position within the Gulf of Guinea, and the locations of 41 surveyed 1-km^2 sample grid squares *i.e.* 12 in primary (P) and 29 in secondary forest (S).

FIGURE 2. Variability in densities across squares between pre- and post-breeding seasons, shown as deviance from their non-significant correlation with 95 % confidence interval.

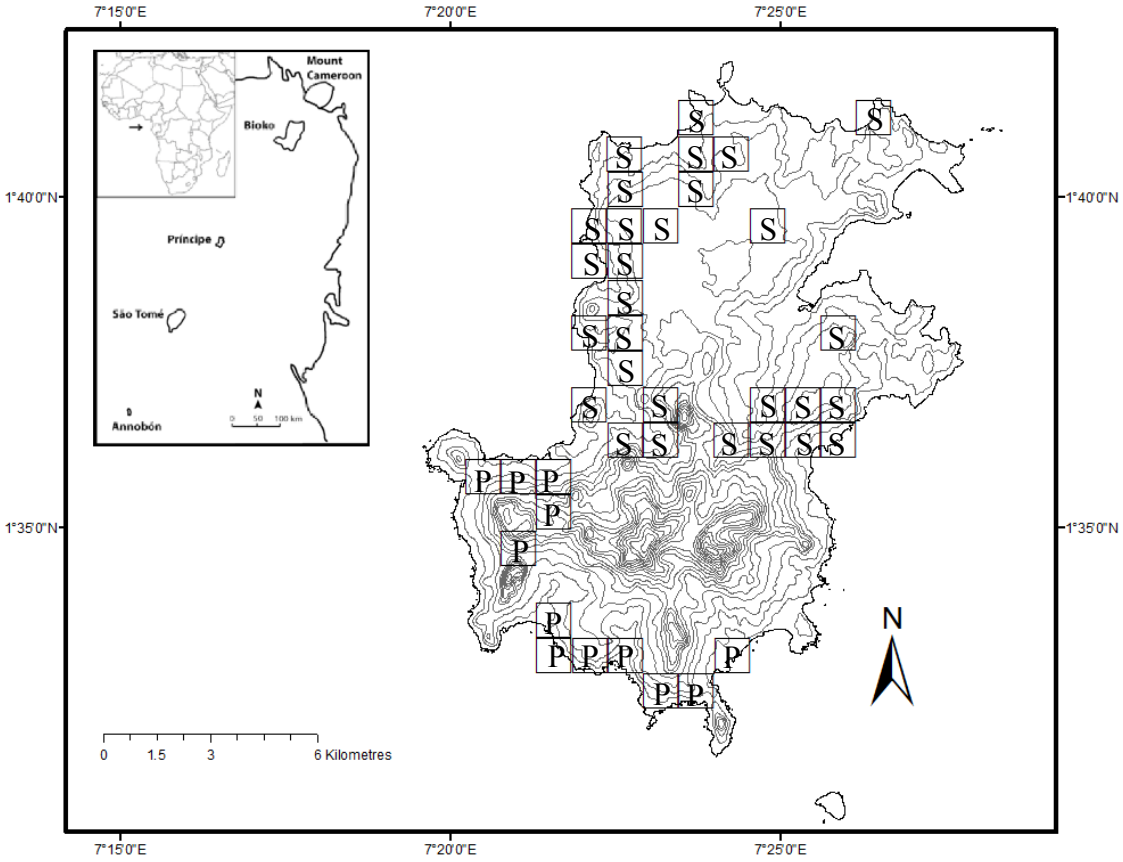
FIGURE 3. Distribution of densities across squares in pre-breeding (a) and post-breeding seasons (b).

FIGURE 4. Importance of habitat variables, measured as 'mean decrease in accuracy' in predicting parrot density after each tree permutation for: a. pre-breeding and b. post-breeding seasons.

FIGURE 5. Grey parrot density in relation to the probability of finding nest-tree species (F=2.99, P=0.07) in the pre-breeding season (continuous line) with 95 % confidence interval (dashed line).

