

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

3 Simon Valle^{1*}, Nigel J. Collar², Edwin Harris¹ and Stuart J. Marsden¹

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5 ¹ *Division of Biology & Conservation Ecology, School of Science & the Environment,*

6 *Manchester Metropolitan University, Chester Street, Manchester M1 5GD, U.K.*

7 ² *BirdLife International, Pembroke Street, Cambridge CB2 3QZ, UK*

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

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1 **Abstract**

2

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

17

18 **Introduction**

19

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

1 causes of worldwide parrot population declines (Snyder et al., 2000, Olah et al., 2016). However,
2 despite their threatened status, little is known about the size of parrot populations in the wild
3 (Marsden and Royle, 2015), their habitat requirements (Snyder et al., 2000), or the seasonality of
4 these requirements (Renton, 2002). Parrot habitat is defined by a number of limiting factors,
5 namely food (Saunders, 1990, Berg et al., 2007), nest sites (Beissinger and Bucher, 1992, Wiebe,
6 2011), roost sites (Chapman et al., 1989), and water and mineral licks (Lee et al., 2010).
7 However, the availability of these resources can vary significantly in space and time, and over
8 the annual cycle parrots may require a variety of habitats and forest types (Marsden and Pilgrim,
9 2003, Renton, 2002). Thus, understanding seasonal changes in habitat use by parrots is important
10 for conservation monitoring, which can be particularly challenging owing to their flocking
11 behaviour and low detectability (Marsden and Fielding, 1999, Lee and Marsden, 2012, Marsden
12 et al., 2015).

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

1 2015). Thus, Príncipe's population presents an opportunity to study grey parrot ecology without
2 the bias of anthropogenic pressures present in mainland populations.

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

7

8 **Material and methods**

9

10 *Study area*

11 The island of Príncipe (1°32'–1°43'N 7°20'–7°28'E; 139 km²), part of the nation of São Tomé
12 and Príncipe, lies 220 km off West Africa, in the Gulf of Guinea (Fig. 1). Príncipe is broadly
13 divided in two geographically and climatically distinct regions: a low-lying basalt platform in the
14 north, with hills below 180 m asl, and a mountainous region in the south (Jones and Tye, 2006).
15 By the beginning of the twentieth century the forest in the north had been modified in many
16 places by clear-felling, selective felling and the creation of cocoa, coffee and coconut plantations
17 (Exell, 1973), while the south remains covered in pristine forest with much floral endemism
18 (Figueiredo et al., 2011). The rainy season lasts from September to May and the dry season
19 (*gravana*) from July to August, while a shorter dry season runs from December to early January,
20 with the north being always drier than the south (Jones and Tye, 2006).

21

22 *Population and density estimation*

1 The island was divided into 133 one-km² grid squares based on the Universal Transverse
2 Mercator (UTM) geographic coordinate system. To account for habitat heterogeneity, these were
3 then classified as primary or secondary forest, according to the latest vegetation surveys
4 (Albuquerque et al., 2004) and visual ground-truthing. Fifty-nine squares (44%) were assigned to
5 the primary forest habitat category. The remaining 74 squares (56%) fell into the secondary
6 forest category, which included lowland forest (26%), as well as overgrown cocoa (*Theobroma*
7 *cacao*) plantations (31%), coconut palm (*Cocos nucifera*) groves (29%), and oil palm (*Elaeis*
8 *guineensis*) estates (11%). Forty-one squares (i.e. one in every five, cyclically) were selected
9 systematically on a map (12 in primary and 29 in secondary forest). However, in most of these
10 (63% of squares), owing to issues of accessibility logistics and safety, the nearest accessible
11 square had to be visited instead (Fig. 1).

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

1 flocks, cluster sizes was recorded without error; and (e) the sampled strips were representative of
2 the surveyed region square (Buckland et al., 2008). In each grid square, a transect (mean 1 km \pm
3 0.4 SD, min – max = 0.3–1.9) was walked at a rate of 1 km h^{-1} regardless of terrain. Steep terrain
4 and dense vegetation often prevented safe navigation, so only existing paths (width \leq 0.5 m) and
5 natural openings in the otherwise impenetrable vegetation were used. All grey parrots heard and
6 seen perched along the transect route were counted, and their perpendicular distance from the
7 transect line measured. A cut-off distance of 50 metres was established, since exploratory
8 fieldwork showed that birds beyond this distance were very hard to detect and their contribution
9 to the building of the detection function negligible (Buckland et al., 1993). All flying birds, since
10 they were not detected at their initial location, were excluded from the counts unless they had
11 been flushed, in which case their take-off point was recorded (Marsden, 1999). Transects were
12 walked between 0700h and 1100h, when parrot activity is expected to be highest (Blake, 1992).
13 All counts were conducted in calm dry conditions, by SV alone. Depending on terrain conditions
14 and logistics, between one and four transects per day were surveyed, within a given area (i.e.
15 some squares would be adjacent). Transects were initially walked once after the fledging period
16 (March–April 2014; ‘post-breeding’) and again just before the following breeding season
17 (August–September 2014; ‘pre-breeding’). Distance sampling is most efficient when birds are
18 spread relatively evenly through the survey region (Buckland et al., 2008). Thus, since nesting
19 grey parrots movements are much more secretive and restricted during all phases of breeding
20 (Valle, 2015), no surveys were conducted in this period to avoid sources of bias.

