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Nest-site selection and nest predation in a tropical passerine in relation to food, friends and foes

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Conflict of interest statement

The authors declare no conflict of interest.

Ethics statement

The study followed the ASAB/ABS Guidelines for the ethical treatment of animals in research. The fieldwork was conducted with the permission of the Seychelles Bureau of Standards and the Seychelles Ministry of Environment, Energy and Climate Change, and complied with all local ethical guidelines and regulations. Nature Seychelles granted permission to conduct fieldwork on Cousin Island.

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Author contributions

M.H. conceived the idea, A.O.K.V.E., M.H. & J.K. formulated the hypotheses and design of the study. A.V.E. & M.H. collected data during the main fieldwork season and J.K., D.R. & H.D. collected long term data as part of ongoing research on Cousin island. A.V.E. analyzed the data. A.V.E. wrote the initial draft and M.H., J.K., D.R. & H.D. substantially edited the manuscript.

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ABSTRACT

Nest-site selection is an important determinant of avian reproductive success, mainly through its effect on predation risk. However, how environmental and social factors affect nest-site selection and predation risk remains less well understood. Optimal nest positioning may depend on the balance of many distinct factors such as nest predation, food availability, extra-pair mating opportunities, and interactions with neighbouring conspecifics. We investigated how these factors may affect nest-site selection and nest survival in the Seychelles warbler (*Acrocephalus sechellensis*), a facultatively cooperative-breeding passerine that defends stable territories year-round. We found that nest survival was higher when nests were built in higher vegetation layers and that nests were more likely to be located in food-rich parts of the territory, especially in territories with lower food availability. Further, we found that nests in territories with helpers were built in areas with higher food availability, whereas nests in territories without helpers were built in areas with fewer nest-predators. Finally, we found that females paired with younger males tended to build their nest closer to the territory border. Our results suggest that nest-site selection in the Seychelles warbler is affected by nest-predation, food availability and, possibly, the female's opportunity for extra-pair copulations. Clarifying the relative importance of these different selective factors is key to the understanding of optimal nest-site selection to maximize reproductive success.

Key words: nest-site choice, spatial ecology, nest predation, territory quality, social neighbours.

LAY SUMMARY

- Nest site selection in Seychelles warbler territories was associated with predator density, nest height, food availability, tree species, and proximity to potential extra-pair mates.
- Warblers built nests in areas with fewer predators, higher in the canopy, and closer to food resources compared to other areas in their territories.
- Breeders that were assisted by helping subordinates built nest in areas with higher food availability, whereas nests in territories without helpers were built in areas with fewer nest-predators.
- Females paired to younger males built nests closer to the territory border, possibly to gain access to older extra-pair males.
- Nest height relative to the mean territory canopy was associated with higher nest survival rates.
- Nest site selection involves a trade-offs between like food availability and predation risk, which is mediated by the presence of helpers at the nest.

INTRODUCTION

Nest-site selection has pivotal consequences for an individual’s reproductive success (Martin, 1995; Ricklefs, 1969). In birds, many factors influence nest-site selection, such as predation risk (Forstmeier & Weiss, 2004), proximity to food resources (Bonnot et al., 2009), mate-guarding (Møller, 1990), and proximity to potential extra pair mating partners (Mennill et al., 2004; Ramsay et al., 1999). However, few studies have investigated the interacting effect of both the environment and conspecifics on nest-site selection. Social systems where individuals defend stable year-round territories are particularly suitable for studies on nest-site selection as individuals are expected to have extensive knowledge of their territory, allowing them to make a well-considered nest-site selection decision to maximize nest success.

In this study, we investigate how spatial variation in environmental and social factors influences nest-site selection and nest survival in the Seychelles warbler (*Acrocephalus sechellensis*) on Cousin Island, Republic of Seychelles. This well-studied Seychelles warbler population (Hammers et al., 2015; Komdeur et al., 2016) provides an excellent opportunity to comprehensively assess factors influencing nest-site selection within a territory and, subsequently, nest survival, which is challenging in most species.

The Seychelles warbler is a facultatively cooperative breeding, nonmigratory, tropical passerine that now occurs on five islands (Wright et al., 2014) and displays a high degree of year-round territoriality (Groenewoud et al., 2019; Komdeur, 1992, 1996a; Raj Pant et al., 2020). Once paired, breeding pairs remain in the same territory until one of them dies and is replaced by a new partner in the same territory (Komdeur et al., 1991). Extra-pair paternity is common: 42% of offspring are sired by males from another territory (Raj Pant et al., 2020). Dominant females normally only lay one egg per breeding attempt (Richardson et al., 2002), therefore the loss of the egg often equals nest failure. This makes egg predation an important determinant of reproductive success in this species (Komdeur & Kats, 1999). Seychelles fodies (*Foudia sechellarum*), hereafter “fodies”, are the primary predators of warbler eggs on Cousin Island and an experimental study has shown that fake eggs in unattended nests were predated within three days in 75% of cases (Komdeur & Kats, 1999). Egg predation generally only takes place when nests are unattended (Komdeur & Kats, 1999). Therefore, to minimize egg predation, Seychelles warblers are expected to build their nests in areas of their territory where nest predators are less likely to visit and/or in areas with high food availability, allowing short-range foraging trips and thus greater nest attendance (Groenewoud et al., 2019; Komdeur & Kats, 1999). Optimal nest positioning may depend on the balance of many distinct factors such as nest predation, food availability, extra-pair mating opportunities, and interactions with neighbouring conspecifics. For species holding year-round territories like the

Seychelles warbler, individuals are expected to have extensive local knowledge to inform optimal nest site choice. However, past studies remain inconclusive as to whether birds are able to select the best nest-site characteristics to maximise fitness (as reviewed by Chalfoun & Schmidt, 2012) and have not, to our knowledge, evaluated both environmental and social aspects simultaneously.

We capitalized on the well-studied population of Seychelles warblers on Cousin Island (Komdeur et al., 2016) to assess multiple hypotheses on how key ecological and social variables may affect nest-site selection and subsequent nest survival. We specifically investigated the roles of nest predator density, nest concealment, nest height, tree species, proximity to interspecific breeders, food abundance, density of neighbouring individuals, age of male neighbours, presence of helpers. We also investigated whether nest characteristics changed after a failed nesting attempt (see Table 1 for an overview of the hypotheses tested in this study).

Hypothesis	**Explanation**
Nest predator avoidance	Nests are placed in areas with lower densities of nest predators (Dinkins et al., 2012).
Nest concealment	Nest concealment may reduce the risk of predation (Martin, 1993)
Nest height	Nest height may affect the risk of nest predation (Alonso et al., 1991).
Tree species selection	Lower nest predation by using the most common tree species to nest in, thereby making a searching pattern more difficult, as per the "needle in a haystack" hypothesis (Martin & Roper, 1988).
Proximity to interspecific breeders	Breeding away from interspecific breeding birds (here tree colony breeding lesser noddies *Anous tenuirostris*), which may attract a higher number of nest-predators.
Proximity to food	Higher local food resources can decrease the time spent foraging away from the nest, increasing incubation and nest guarding time. (Rastogi et al., 2006).
Proximity to neighbours	Nesting near borders could increase the opportunity for extra-pair mating copulations (Westneat & Mays Jr, 2005) but could reduce nest success as a result of territorial conflict (Bebbington et al., 2017).

Presence of helpers	Helpers reduce predation of nests (Komdeur, 1994b), which could alleviate the role of nest predation in nest-site selection, thereby shifting the focus to other components.
Renesting location	Failed nests may be relocated to reduce predation risk (Marzluff & Balda, 1988).

Table 1. Hypotheses and their explanations on nest site selection and nest survival in the Seychelles warbler. All these hypotheses are tested in this study.

We evaluated these non-mutually exclusive hypotheses to comprehensively investigate the determinants of nest placement decisions in a year-round territorial songbird. Clarifying the relative importance of these different selective factors is key to the understanding of optimisation of nest-site selection in order to maximize reproductive success.

METHODS

Study System

The study was carried out on the population of Seychelles warblers inhabiting Cousin Island (29 ha; 04° 20′ S, 55° 40′ E), which has been monitored as part of a long-term research project since 1985 (Davies et al., 2021; Hammers et al., 2019; Komdeur, 1992). At the time of data collection (June – August 2018), the population consisted of 314 independent (≥3-month-old) individuals spread over 110 territories. Almost all individuals (>96%) had been individually marked with a unique combination of a British Trust for Ornithology (BTO) metal ring and three plastic colour rings (Richardson et al., 2001).