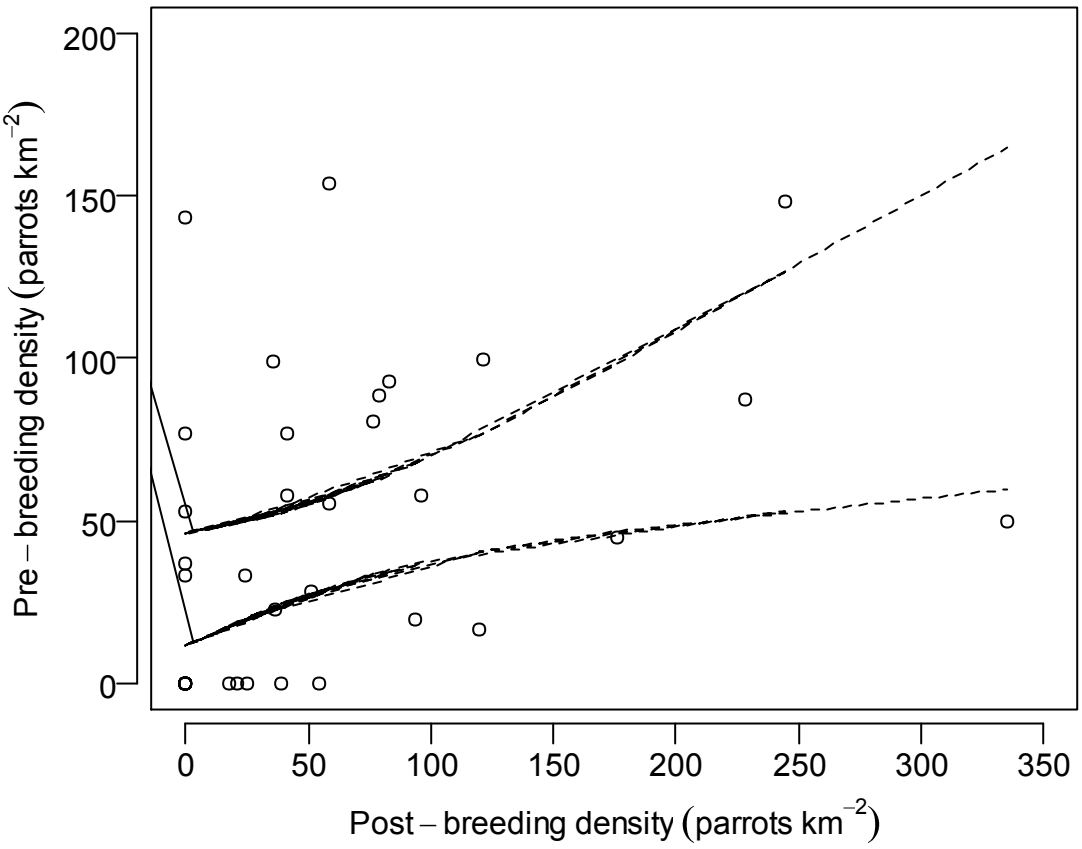
FIGURE 6. Relationships, from GAMs, between grey parrot density and a . slope, b. the probability of finding food--tree species, in the post-breeding season (continuous line) with 95 % confidence interval (shaded area) ($F = 2.69$, $P < 0.05$, and $F = 8.04$, $P < 0.01$, respectively).