21 DISTANCE 6.0 (Thomas et al., 2010) software was used to estimate grey parrot density
22 (individuals/km²) in each of the surveyed grid squares using a shared detection function across
23 squares. A measure of forest regeneration (see ‘*Habitat characterization*’ below) was included as

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

10

11 *Habitat characterization*

12 Every 500 m along each transect, the following habitat measures were taken within a 20 m radius
13 sample plot: geographic coordinates and altitude (GPS); slope (clinometer); aspect (compass);
14 maximum canopy height (clinometer and range finder); canopy closure in five equidistant points
15 (type-A spherical densitometer); number of woody stems at 1 m height (counted by swinging a
16 1-m-long stick through 360° at 1 m height, and hereafter referred to as 'regeneration'); diameter
17 at breast height (DBH) of the three largest-girthed trees (tape measure); and estimated percentage
18 of ground covered by understorey, estimated by eye (hereafter 'ground flora'). Measurements
19 were then averaged across sample plots to give a single value per variable per grid square. In
20 each vegetation plot, presence or absence was recorded for all tree species which, from according
21 to the available literature on the species's habitat use and local knowledge, grey parrots were
22 known to feed on or nest in (Table S1). Also recorded were 12 widespread introduced/cultivated
23 tree species as an indicator of anthropogenic disturbance (Lee and Marsden, 2008). For each

1 square, the proportion of vegetation sample plots holding each of the above tree species was
2 calculated, and this was then averaged for three categories, namely ‘food-tree species’, ‘nest-tree
3 species’ and ‘introduced/cultivated species’. In two grid squares the length of the transect was
4 <500 m and, thus, no vegetation sampling was carried out. These squares were excluded from
5 any further habitat association analysis. Habitat variables were sampled in a total of 99 plots
6 across the island, i.e. 2.5 per square.

7 8 *Seasonality in parrot-habitat associations*

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

23

1 **Results**

2

3 *Population size and density estimate*

4 The total population was estimated at $6,517 \pm 361$ (mean \pm SE) grey parrots in the pre-breeding
5 season, and at $7,996 \pm 568$ in the post-breeding season, with mean densities of 47.9 ± 2.7 and
6 58.78 ± 4.2 parrots/km² respectively (Table S2). The total number of detections did not vary
7 greatly between the two seasons (125 and 139 in pre- and post-breeding season respectively),
8 and in each of them parrots were detected in the majority of the surveyed squares (58% in each
9 season), with no particular inclination for either type of forest ($\chi^2 = 2.98$, $df = 1$, $P = 0.08$). In
10 both seasons, 17 grid squares (5 in primary and 12 in secondary forest in pre-breeding season; 8
11 and 9 in post-breeding season) had no records, and thus had an estimated zero density. There was
12 no systematic difference (i.e. increase or decrease) in abundance within the 41 grid squares ($W =$
13 260 , $P = 0.36$), between pre- and post-breeding season. However, there was considerable
14 variability in densities across squares between the two seasons (Fig. 2). In the pre- and post-
15 breeding seasons, three and four grid squares respectively had a density between 100 and 200
16 parrots/km² (max \pm SE = 154.06 ± 8.24 ; Fig. 3a,b). In the latter season, three grid squares had a
17 density ≥ 200 parrots/km² (max \pm SE = 336 ± 24 ; Fig. 3b). Parrot density was significantly
18 lower in primary than in secondary forest in the post-breeding season ($W = 64$, $P < 0.01$), but
19 there was no significant difference between forest types in the pre-breeding season ($W = 139$, $P =$
20 0.85).

21

22 *Seasonality of parrot-habitat associations*

1 RF analyses indicated that the presence of nest-tree species was the best predictor of local parrot
2 density in the pre-breeding season, while slope and presence of food-trees were the strongest
3 predictors in the post-breeding season (Fig. 4). GAM shows a near-significant nonlinear
4 relationship between local parrot density and nest-tree species ($F = 2.99, P = 0.07$; Fig. 5). In the
5 post-breeding season, local density was related to slope in a nonlinear way, with gently sloping
6 terrain ($0-20^\circ$) associated with high densities ($F = 2.69, P < 0.05$, Fig. 6a), and linearly with
7 presence of feeding trees ($F = 8.04, P < 0.01$, Fig. 6b). There was no correlation between terrain
8 slope and the presence of food-tree species ($r_s = +0.08, P = 0.63, N = 39$).

10 Discussion

11
12 On Príncipe, grey parrots show both geographical and seasonal preferences in their use of
13 available habitat. Densities were estimated to be in the range of 48–59 individuals $/\text{km}^2$ on the
14 island, which is the highest ever recorded for the species previous maxima being 29 and 10.7
15 birds $/\text{km}^2$ estimated in Lobeke and Campo Ma'an National Parks, Cameroon, respectively
16 (Marsden et al., 2015). These densities are also relatively high compared to other psittacines. Out
17 of 90 parrot species for which at least one density estimate is available, only 17 have densities
18 higher than 50 birds $/\text{km}^2$, and all but two of these (Red-faced Parrot *Hapalopsittaca pyrrhops*
19 and White-crowned Parrot *Pionus senilis* in Ecuador) are island populations (Marsden and
20 Royle, 2015). This pattern may be the consequence of a combination of Príncipe's particular
21 environmental conditions, but is also consistent with the phenomenon known as 'density
22 compensation', where the summed high population densities of the few species on islands is
23 similar to the summed lower densities found on the species-rich mainland (MacArthur et al.,

1 1972). Whatever the cause, such high densities may have important conservation implications for
2 the species. Príncipe is clearly serving as a small stronghold for the otherwise declining global
3 population, as other islands are for other parrot species, for example the Bolama-Bijagós
4 Archipelago for the Timneh Parrot (*Psittacus timneh*) (Clemmons, 2003).

5 Parrot abundance varied greatly across the island, to the point where it was entirely absent
6 from some areas in both seasons (26% of surveyed grid squares). This suggests that some areas
7 may be permanently unattractive to the species despite the small size of the island, the large
8 population present, and the well-known mobility of grey parrots (Collar, 1997, Juniper and Parr,
9 1998). By contrast, in the post-breeding season, there were three grid squares in secondary forest
10 which had very high densities (i.e. ≥ 200 parrots/km⁻²). Owing to their environmental
11 characteristics, these areas are likely to host periodically high concentrations of important
12 resources, as indicated by the positive relationship we found between parrot density and food-
13 tree species. Such large densities could also be attributable solely to the influx of newly fledged
14 juveniles, or to some more complex post-breeding behaviour, as some parrot species are known
15 to establish crèches as an anti-predator behaviour or for flight training (Rowley, 1980, Wanker et
16 al., 1996, Taylor and Perrin, 2006). Both densities and total population estimates were consistent
17 with results from a similar survey carried out in 2012 and with what is known about the species's
18 nest densities and reproductive output on the island (Valle, 2015).