Seychelles warblers experience high annual adult survival (mean ± SE; 84%, 4%) and have a relatively long lifespan for a small passerine (mean = 5.5 years after fledging, SE + years after fledging; max. 19 years, (Brouwer et al., 2006; Hammers & Brouwer, 2017). A dominant pair is present in each territory along with (in about 50% of the territories) a variable number (most times 1, up to 5) of subordinates of both sexes, which include retained offspring from previous broods, deposed dominant breeders, and individuals from other territories

(Richardson et al., 2003, 2007). Cooperative breeding occurs frequently as these subordinates often provide alloparental care (incubation and feeding offspring; Hammers et al., 2019; 2021. The open cup nests are typically built in trees between the forks of branches (Komdeur, 1996a) and most frequently contain single-egg clutches (Raj Pant et al., 2019; Richardson et al., 2001). Eggs are vulnerable to predation by avian predators such as the Seychelles fody and the Seychelles magpie robin (*Copsychus sechellarum)*, and reptiles such as Wright's skink (*Trachylepis wrightii),* Seychelles skink (*Trachylepis seychellensis*), and bronze-eyed gecko (*Ailuronyx seychellensis)*. Fodies are the main egg predators, and in the absence of guarding warblers can toss an egg out of the nest in seconds and consume the contents from the ground (Komdeur & Kats, 1999). Seychelles Warblers forage solely within the boundaries of their territory and defend their borders vigorously from invading conspecifics, which allows precise territory boundaries to be mapped and the number of helpers to be assessed (Bebbington et al., 2017)

Data Collection

Data were collected from 16 June - 14 August 2018 during the warblers' main breeding season (Komdeur, 1996a). We monitored each territory on the island to ascertain the identity, status, and number of group members. The male and female displaying dominant behaviour were identified as the dominant breeders for each territory (Richardson et al., 2002). Dominant females were followed for at least 15 minutes every seven days to assess when nest building was initiated. Each breeding attempt was monitored after a nest was built with nest observations conducted every 3-4 days until chicks fledged or the nest failed. Three GPS coordinate readings (3m accuracy) were taken at each nest location and averaged to increase accuracy. We checked the nests for incubating (egg present) or feeding behaviour (nestlings present) every three days. We estimated the height of each nest in a nesting tree in meters by eye to the nearest meter and calibrated our estimates with three observers. We scored the direct concealment of each nest by foliage on an ordinal scale ranging from 1 to 5, where 1 indicated 0-20% concealment, 2: 21-40%, 3: 41-60%, 4: 61-80% and 5: 81-100%. A complete walk-around was conducted around each nest to get a good estimation of the direct concealment around the nest from each angle.

In territories where subordinates were present, we observed the nest for 60 minutes during both the incubation and feeding stages to determine if subordinates were actively participating in nest care. We recorded all incubation bouts, nest defence efforts, and feeding events for each adult individual (Hammers et al., 2019, 2021). Subordinates observed incubating (females only) or feeding nestlings (males and females) were identified as ‘helpers. Subordinates in territories where the nest failed before observation could not be assigned helper status and were excluded in the analyses of the effect of helper presence (see below).

Territory boundaries were determined by tracking the position of the dominant breeders in the territory (using a portable GPS) during the 15-minute watches undertaken every 7 days (and using any ad hoc sighting during mistnetting and/or nest watches) to revise/change territory boundaries determined in the previous season. Observations of colour-ringed individuals engaging in boundary conflicts were used to determine the exact borders of the territories (Eikenaar et al., 2008). At the end of the season, the final territory map was updated in ArcMap 10.5.1 (ESRI Inc., Redlands, CA, USA).

Following Komdeur (1992), vegetation cover was assessed by looking vertically through a cardboard tube (10 cm long, 5 cm diameter), recording the presence (y/n) and species of vegetation at multiple height intervals, ranging from 0-20 m. Vegetation was considered present when it covered more than half of the viewing field of the tube at each height interval

(2m apart from the lowest intervals that ranged from 0-0.75 m and 0.75-2 m. In total, four points (N, E, S, W) around each nest at 1 m horizontal distance were surveyed for vegetation presence at the nest-location and the mean was taken. To compare the vegetation near the nest with that found elsewhere in the territory, we took 20 measurements evenly distributed within each territory based on the territory maps, ensuring representative coverage over the whole territory. The distance between any two measurements depended on the size of the territory.

Surveys were carried out to estimate the mean invertebrate density per leaf surface area of each tree species present. Arthropods were counted underneath leaves, as warblers forage on arthropods by gleaning them from the undersides of leaves (Komdeur et al., 1991). Arthropods were counted once every month (i.e., three times within the study period) for 50 leaves for the 6 most abundant tree species (Komdeur et al., 1991). Arthropods were grouped into 10 groups: *Orthoptera, Diptera, Coleoptera, Lepidoptera, Formicidae, Aculeates, Hemiptera, Dictyoptera, Arachnida,* and ‘other arthropods’. To obtain arthropod abundance, we used the following formula: $\sum(c_x i_x)$, where c_x equals foliage cover per tree species *x* and i_x equals the arthropod count for tree species *x* per unit leaf area measured in dm^2 (Komdeur, 1996b; van de Crommenacker et al., 2011).

On three consecutive days at the end of July, we conducted point counts to obtain the density of fodies across the island and mapped nests of lesser noddies (*Anous tenuirostris,* a colony breeding seabird that exists at high densities on Cousin, see Table 1). Counts were performed for three minutes at each of the 648 evenly distributed point locations. All fodies and noddy nests detected within a 12.5m radius vertical column surrounding the point were recorded. We chose a 12.5m radius as it provided reasonable coverage within the territory based on an average territory and allowed for consistent data collection across different-sized territories. For each warbler territory, we completed 4 (small territory) to 8 (large territory) nonoverlapping point counts as the size of the territory allowed. For each nest site, we conducted a count from underneath the nest itself to be able to compare this against the territory mean. For finer scale comparison, we conducted additional lesser noddy nest counts in 4m and 8m radius spheres surrounding each warbler nest. Densities were calculated as the number of active noddy nests per unit surface (m^{-2}) or volume (m^{-3}). We thus used the point count data to generate fody and noddy nest densities at two levels of habitat scale: territory level and nest-site level.

To investigate where Seychelles warblers, in relation to the territory border, build their nests, we measured the distance from the nest to the closest four neighbouring territorial boundaries. For each of the 4 closest neighbouring territories we calculated the warbler density as warblers per surface area. To avoid biased data due to edge effects, territories with fewer than four neighbouring territories were excluded (e.g., isolated territories and those located on the coast). As females may prefer to sire offspring with older males (Raj Pant et al., 2020), we examined if females build their nests closer to older males in neighbouring territories. Therefore, we measured the distance from the nest to the closest four territory borders and recorded the age of the focal breeding male compared to that of the 4 nearest surrounding males. To avoid biased data due to edge effects, territories with fewer than four neighbouring territories were excluded from the analysis (e.g., isolated territories and those located on the coast).

Spatial Analyses

Spatial analyses were performed using the ‘sp’ package (Bivand et al., 2013) in combination with the ‘sf’ package (Pebesma, 2018) in R version 3.4.4 (R core team, 2022). Distances between nests, boundaries and centers were calculated by the ‘nngeo’ package (Dorman, 2018). To test if nest-sites followed a random spatial distribution within a territory or not we tested if the observed nest locations followed different spatial distributions compared to simulated random nest-site data. Simulated data are based on 1000 draws simulating bootstrapped random nest-sites using the 'spsample' function of the 'spdep' R package (Bivand & Wong, 2018). We used the mean distance of all bootstrapped random draws within a territory and compared those with the actual distances measured around real nest-sites.

Statistical Analyses

All statistical analyses were conducted in R, version 3.4.4 (R Core Team, 2022), using the 'brms' package (Bürkner, 2017). Throughout we show the posterior medians of Bayesian estimations and their 95% Highest Density Intervals (HDI). Statistically significant results occur when the 95% HDI excludes zero. Models were checked for convergence by the Gelman-Rubin statistic (R-hat) which should be close to 1 (<1.1). Effective sample sizes (ESS) were all greater than 100. Next, we checked if the posterior predictive distributions were able to reproduce the observed data patterns. Lastly, we visually inspected the trace plots of all parameters over all iterations within each MCMC chain.

We modelled nest concealment over a cumulative distribution, accounting for the ordinality of the nest concealment data. To test if warblers preferred a specific nest height, we tested whether nest height differed from the mean canopy height of the territory using a Student's *t* distribution. We did a similar analysis for vegetation height surrounding the nest compared to the vegetation height of the territory as a whole.