Figures

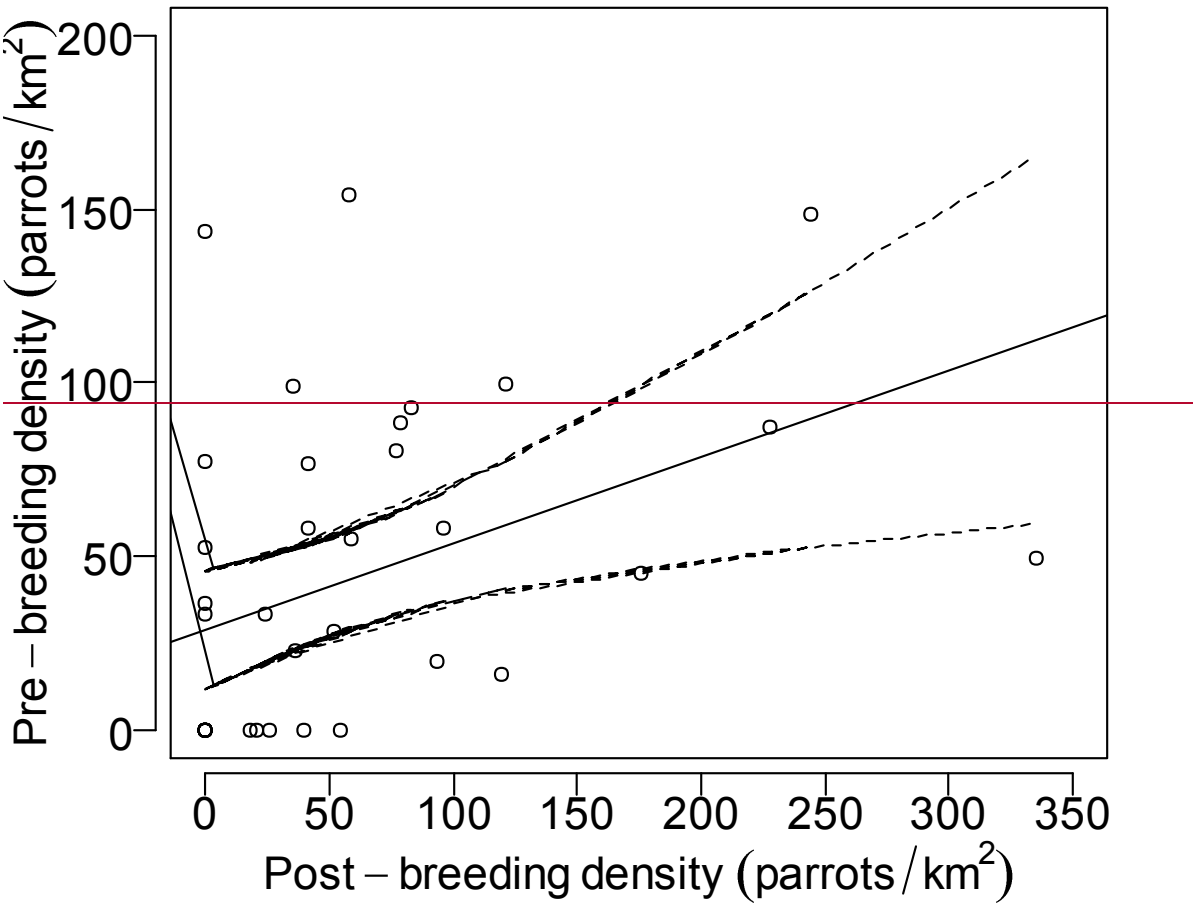

7°15'0"E
7°20'0"E
7°25'0"E
1°40'0"N
1°35'0"N
Mount Cameroon
Bioko
Príncipe
São Tomé
Annobón
N
0 50 100 km
0 1.5 3 6 Kilometres
S
P

1

2 **FIGURE 1.**


200
150
100
50
0
Pre – breeding density (parrots km^{-2})
0
50
100
150
200
250