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

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

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

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

9

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22 **Figure legends**

1 FIGURE 1. Orographic map of Príncipe and its position within the Gulf of Guinea, and the
2 locations of 41 surveyed 1-km² sample grid squares *i.e.* 12 in primary (P) and 29 in secondary
3 forest (S).

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

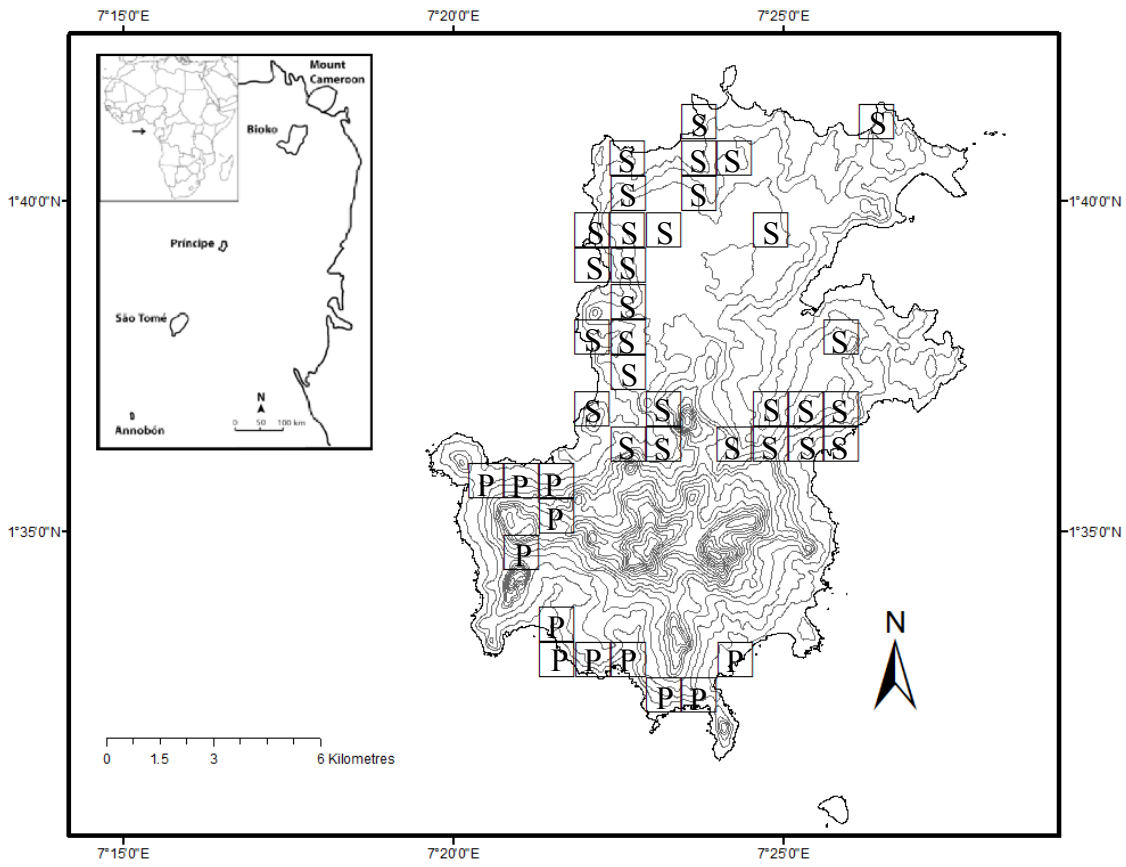
6 FIGURE 3. Distribution of densities across squares in pre-breeding (a) and post-breeding
7 seasons (b).

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

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

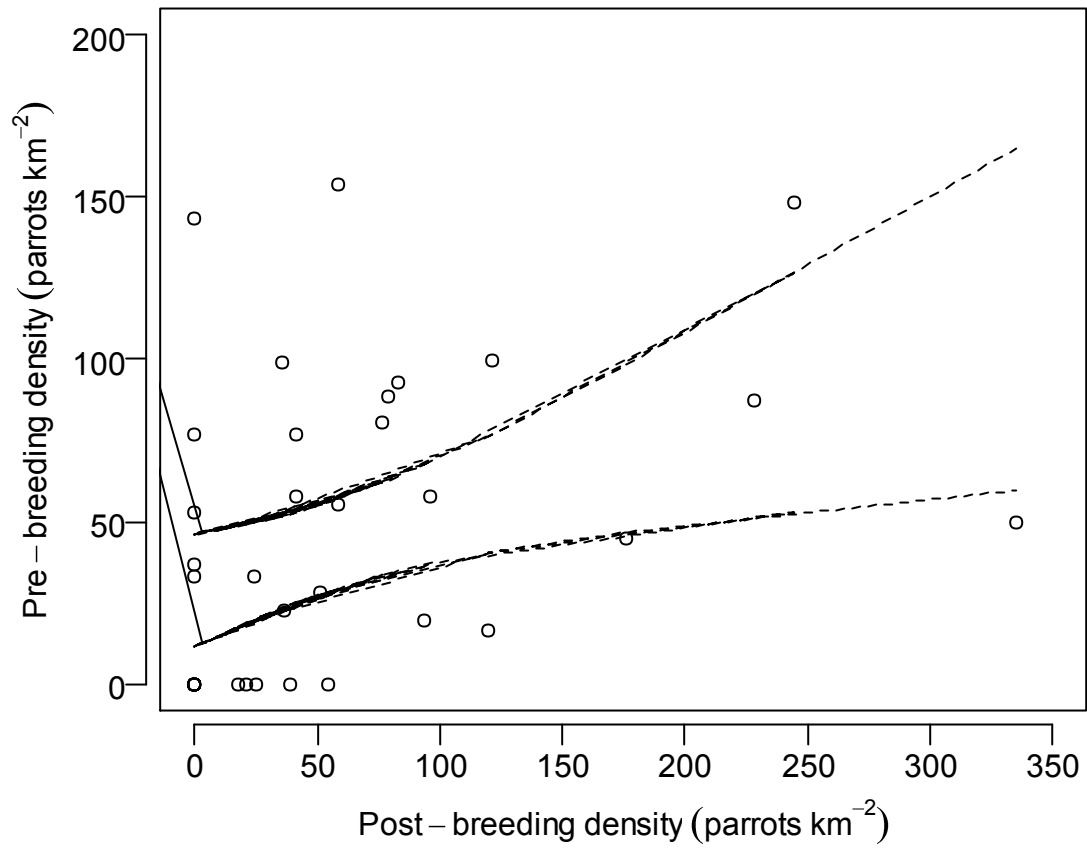
14 FIGURE 6. Relationships, from GAMs, between grey parrot density and a . slope, b. the
15 probability of finding food-tree species, in the post-breeding season (continuous line) with 95 %
16 confidence interval (shaded area) (F = 2.69, P < 0.05, and F = 8.04, P < 0.01, respectively).