To investigate whether some tree species are preferred over others for nesting , we used a multinomial model based on the contingency tables of trees present on the island and all nesting trees. This method accounts for the different sample numbers between the larger number of observations at the island level compared to all observations of nesting trees. Outcomes were scaled to probability levels ranging from 0-1 allowing for pair-wise comparisons between the expected probability of tree species present on the entire island, and the observed probability of tree species used as nesting tree.

To test if nests were placed in areas with fewer lesser noddies, we modelled the difference in the number of noddies present at a 12.5 m radius around the nest-site minus the mean number of noddies in the territory and modelled this over a Student's t distribution. We also tested whether the number of lesser noddies differed between spheres of 4m and 8m radius around the nest by calculating the number of lesser noddies m^{-3} and comparing with those per warbler nest to evaluate it on a finer scale.

We modelled the distance to the border over a truncated Gaussian distribution with lower bound set to 0 as only positive values are possible. To test if a new post-predation nesting attempt differed in nest characteristics compared to the predated nest, we tested for differences in number of fodies, nest concealment, nest heights, number of lesser noddies, and food availability between the failed and the new nest.

To test if nests were placed in food-rich areas of the territory we tested if nest-arthropod abundance differed from the average of the territory. Again, we modelled this over a Student's *t* distribution. To check if nests with helpers had different nest characteristics, we included helpers (y/n) as a fixed effect for each previous model.

To model nest survival we used the cumulative hazard function $H(t) = -ln\left(\frac{S(t)}{1-S(t)}\right)$ where *H(t)* is the cumulative hazard function, *S(t)* is the survival probability at time *t*, and *t* is the length of time the nest is at risk of failure. The cumulative hazard function can be modelled as a function of a linear predictor, η and the exposure time, *t*. This leads to $H(t) = ln\left(\frac{1}{S(t)}\right) =$

$\eta + \lambda_0 t$ where λ_0 is the baseline hazard rate and η includes predictor variables. The survival probability can then be calculated as $S(t) = exp(-H(t)) = exp(-\eta - \lambda_0 t)$ (Clark et al., 2003).

RESULTS

Of the 110 territories that were censused, 92 (84%) had nests. In one territory a nest was located but could not be observed and was therefore excluded from analysis. In total, we monitored 125 nests in 91 territories (the average number of nests per territory is greater than one because individuals often build a new nest when a nest fails early during the breeding season). We found 1 nesting attempt in 91 territories, 2 in 22 territories, 3 in 2 territories, and 4 in 2 territories. See Figure 1 for the locations of all nests.

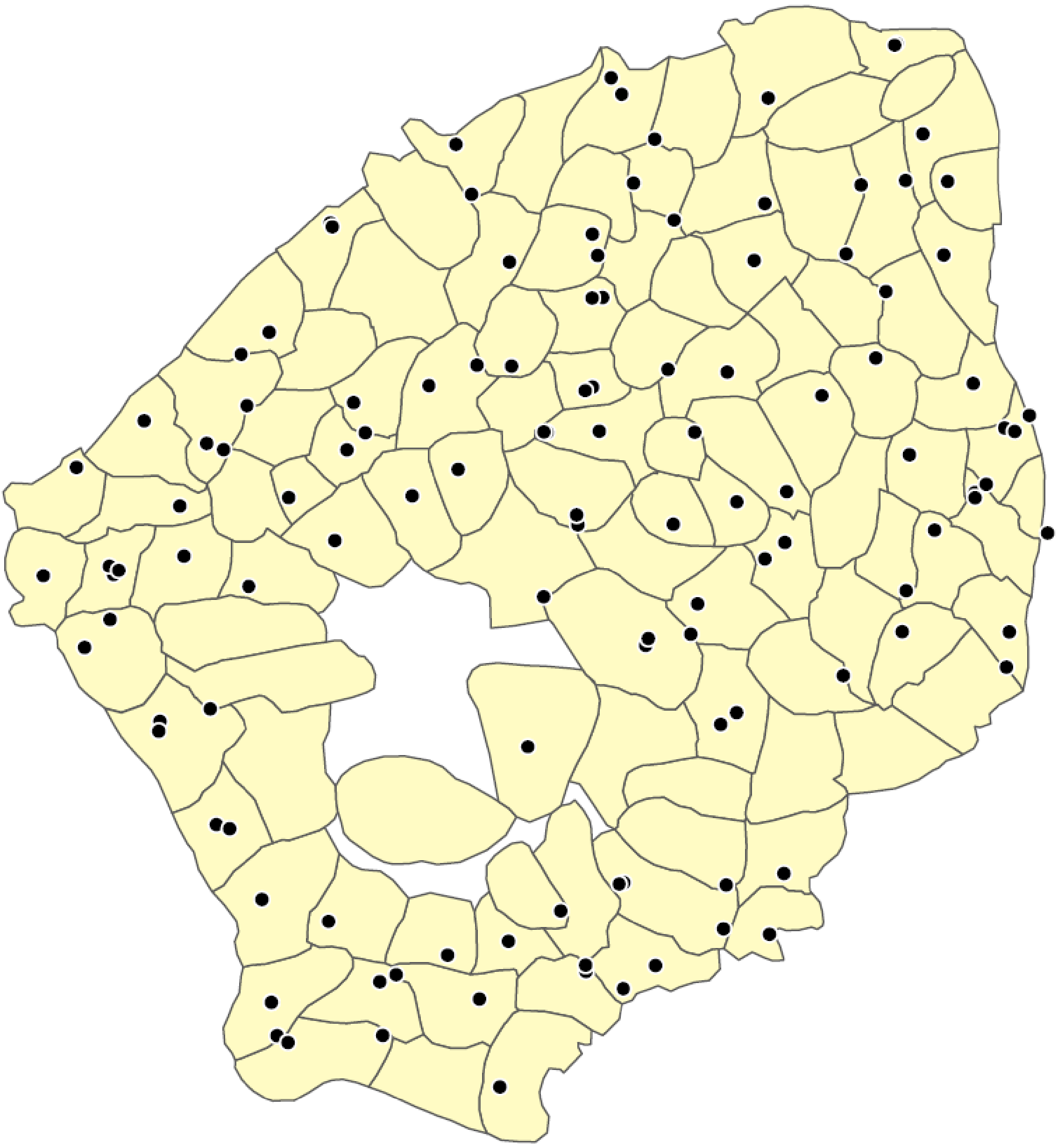

Figure 1. Map showing the territories of Seychelles warblers on Cousin Island during the main breeding season in 2018. Territories are colloured in with their boundaries indicated by black lines. The black dots indicate nest sites.

Nest predators

In Seychelles warbler territories we observed a mean of 5.67 (± 3.17 SD) fodies. The fody density within a 12.5 m radius of the nest was lower than the mean fody density elsewhere in the territory ($\Delta\mu$ = –0.26, [–0.45, –0.06]). This difference increased with higher mean fody density in a territory (β = -0.98, [-1.09, -0.89]). Nests without helpers were built in areas with fewer fodies compared to the rest of the territory ($\Delta\mu$ = -0.33, [-0.57, -0.04]); whereas nests with helpers where not ($\Delta\mu$ = -0.05, [-0.44, 0.32]; figure 2). In renesting attempts after a predation event, there was no change in the number of fodies around the nest compared to the first nesting attempt ($\Delta\mu$ = 0.020, [–0.029, 0.20]).