300
350
Post – breeding density (parrots km^{-2})

1


Pre – breeding density (parrots / km²)
200
150
100
50
0
0
50
100
150
200
250
300
350
Post – breeding density (parrots / km²)

1

2 **FIGURE 2.**

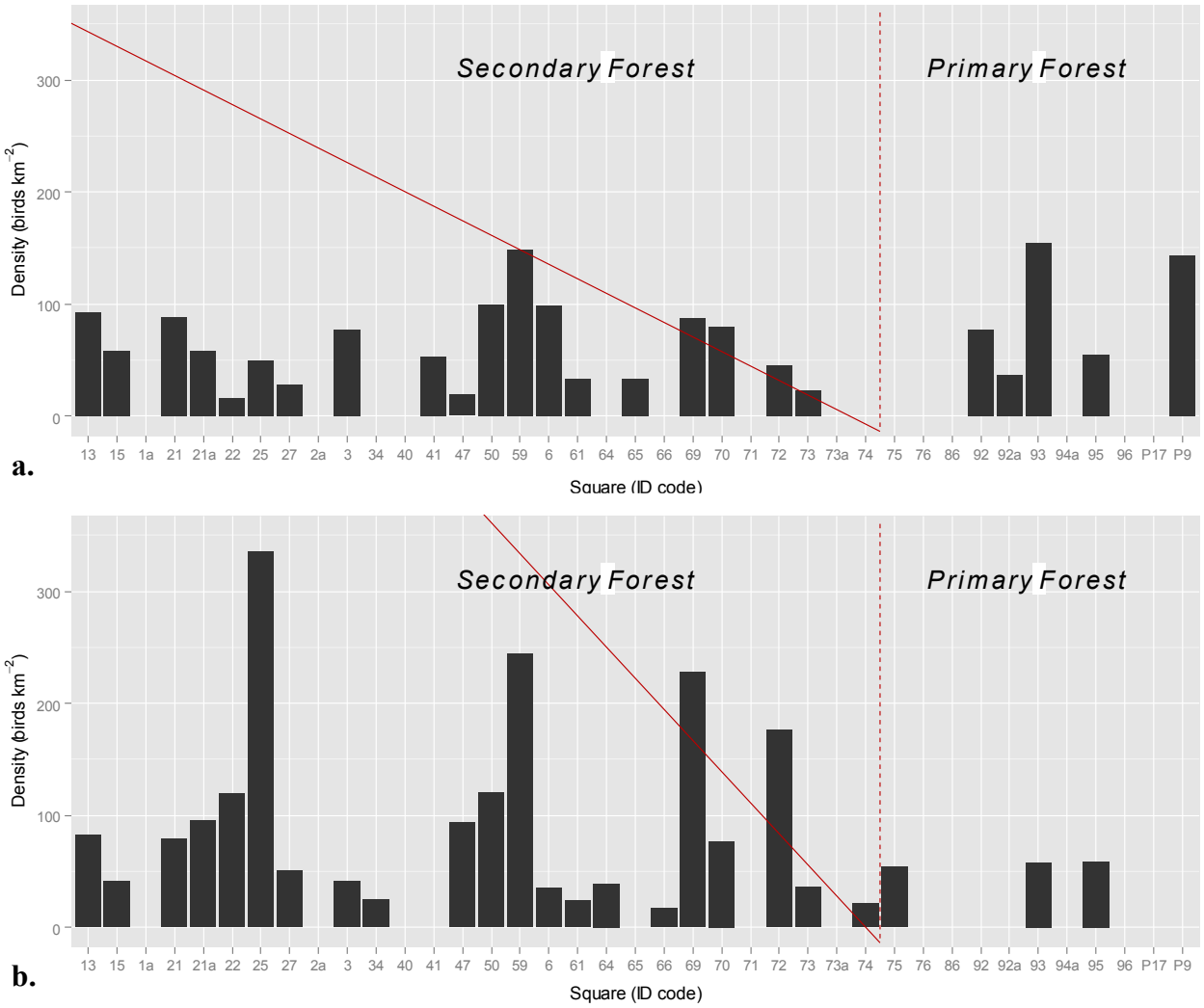
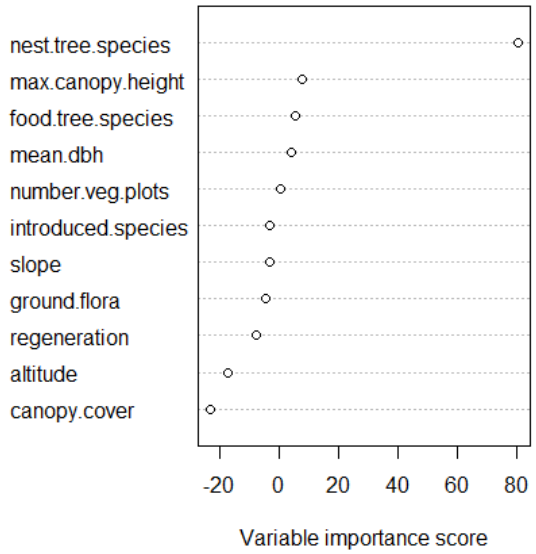