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22 **Figures**

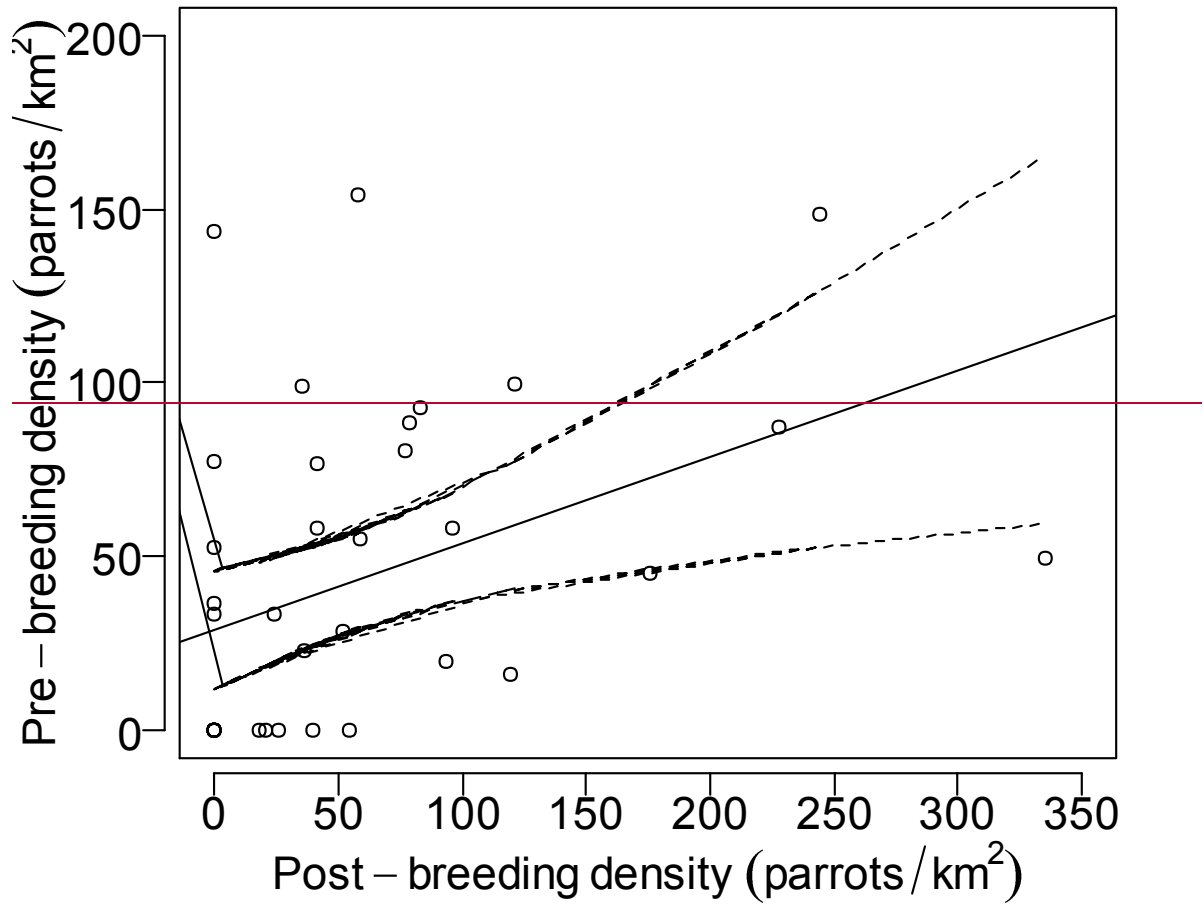


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2 **FIGURE 1.**

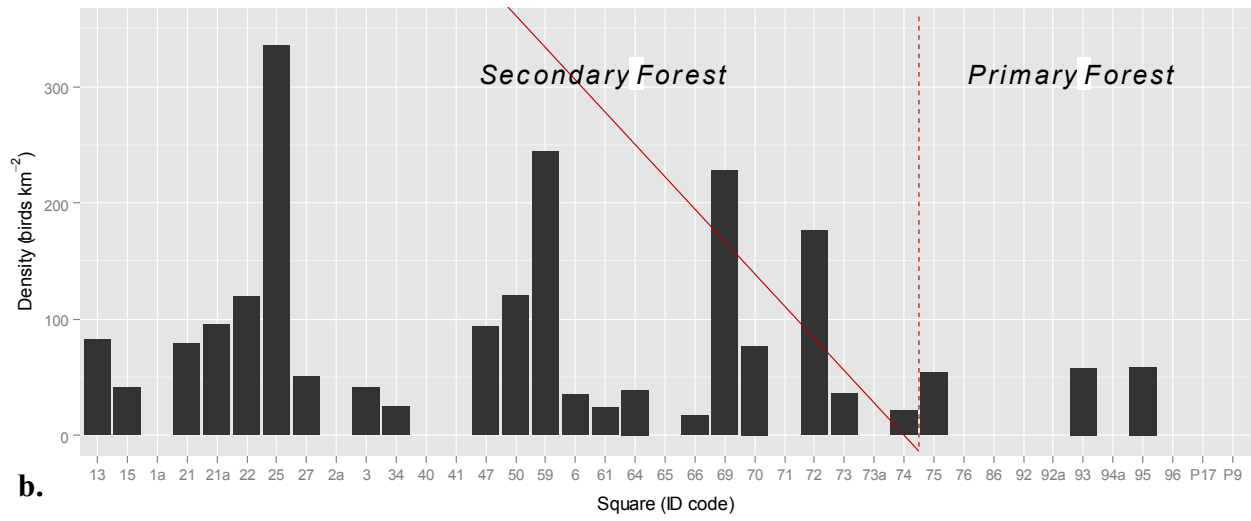
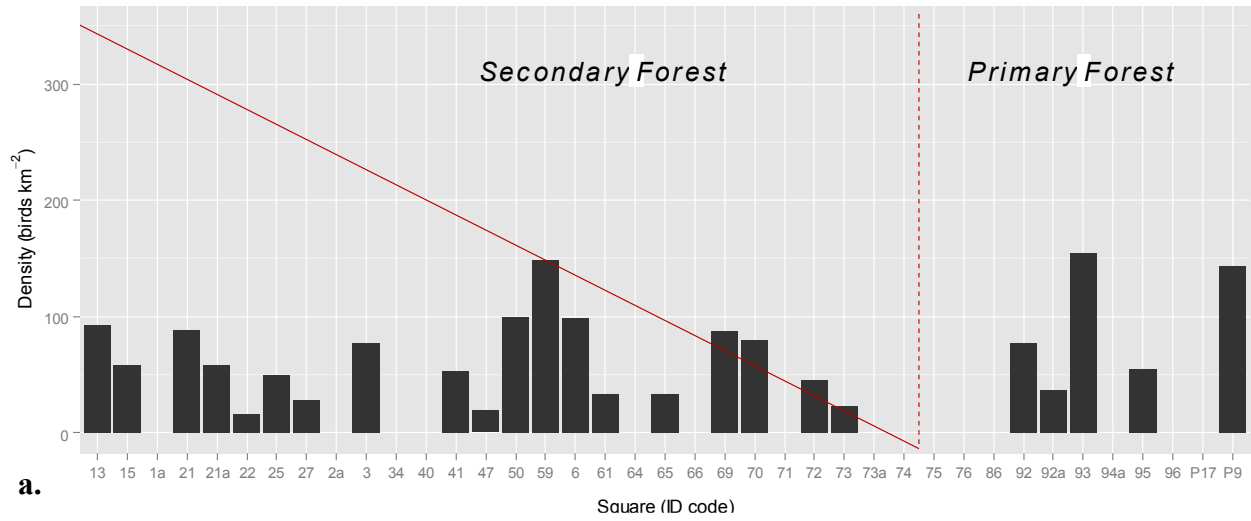