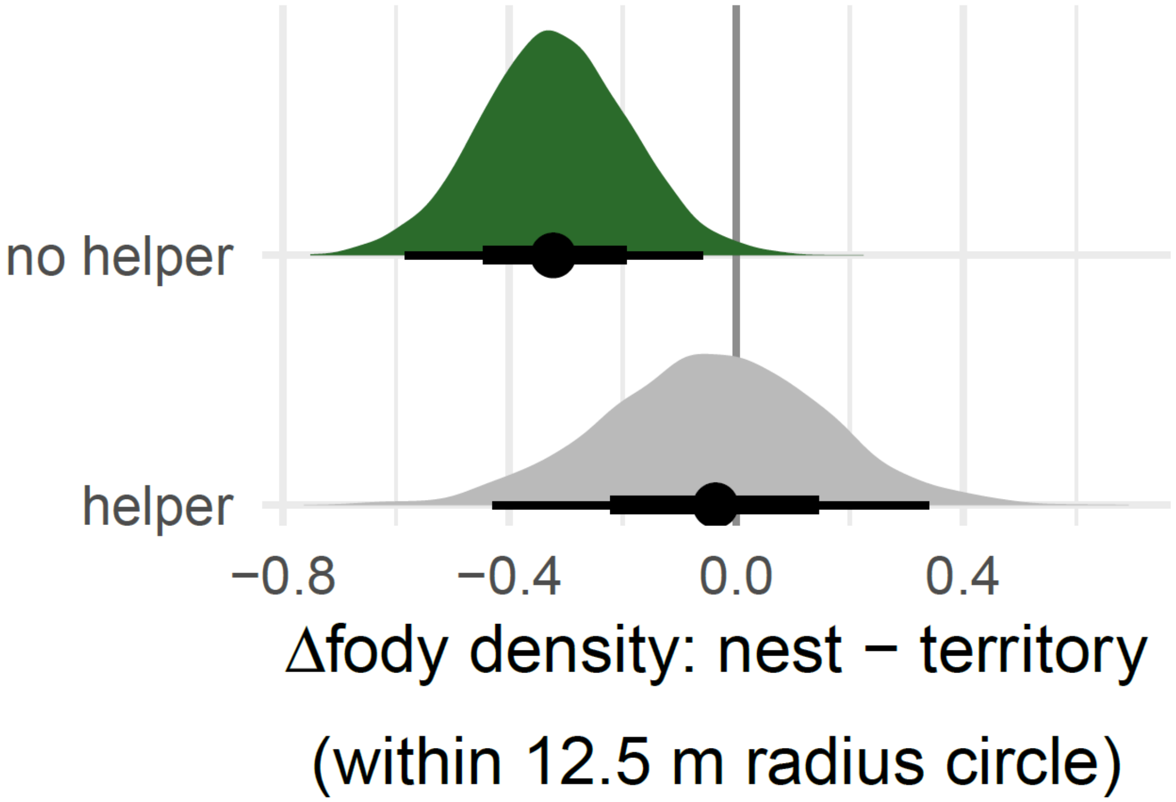

Figure 2. Posterior distributions of the mean difference between the number of fodies near Seychelles warbler nests and their territorial mean. Values below 0 indicate less fodies around the warblers' nest and values above 0 indicate more fodies near the warblers' nest compared to the territorial mean. The green hue indicates a credible difference, whereas the grey hue indicates no credible difference. The shaded areas represent the full posterior density

of the mean, whereas the thin line indicates 95% HDI, the thick line indicates 66% HDI and the point indicates the point estimate. Breeding pairs without helpers at the nest placed their nests within their territory in areas with lower fody densities within the territory, whereas this was not the case for pairs with helpers.

Nest concealment

Nests concealment was quite uniformly distributed over the territories: three nests had a concealment score of 0, 15 of 1, 21 of 2, 21 of 3, 21 of 4, and 24 of 5. Nest concealment did not increase with fody abundance (β = 0.35, [-0.54, 1.19] and neither did the concealment of replacement nest attempts following a predated nest. ($\Delta\mu$ = –0.26, [–1.42, 0.98]).

Nest height

Nests were built at a mean height of 10.77 m (± 5.38 SD) compared to the surrounding maximum vegetation height of 8.08 m (± 3.26 SD) (see figure 2). Nests were built 2.98 m higher (HDI = [2.01, 3.84]) than the average canopy height in the territory (see figure 3). Mean canopy height near nest sites (1 m radius) was on average 1.92 m higher than the mean canopy height of the territory ($\Delta\mu$ = 1.82 m, [0.89, 2.86]). We found no difference in relative nest height between nests with and without helpers ($\Delta\mu$ = 0.60 m, [-1.68, 2.74]). Nesting attempts following a predation event did not show a difference in nest height compared to the earlier nesting attempt ($\Delta\mu$ = –0.56 m, [–2.34, 1.19]).

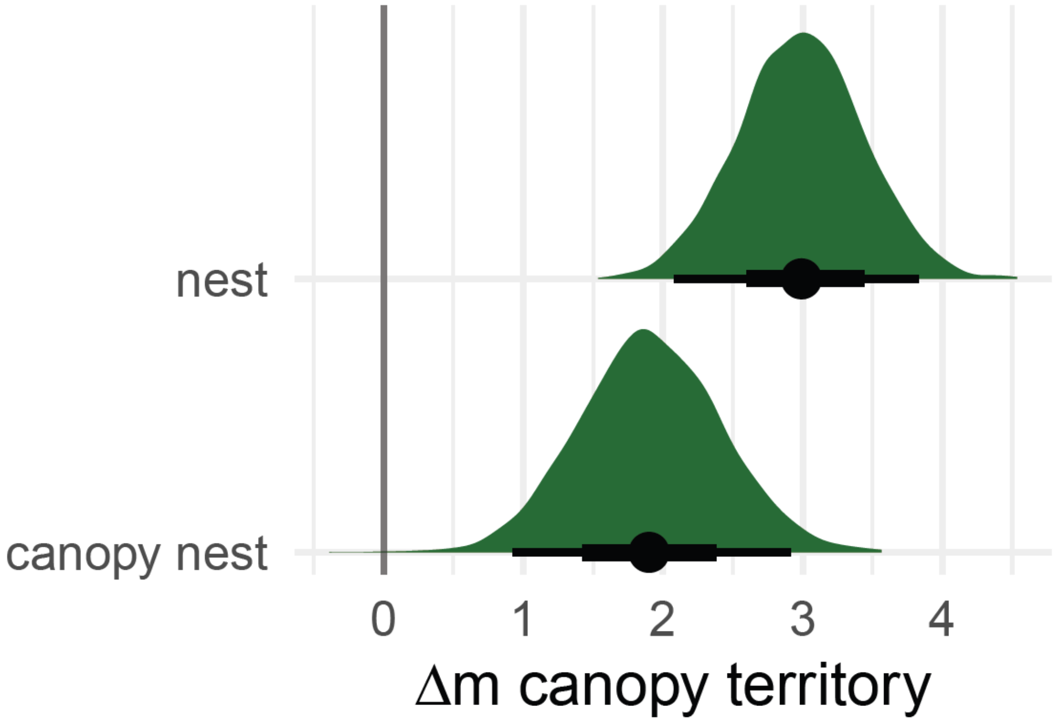

Figure 3. Posterior distributions of the mean difference in height between Seychelles warbler nests and the mean canopy height of their territory, and the mean canopy height around their nest and the mean canopy height of their territory. Values below 0 indicate nests are placed lower than the mean territorial canopy height and values above 0 indicate that nests are placed higher than the mean territorial canopy height. The green hue indicates a credible difference. The shaded areas represent the full posterior density of the mean, whereas the thin line indicates 95% HDI, the thick line indicates 66% HDI, and the point indicates the point estimate of the posterior mean. Nests were built higher than the mean canopy of the corresponding territory.

Tree species selection

Pisonia grandis trees dominated the island (43%), followed by *Ochrosia oppositifolia* (21%), and *Ficus reflexa seychellensis* (7%; see Table 2). Seychelles warblers bred in more than 20 species of trees (Table 2). Nests were built more often than expected in *Ficus reflexa* *seychellensis* ($\Delta\mu$ = -0.096, [-0.17; -0.03]; see figure 4). However, nests were built less often than expected in *Ochrosia oppositifolia* ($\Delta\mu$ = 0.20, [0.16; 0.23]), *Morinda citrifolia* ($\Delta\mu$ = 0.04, [0.01; 0.06]), and *Scaevola taccada* ($\Delta\mu$ = 0.008, [0.002; 0.013]).

Tree species	Island		Nesting trees	
	N	**%**	**N**	**%**
Pisonia grandis	**1350**	43%	**63**	(53%)
Ochrosia oppositifolia	**671**	21%	**4**	(3%)
Ficus reflexa seychellensis	**221**	(7%)	**21**	(18%)
Morinda citrifolia	**183**	(6%)	**3**	(3%)
Ficus lutea	**151**	(5%)	**10**	(8%)
Thespesia populnea	**88**	(3%)	**6**	(5%)
Euphorbia pyrifolia	**61**	(2%)	**3**	(3%)
Pandanus balfourii	**52**	(2%)	**2**	(2%)
Avicennia marina	**41**	(1%)	**2**	(2%)
Hibiscus tiliaceus	**29**	(1%)	**2**	(2%)
Scaevola taccada	**25**	(1%)	**0**	(0%)
Casuarina equisetifolia	**15**	(<1 %)	**0**	(0%)
Cocos nucifera	**10**	(<1 %)	**0**	(0%)
Calophyllum inophylum	**8**	(<1 %)	**0**	(0%)
Bambuseae spp.	**7**	(<1 %)	**1**	(1%)
Cordia subcordata	**7**	(<1 %)	**2**	(2%)
Terminalia catappa	**6**	(<1 %)	**0**	(0%)
Timonius sechellensis	**3**	(<1 %)	**1**	(1%)
Carica papaya	**2**	(<1 %)	**0**	(0%)
Eucalyptus camaldulensis	**2**	(<1 %)	**0**	(0%)
Total	**2935**		**120**	

Table 2. Tree species ranked from most frequent to least frequent on Cousin Island and their relative presence versus the number of trees used by Seychelles warblers to nest in. The "N" in island represents the total number of trees surveyed in all warbler territories. Data on 5 nests regarding their specific nesting tree is missing.