Secondary Forest
Primary Forest
Density (birds km^{-2})
0
100
200
300
13 15 1a 21 21a 22 25 27 2a 3 34 40 41 47 50 59 6 61 64 65 66 69 70 71 72 73 73a 74 75 76 86 92 92a 93 94a 95 96 P17 P9
Square (ID code)
a.
Secondary Forest
Primary Forest
Density (birds km^{-2})
0
100
200
300
13 15 1a 21 21a 22 25 27 2a 3 34 40 41 47 50 59 6 61 64 65 66 69 70 71 72 73 73a 74 75 76 86 92 92a 93 94a 95 96 P17 P9
Square (ID code)
b.

FIGURE 3.

a.


nest.tree.species
max.canopy.height
food.tree.species
mean.dbh
number.veg.plots
introduced.species
slope
ground.flora
regeneration
altitude
canopy.cover
-20
0
20
40
60
80
Variable importance score

b.

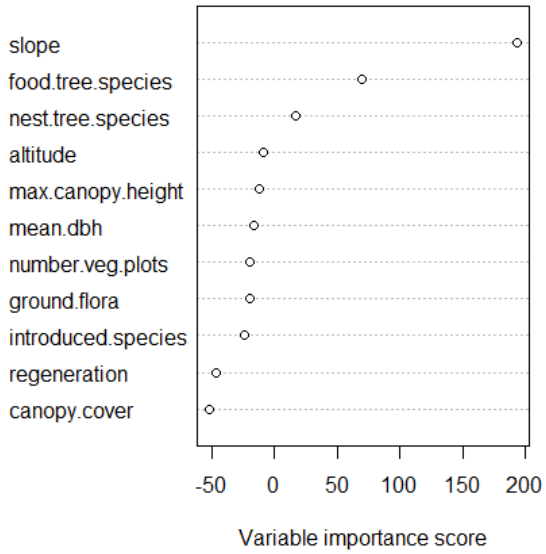
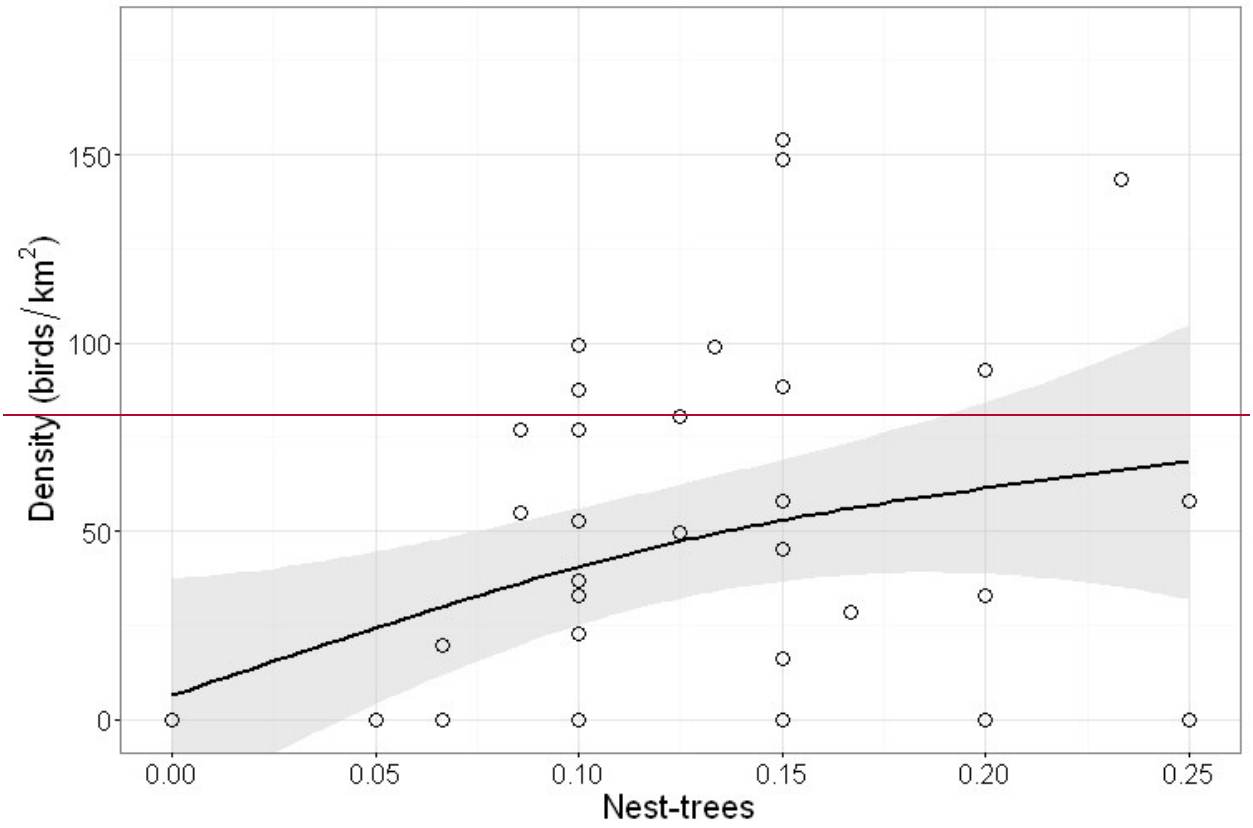
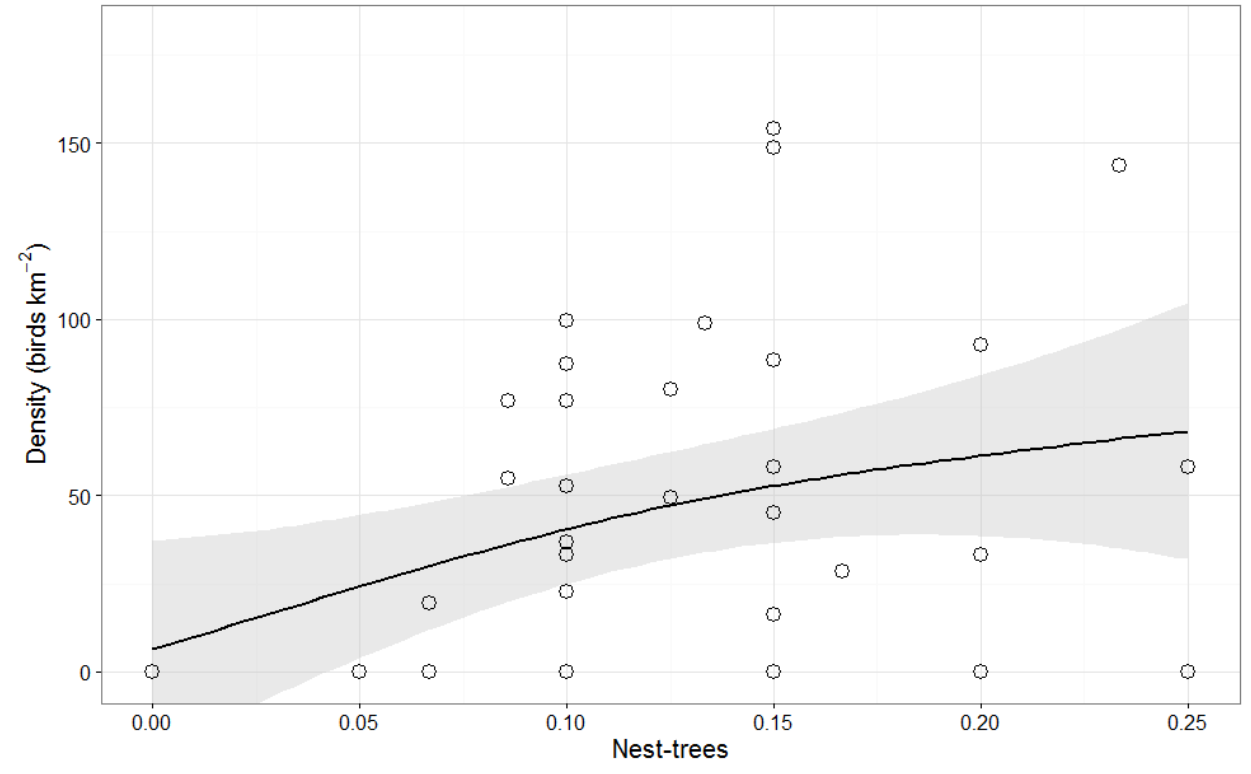