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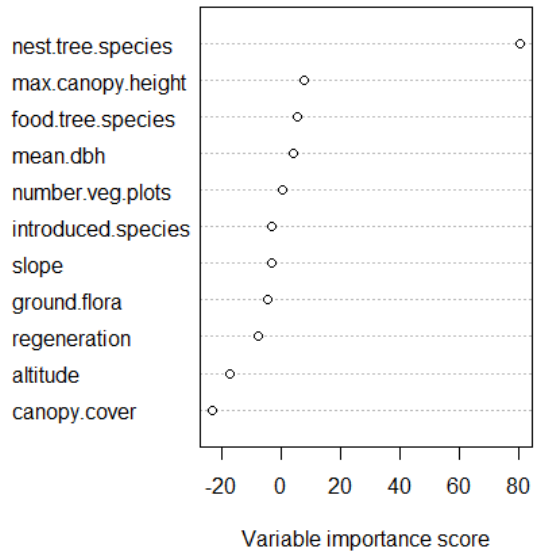
2 FIGURE 2.



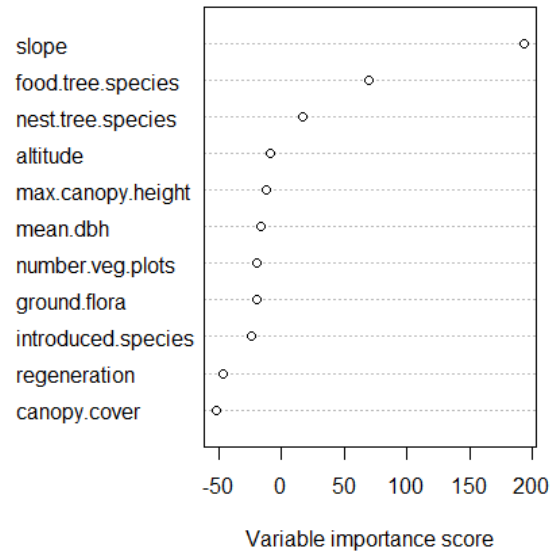
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FIGURE 3.

a.



b.