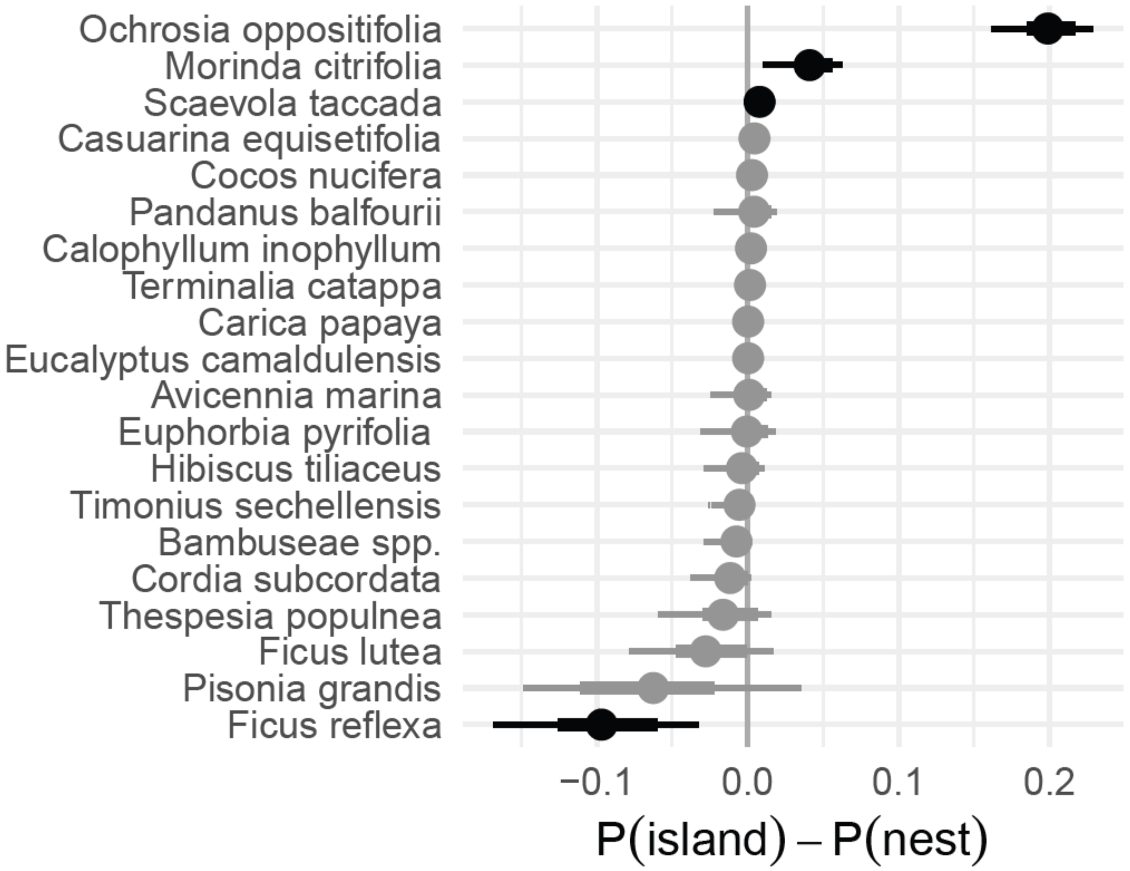

Figure 4. Nesting trees ordered from least selected towards most selected by the Seychelles warbler to nest in. The x-axis displays the difference between the probability of tree species in territories (N=2935) and the probability of tree species of nest-sites (N=120). The thin bars indicate the 95% HDI, the thick bars the 66 % HDI, and the point the point estimate of the posterior median. More positive (to the right) estimates indicate tree species are less abundant as nesting tree, whereas positive values (to the left) indicate tree species are more abundant as nesting tree compared to the trees available at the territories.

Proximity to other breeding birds

Lesser noddies were present throughout the island but at higher densities in the northern part (see appendix 2). We found no difference in the number of noddies at the nest-site compared to other locations within the same territory ($\Delta\mu$ = –0.59, [–4.19, 3.06]). The density of noddy nests was lower in 4 m versus 8 m radius around warbler nests ($\Delta\mu$ = -0.0015 noddies m^{-3}, [-0.0031, -0.00029]). No difference in noddy density was found for nests with and without helpers ($\Delta\mu$ = 0.00, [-0.003, 0.003]). We also found no difference between noddy density around the nest and the territory average ($\Delta\mu$ = -0.40 [-7.93, 8.07]). Renesting attempts also showed no change in the number of lesser noddies in a radius of 12.5 m around the nest ($\Delta\mu$ = 7.91, [–1.20, 16.75]).

Proximity to Food

Arthropod density was higher near the nest compared to across the rest of the territory ($\Delta\mu$ = 0.026 dm^{-2}, [0.003, 0.048]). In territories with lower overall food availability, this difference was greater (β = -0.58 dm^{-2}, [-0.91, -0.24]; see figure 5). Nests with helpers were in locations with more arthropods than the territory mean ($\Delta\mu$ = 0.066, [0.030, 0.106]), whereas nests without helpers had arthropod densities similar to the territory mean ($\Delta\mu$ = -0.004, [-0.030, 0.025]; see figure 6). In addition, no change was detected in the density of arthropods near the renesting attempt compared to the preceding attempt ($\Delta\mu$ = –0.020, [–0.084, 0.043]).