slope
food.tree.species
nest.tree.species
altitude
max.canopy.height
mean.dbh
number.veg.plots
ground.flora
introduced.species
regeneration
canopy.cover
-50
0
50
100
150
200
Variable importance score

FIGURE 4

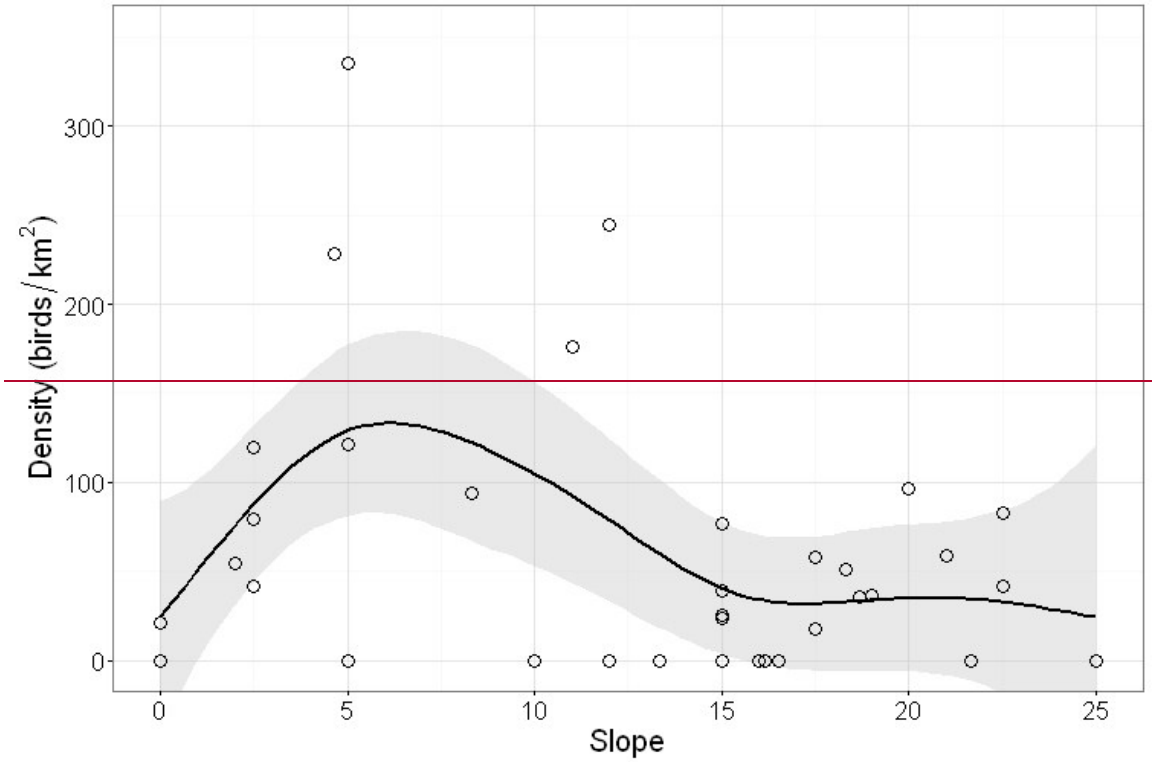

Density (birds / km^2)
150