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2 **FIGURE 4**

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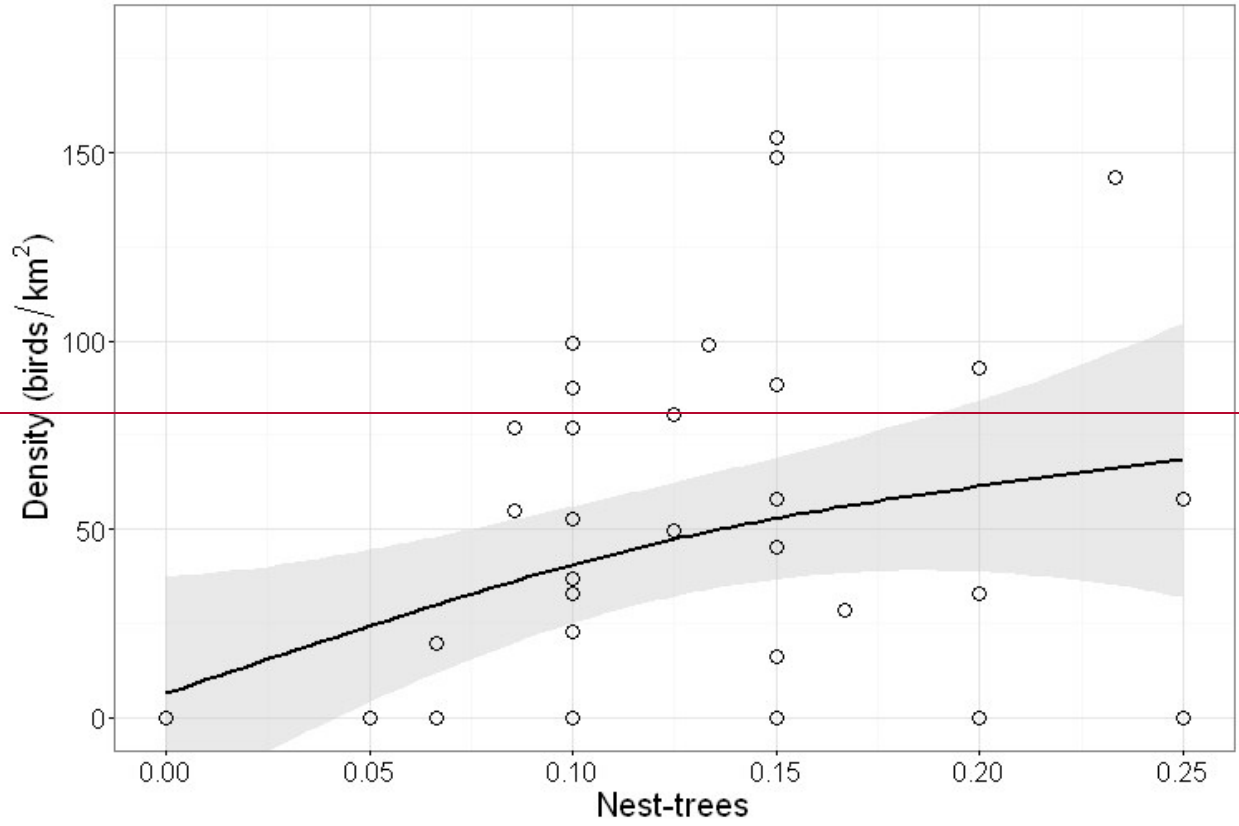
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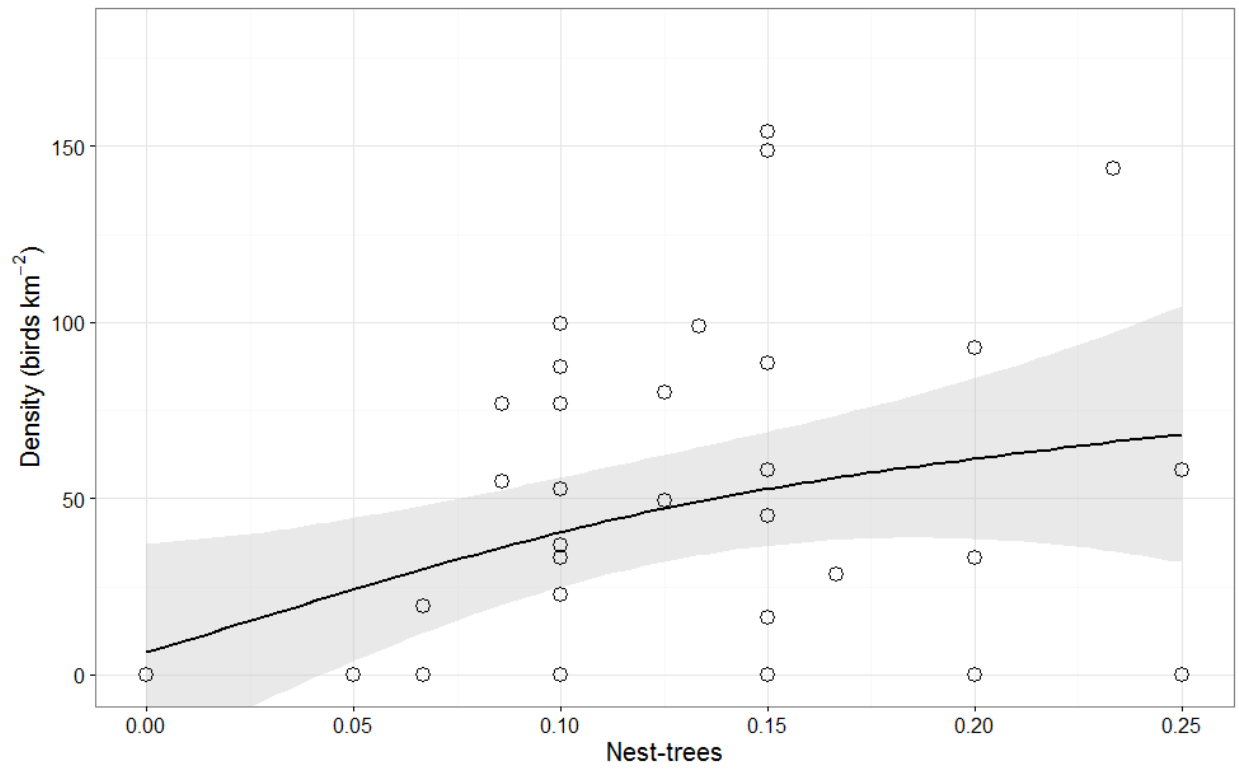
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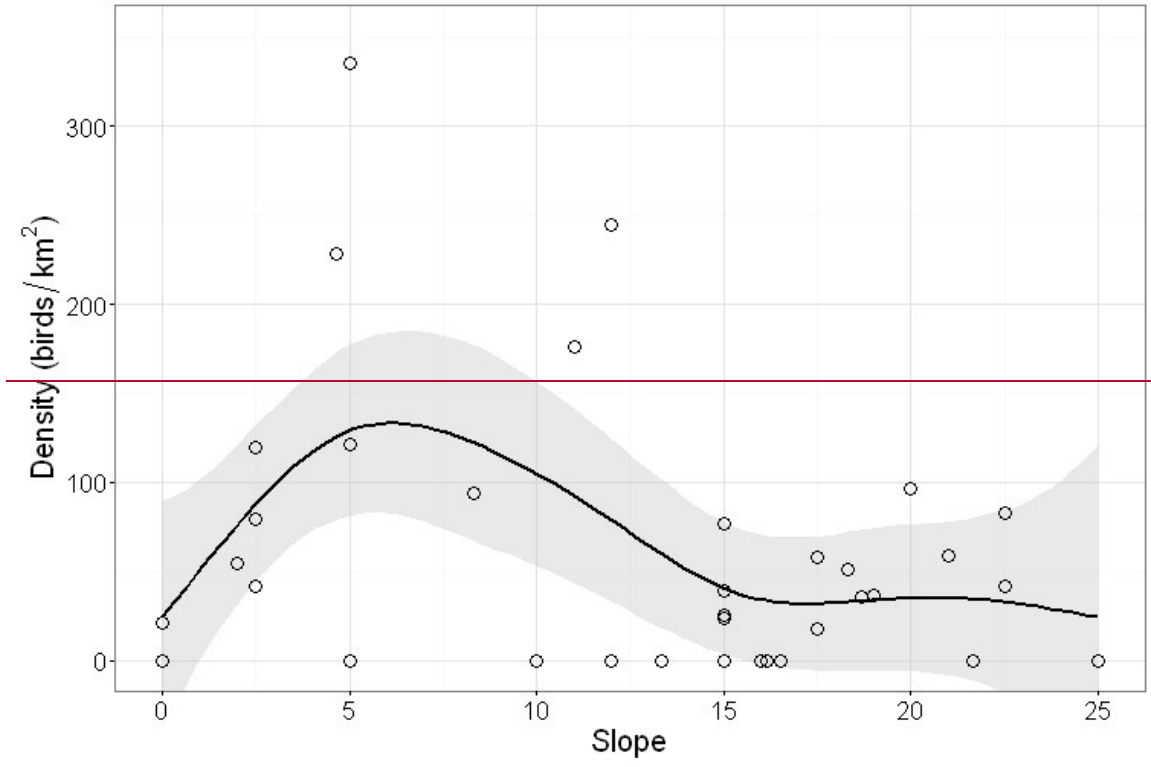
1 **FIGURE 5.**