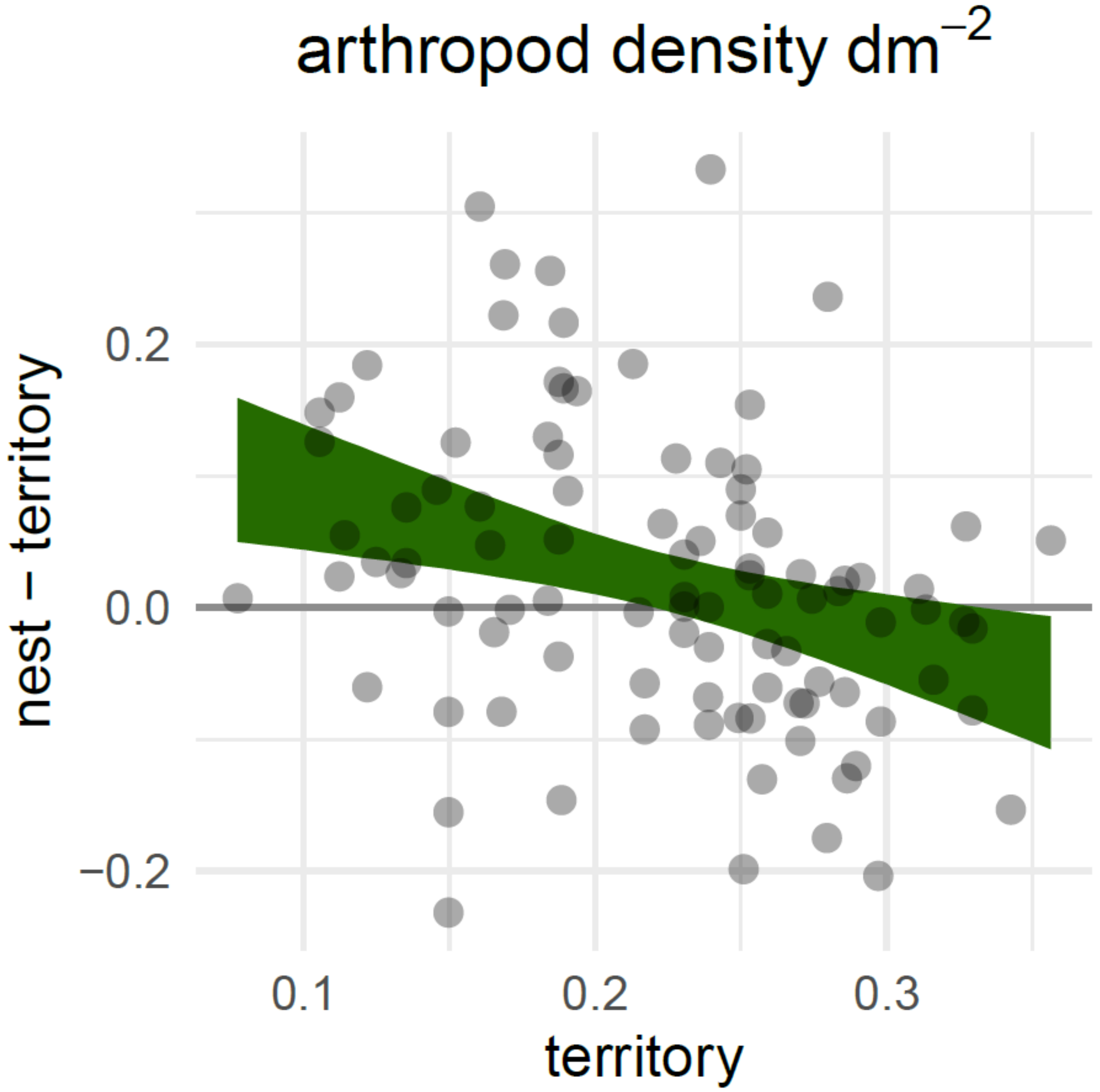

Figure 5. The difference in food availability between nests and the mean food availability within a warblers' territory. The y-axis depicts the difference in density of arthropods calculated as the mean density of arthropods around the nest-site subtracted by the mean of the territory. Positive (higher) values indicate more arthropods near the nest compared the mean of the territory. The shaded area indicates the estimate of the 95% HDI of the posterior mean. Nests were placed more often in arthropod-abundant sites in territories with on average lower arthropod densities, whereas nests in more arthropod-rich territories were not.

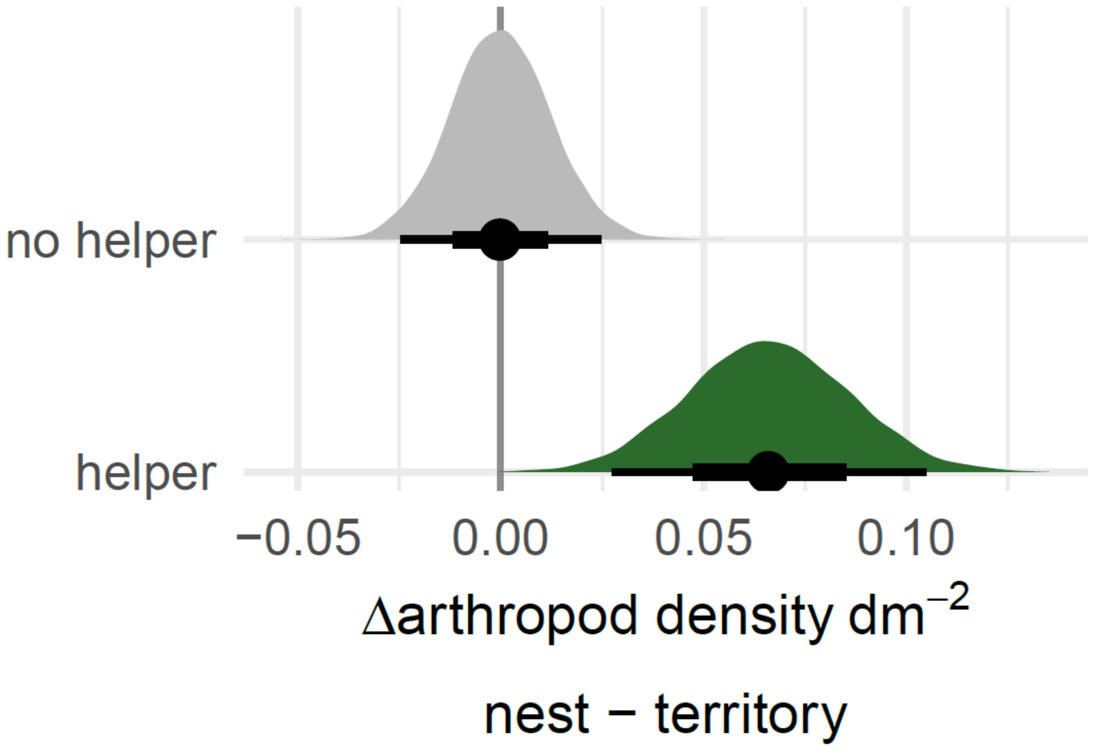

Figure 6. Posterior distributions of the mean difference between the density of arthropods around the nest compared to territory for Seychelles warblers' nests with and without helpers (extra-pair birds cooperating in breeding). Values below zero indicate less, and values above zero indicate higher density of arthropods near the nest compared to the territorial mean. The green hue indicates a credible difference, whereas the grey hue indicates no credible difference. The shaded areas represent the full posterior density of the mean, whereas the thin line indicates 95% HDI, the thick line indicates 66% HDI and the point indicates the point estimate. Breeding pairs with helpers at the nest placed their nests within their territory in areas with higher densities of arthropods, whereas this was not the case for breeding pairs without helpers.

Proximity to Conspecific Neighbours

The mean size of the territories studied was 2342.55 m^2 (± 772.45 SD). Nests were typically located 9.40 m (± 6.77 SD) from the nearest border which is 1.36 m (HDI = [0.20, 2.54]) further from the closest border than would be expected from a random simulation.

The number of warblers inhabiting the nearest territory nearest to the focal nest site did not differ from the number of warblers in the second, third, or fourth closest territories ($\Delta\mu$ = –1.3·10^{-4}, [–2.7·10^{-4}, 1.9·10^{-5}]). Similarly, the number of individual warblers per surface area did not differ among the closest, second closest and third closest territories ($\Delta\mu$ = 0.042 m^{-2}, [–0.17, 0.26]).

Nests were located closer to the border when the closest neighbouring territory was inhabited by an older male than the breeding male of the territory (β = 0.62 m yr^{-1}, [0.16, 1.21]; see figure 7). However, the breeding male of the territory nearest to the nest was on average not older than the average age of the breeding male of the second, third and fourth territory combined ($\Delta\mu$ = –0.60 yrs, [–1.32, 0.12]).

When birds renested the nest was situated 9.74 m (± 1.49 SD) from the first nest. This is nearer than expected ($\Delta\mu$ = –14.36 m, [–17.76, –11.03]), when compared with random simulated nest distances within each territory (mean = 24.05 m, ± 0.85 SD). The distance from the closest border remained unchanged in the renesting attempt ($\Delta\mu$ = -0.08 m, [-2.99, 2.80]).