100
50
0
0.00
0.05
0.10
0.15
0.20
0.25
Nest-trees

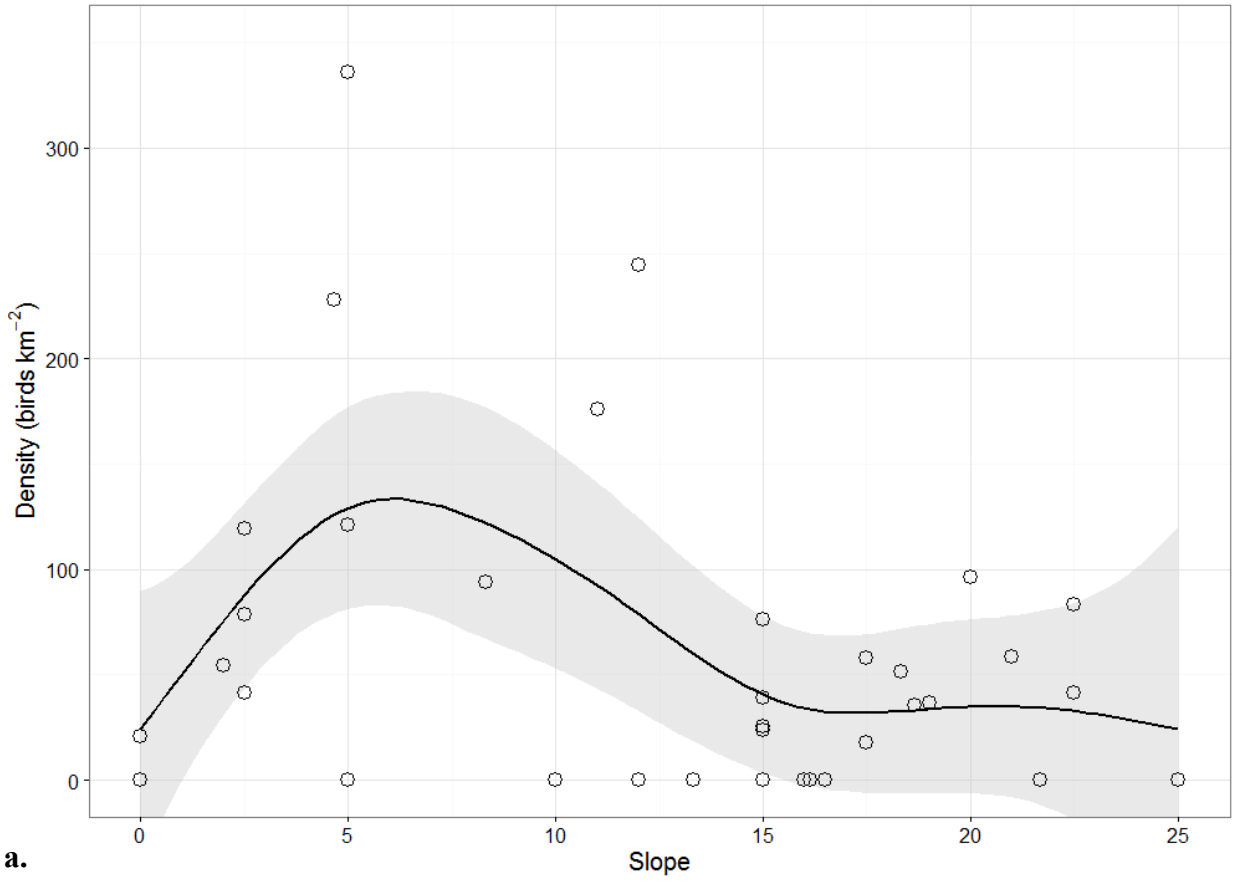
1


Density (birds km^{-2})
150
100
50
0
0.00
0.05
0.10
0.15
0.20
0.25
Nest-trees

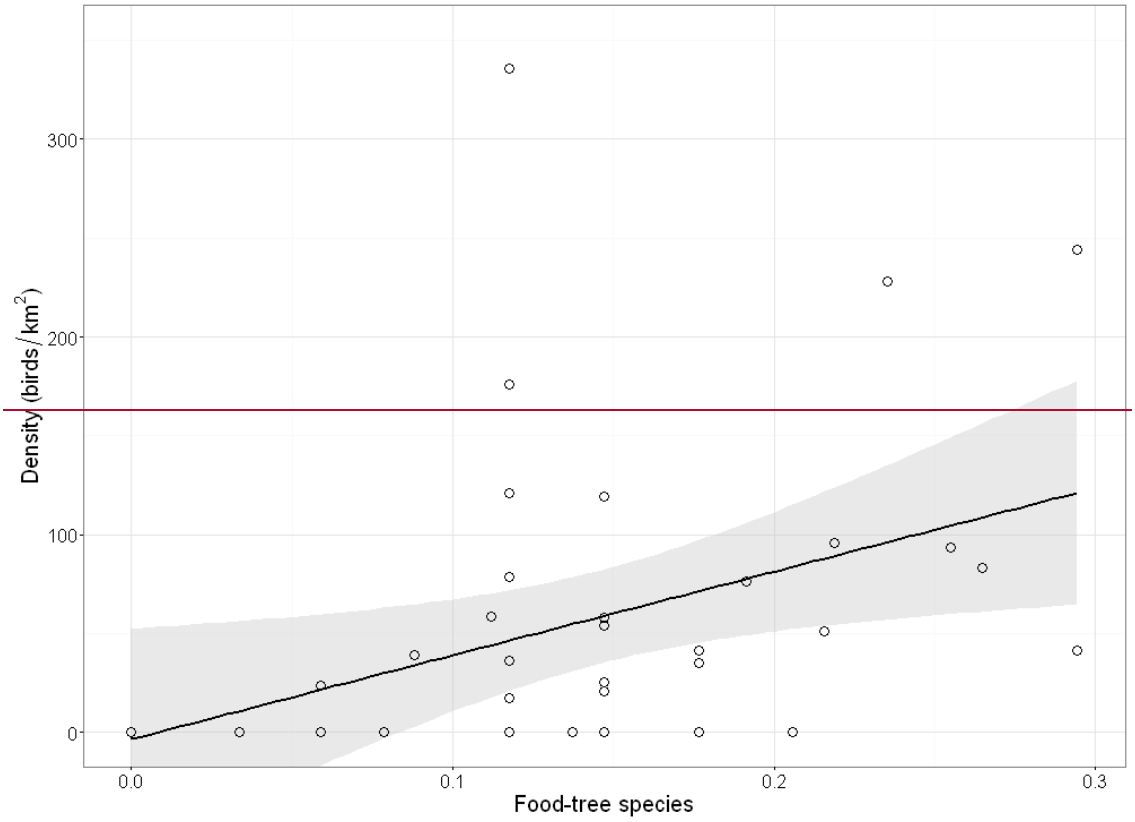
2

FIGURE 5.

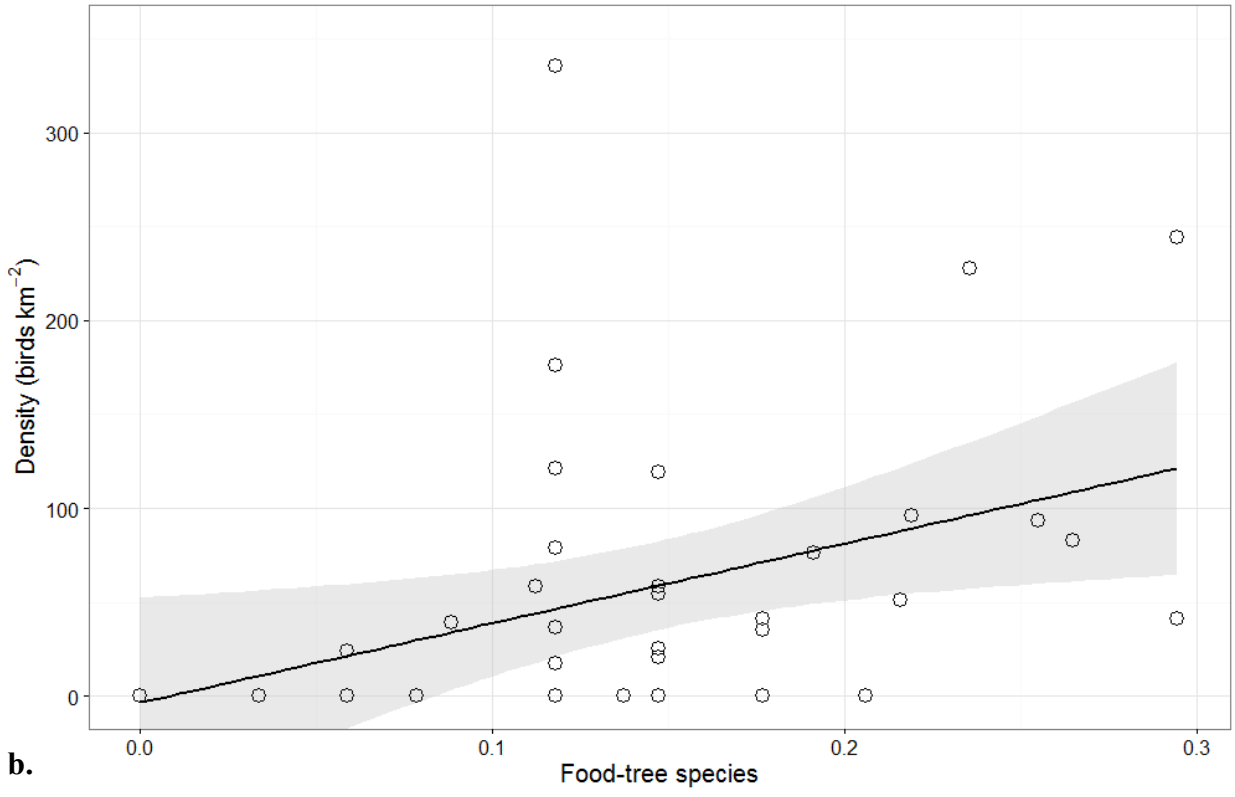

Density (birds / km^2)
300
200
100
0
0
5
10
15
20
25
Slope


Density (birds km^{-2})
300
200
100
0
0
5
10
15
20
25
Slope

a.


Density (birds / km^2)
300
200
100
0
0.0
0.1
0.2
0.3
Food-tree species

1


Density (birds km^{-2})
300
200
100
0
0.0
0.1
0.2
0.3
Food-tree species

b.

2

FIGURE 6.