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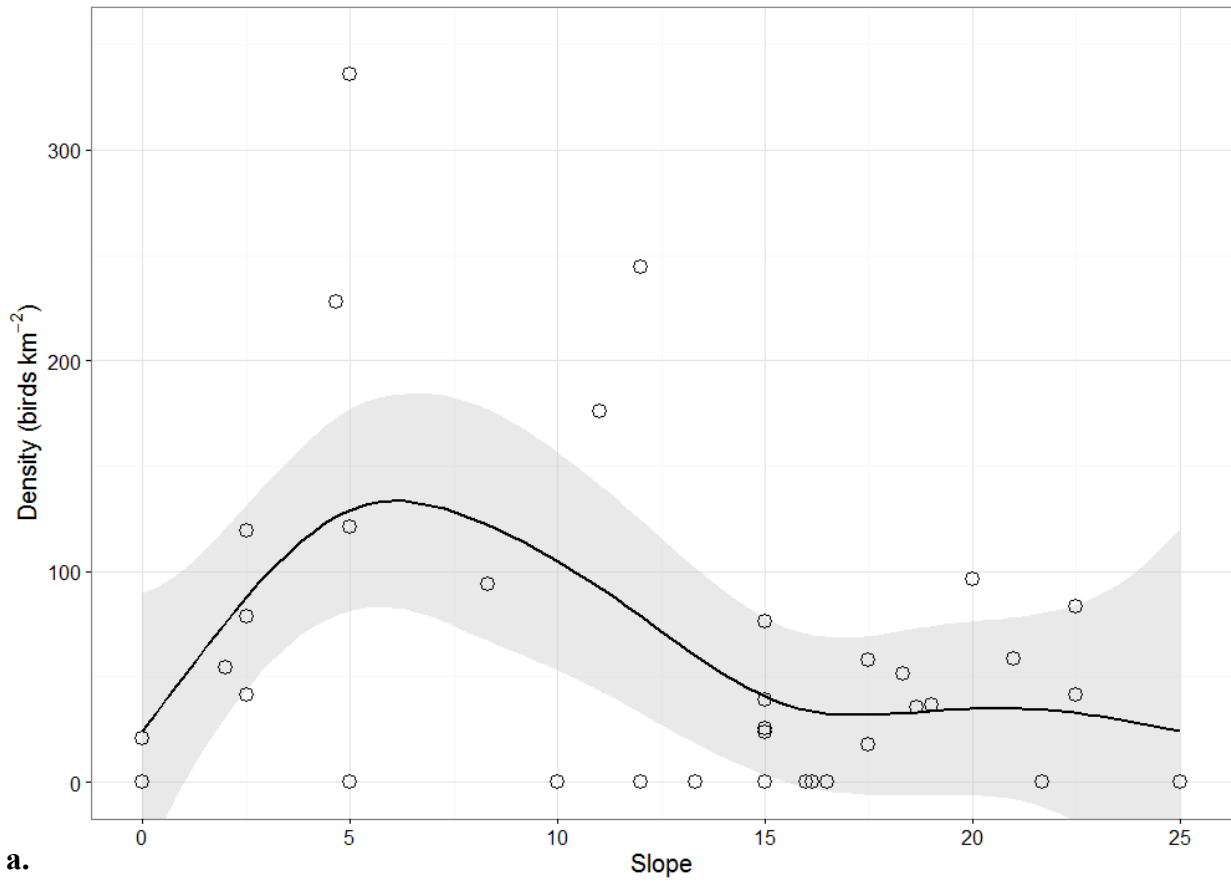
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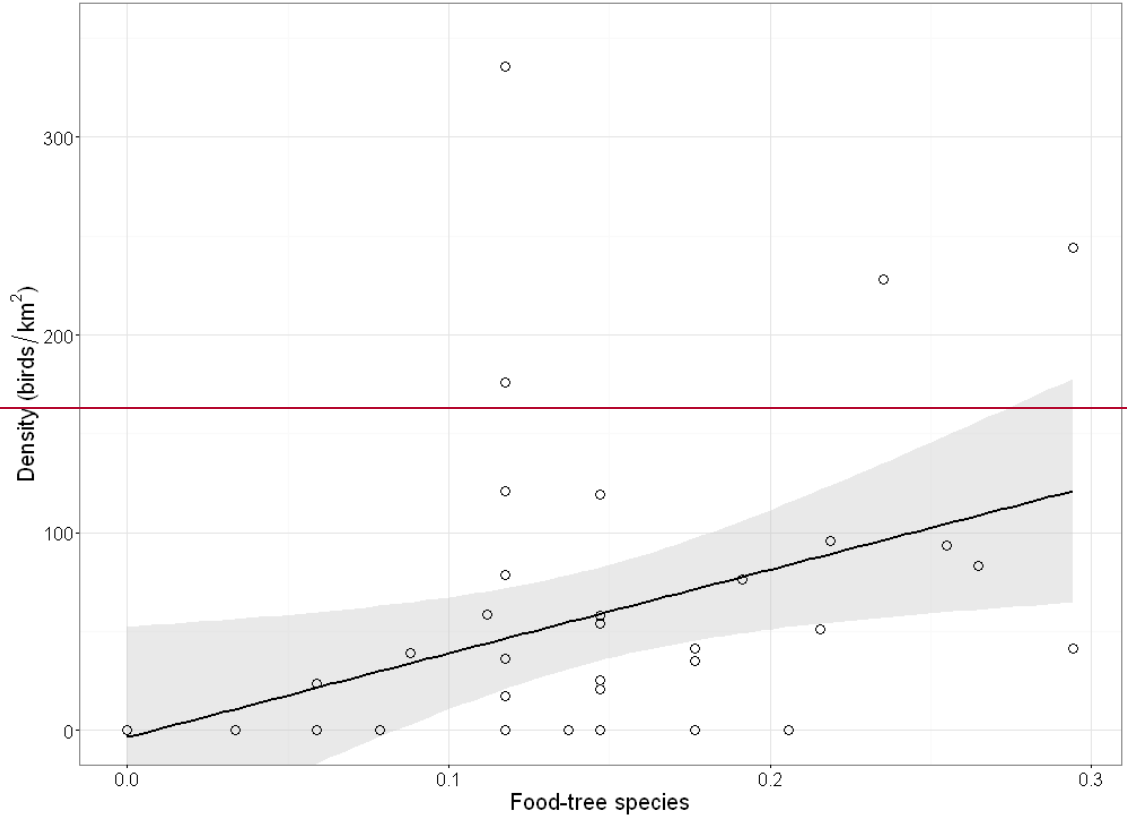