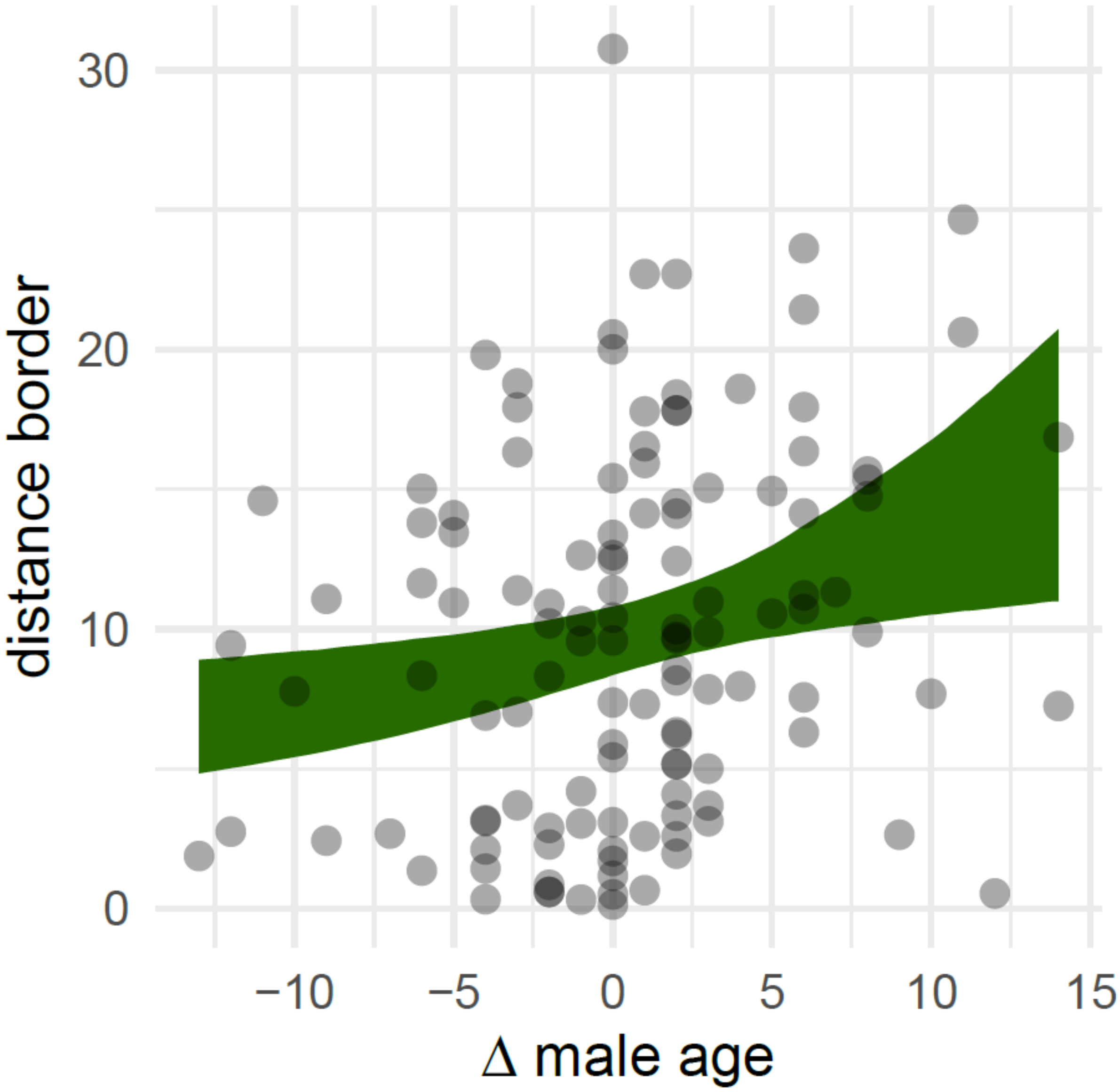

Figure 7. Estimate of the distance to the border in m as a function of the difference in age in years between the dominant male and the closest neighbour in the Seychelles warbler. Positive numbers on the x-axis indicate that the focal male is older than the closest neighbouring male while negative values indicate that the neighbouring male is older than the focal male of the territory. The shaded area indicates the trend of the 95% HDI of the posterior mean. When the male neighbour is older than the focal male, the distance to the border is shorter. Distance to the border is not correlated to territory size.

Egg Survival

In total 38% of all observed nests failed (were predated) during the egg stage, which accounted for 75% of nest failures. Far fewer nests failed during the nestling stage, accounting for 25% of overall nest failure.

Daily nest survival was not affected by the number of fodies present in a warbler territory (η = 0.24, [–0.44, 0.97]), nor in the immediate surroundings of the nest (η = 0.04, [–0.31, 0.43]). Similarly, nest concealment assessed during incubation was not correlated with nest survival (η = 0.02, 95% HDI = [-0.23, 0.28]), nor was concealment during the period of fledglings (η = 0.45, 95% HDI = [-0.16, 1.24]). However, nests that were placed relatively high compared to the average canopy within a territory had increased daily survival rates (η = 0.09, 95% HDI = [0.01, 0.17]; see figure 8). Among the different tree species, only *Cordia* showed a negative effect on daily nest survival (η = -4.49, [-8.17, -1.29]), although all these data points stem from one breeding pair failing 4 breeding attempts in the same tree which was visited frequently by fodies during the study period (A.O.K.E & M.H. personal observation). No other tree species showed an effect on daily nest survival. The presence of lesser noddies near the nest was not correlated with nest survival (η = 0.01, 95% HDI = [-0.01, 0.03]), nor was the distance of the nest to the territory border (η = 0.03, [-0.02, 0.08]).

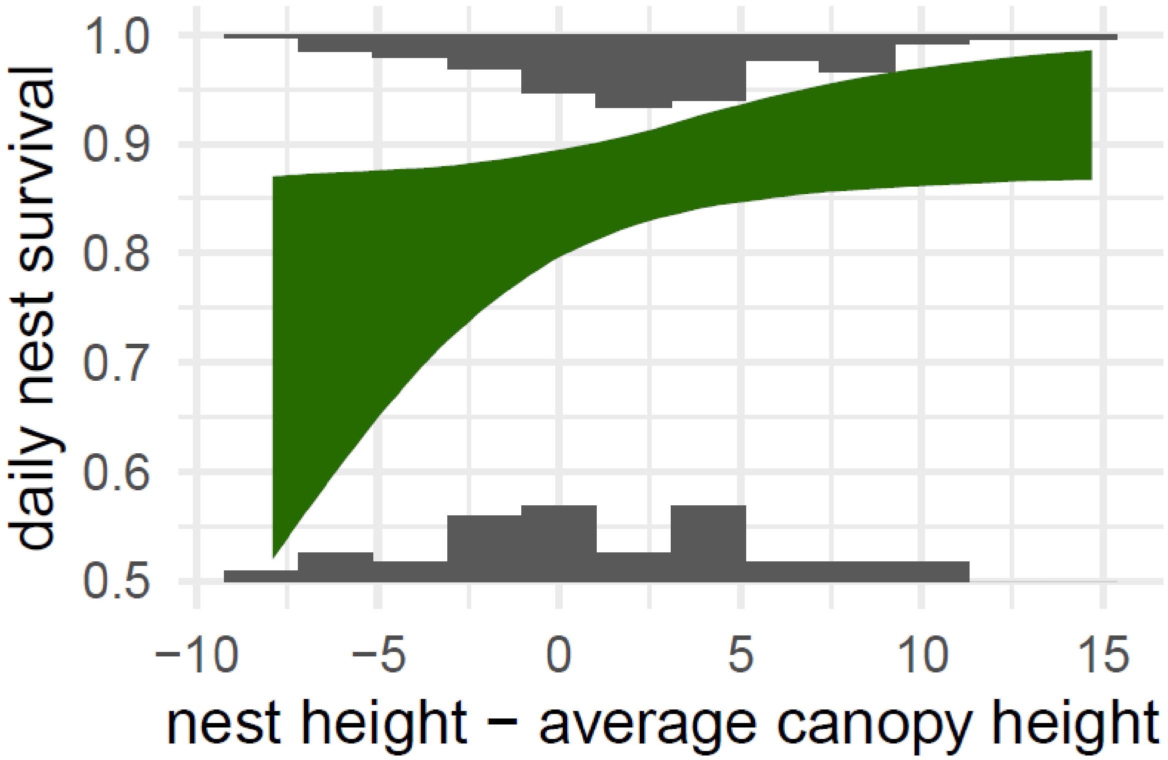

Figure 8. Estimated daily nest survival during incubation in the Seychelles warbler as a function of nest height relative to the surrounding average canopy height. The shaded area indicates the 95% HDI of the posterior of the mean. The histogram on the top indicates the raw binned nest survival in days and the histogram on the bottom indicates the raw binned nests that were predated (both scaled accordingly). Nests placed higher in the canopy have a higher estimated daily survival.

DISCUSSION

Although nest-site selection has been hypothesised to be a non-random process with important consequences for offspring survival, many studies have failed to demonstrate preferred nest-site characteristics or a relationship between nest location and survival (reviewed by Chalfoun & Schmidt, 2012). Our findings suggest that Seychelles warblers do select their nest-sites carefully in relation to predator density, nest height, food availability, tree species, and extra-pair mating opportunities. In contrast, we found no evidence that nest concealment and proximity to colonial breeding seabirds affect nest placement. However, while many factors where associated with nest-site selection, only nest height was found to be directly associated with nest survival.

Do egg predators affect nest-site selection?

Nests were generally built in areas with lower nest predator (i.e. fody) densities, suggesting that Seychelles warblers may choose nest-sites with reduced egg predation risk. This is in accordance with Dinkins et al. (2012), who found that greater sage grouse (*Centrocercus urophasianus*) prefer to nest in areas with lower predator densities. However, the actual relationship between nest predator density and nest survival is not straightforward. While nest predator density may influence initial nest-site selection, it may not determine the actual predation rate (Hollander et al., 2015). For example, in ground nesting ovenbirds (*Seiurus aurocapilla*) and hermit thrushes (*Catharus guttatus*), nests placement in areas with lower predator densities did not directly translate into higher nest survival (Vernouillet et al., 2020). In the Seychelles warbler, active nest defence by adults might be more influential for nest success than nest placement (Komdeur, 1994b). Indeed, an alternative explanation for lower fody densities around warbler nests is that these lower fody densities result from active nest defence, as fody densities were often estimated during nesting events rather than before. However, nests with helpers did not show a difference in the number of fodies near the nest and elsewhere in the territory, which may indicate that nest-site selection rather than active nest defence explains the lower fody densities near the nests.

Does nest concealment influence nest survival?