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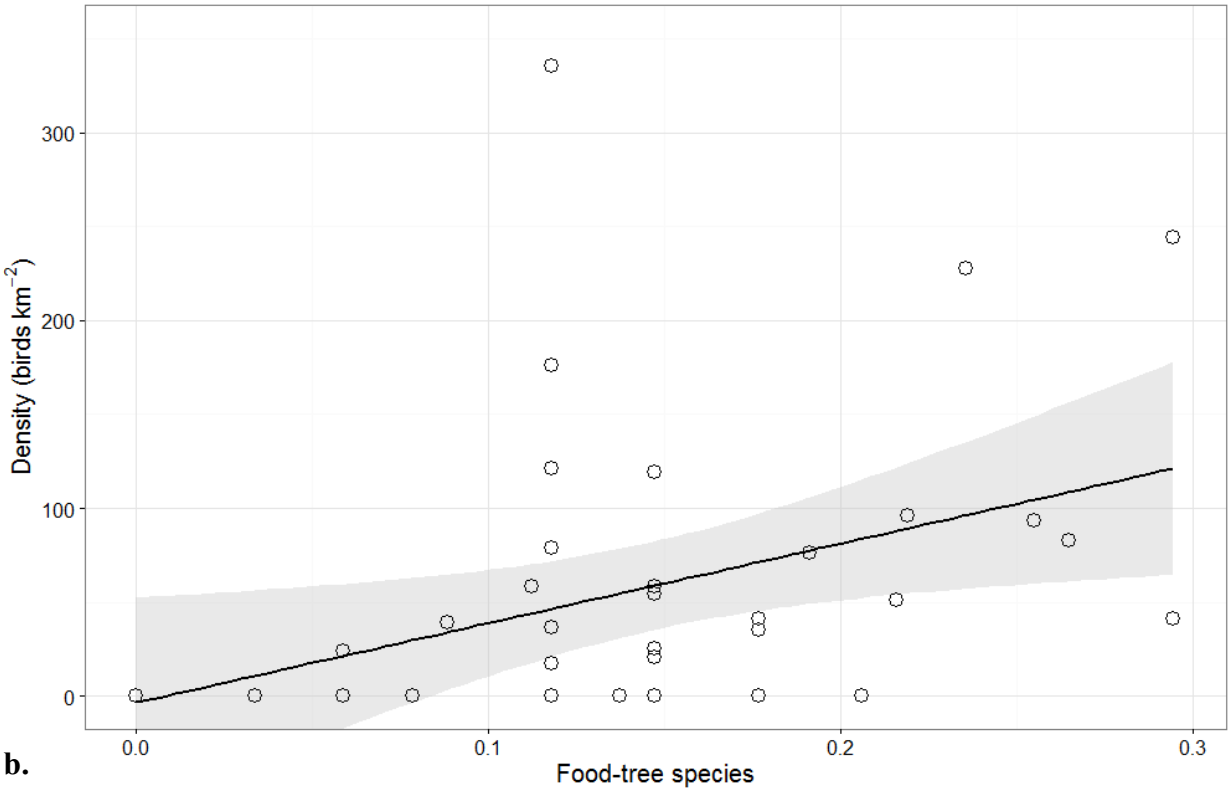


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a.



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1 **FIGURE 6.**