We found no evidence that better concealed nests have higher nest survival. This contradicts previous research that suggests concealed nests are less vulnerable to predation, as reviewed by Martin (1992). However, our findings are consistent with other studies, for instance on northern cardinals (*Cardinalis cardinalis*) and several species of forest birds in southeast Alaska, where no correlation was found between nest concealment and nest survival (Filliater et al., 1994; Willson & Gende, 2000). An explanation for the lack of an association in our study might be that the main egg predator, the Seychelles fody, uses cues other than direct visual observations to locate nests, e.g. by using observations of warblers flying to and from the nest as a cue. Different relationships between nest concealment and predation among species indicate the importance of considering the specific foraging strategies of predators and the species' nesting ecology when evaluating the effectiveness of nest concealment.

Are high-placed nests safer?

Seychelles warblers preferred nest-sites higher than the average canopy height of the territory and this was associated with decreased probability of nest predation. This result is similar to what was found in orange-crowned warblers (*Leiothlypis celata sordida*; Hays et al., 2022)). Nesting in higher vegetation layers may reduce the risk of predation by ground-dwelling and climbing egg predators, such as skinks, geckos, and Seychelles magpie robins, that mainly forage in the leaf litter layer and low vegetation layers (Komdeur, 1996a). Other factors might play a role in the preference for higher nest-sites, such as an increased ability of warblers to detect and fend off potential egg predators. By nesting higher in the canopy, warblers may have an advantage in detecting approaching fodies. Nest-guarding males may have a better vantage point to spot potential threats which allows them to respond and deter fodies approaching the nest more effectively. Additionally, fodies decrease the chance of discovering a Seychelles warbler nest by spending far less time foraging high in the canopy compared to the understory and shrub layer (Komdeur, 1994a).

Does tree species matter for nest-site selection?

The distribution of nest-sites among tree species on the island was uneven and did not conform to the 'needle in the haystack' hypothesis, whereby breeding in rare tree species might be detrimental for nest survival when predators recognize this preference (Martin & Roper, 1988). Nests were less common in *Ochrosia oppositifolia, Morinda citrifolia,* and *Scaevola taccada*. These species may not provide optimal nesting conditions due to factors such as tree structure, food availability, or predator exposure. For example, *Scaevola taccada*, found at the beach-forest interface, has low food abundance per leaf surface area (0.073 cm^{-2}) and remains low shrubs (mean = 1.07 m ± 0.83 SD). *Ochrosia oppositifolia* also has few arthropods (0.13 cm^{-2}) per leaf surface area. *Morinda citrifolia,* on the other hand*,* is the most arthropod-rich tree (0.29 cm-2) and its presence may have a positive effect on reproductive success (Komdeur & Pels, 2005). However, this high arthropod abundance may also make it a favoured tree species for foraging fodies (Komdeur, 1994a), thus increasing the likelihood of nest discovery. In addition, its branch structure consists of single horizontal branches coming out of the tree trunk which does not provide the classic V-shape supported by three branches that the Seychelles warbler prefers (Komdeur, 1996a; Nazimuddin & Qaiser, 2011). Nests were more frequent in *Ficus reflexa seychellensis*, possibly due to its height (mean = 10.54m ± 4.35 SD). In addition to the height preference, the foraging activity of fodies is less in *Ficus reflexa seychelles* compared to other trees such as *Pisonia grandis* (Komdeur, 1994a), which helps warblers' nests to be undetected.

Do other breeding birds influence nest-site selection?

Seychelles warblers were hypothesized to avoid lesser noddy nests as their eggs might attract fodies. Our results do not support this hypothesis. While the density of fodies was positively correlated with the density of lesser noddies (S2), but there was no correlation between lesser noddy density and warbler nest predation. Our study did not find a significant difference in the number of noddies at the warbler nest site compared to other locations within the same territory, but when analysing nest placement on a finer, three-dimensional scale, we observed a lower density of noddy nests in the immediate vicinity (4m radius) of warbler nests compared to a larger radius (8m). This finding might suggest that Seychelles warblers choose nest sites in areas with reduced densities of noddies to minimize predation risk. Alternatively, this effect could stem from the fact that both species have different nesting site requirements. Noddies nest on average lower in the trees and prefer bigger branches, while Seychelles warblers prefer smaller fork shaped twigs to build their nest in. However, this effect was small and only present on a small scale, and therefore seems not to be of major importance in nest-site selection in the Seychelles warbler.

Does food availability influence nest-site selection?

Arthropod prey availability influenced nest-site selection in Seychelles warblers. Breeding pairs in territories with lower overall food resources showed a tendency to nest in specific areas within their territory that had relatively higher abundance of food. Conversely, warblers inhabiting territories with an overall high food abundance did not display such a preference. This tendency to nest in food-rich areas in the face of scarcity within the territory appears to be linked to the optimization of foraging efficiency and reflects the ‘central place foraging theory’ (Martin, 1992). For example, in Eurasian reed warblers (*Acrocephalus scirpaceus*), nest defence increased and incubations brakes shortened when food was supplemented near the nest (Vafidis et al., 2018). In addition, nest placement in food-rich areas could aid the strategic securing of pivotal parts of the territory from annexation by conspecifics, especially in territories where food resources are generally scarce. In territories where the general food abundance is high, the pressure on warblers to select food rich breeding locations diminishes. Contrary to expectation, we did not find a relationship between arthropod availability and nest survival. As arthropods are also the main food type for Seychelles fodies (Komdeur & Kats, 1999), breeding in arthropod-rich sites could attract more nest predators which could counterbalance the positive effects on nest guarding and incubation attendance.

Nest location relative to territory borders?

Females paired with younger males placed their nests closer to the border than expected by random nest-site selection. This finding is in line with a study on black-capped chickadees (*Poecile atricapillus*), where females paired with a low-ranked male nested closer to the border of a high-ranked male (Mennill et al., 2004). An explanation for this finding could be that females paired with younger males may choose to build their nests closer to older neighbouring males to engage in extra-pair matings (Mennill et al., 2004; Richardson & Burke, 1999). Indeed, in many species, including the Seychelles warbler, older males are more likely to sire extra-pair offspring (Raj Pant et al., 2020; Richardson & Burke, 1999). We found no relationship between nest distance to the territory border and daily nest survival.

Do helpers at the nest influence nest-site selection?

The presence of helpers at the nest in the Seychelles warbler was associated with nest-site selection, particularly in relation to predation risk and food availability. Compared with nests in territories without helpers, nests in territories with helpers were found in areas with higher densities of fodies and higher arthropod densities than the surrounding areas. This may indicate that helpers affect the trade-off between predation risk and food availability. Kingma et al. (2018) and Komdeur (1994b) found that Seychelles warbler nests with helpers are better equipped to defend against predators and have a higher nest survival. However, we found no influence of the presence of helpers on direct nest survival. One explanation for this lack of a positive effect of helpers on nest survival could be that a reduction in egg predation risk due to the presence of helpers is offset by breeding in areas with higher nest predation risk. Another explanation is that the absence of a credible result may be attributed to the limited sample size in our study. Ultimately, helpers may provide breeding groups with increased flexibility in nest-site selection, allowing them to breed in areas with higher predator densities and higher food availability.

Does nest-site change affect predation?

We observed that the distance between first and second nesting attempts was significantly shorter than what would be expected under random nest-site selection. This suggests a deliberate selection of the following nest-site, possibly driven by factors such as familiarity with the area. Interestingly, no differences were found in relation to nest height, food availability or predator presence between first and second nesting attempts, so the main factors that determine nest site selection for replacement nests remains unclear. The absence of changes in nest-site selection following a predation event is in line with earlier studies on bell miners (*Manorina melanophrys*) and blue-gray gnatcatchers (*Polioptila caerulea*), which showed that renesting attempts during the same breeding season did not differ between failed or successful nests with respect to distance from the first nest-site (Beckmann & McDonald, 2016; Kershner et al., 2001).

Limitations and future perspectives

Our study provides a comprehensive view of the environmental and social factors influencing nest-site selection in the Seychelles warbler. However, there are some limitations to our study, such as the challenge of detecting effects on nest survival due to the limited sample size of failed nests (N = 36) and the inclusion of nests and nest fates of only one breeding season (N = 125). Additionally, there may be relatively large intra-territory variation that masks territory-level patterns. For a potential multi-facetted decision as nest-site selection, subtle additive effects are less likely to be detected and should be considered in future studies..

Future research should consider experimental manipulations to reveal the impacts of key factors on nest-site selection. We suggest experimentally removing helpers before nest initiation to experimentally test the role of helpers on nest-site selection, food suppletion experiments and predator removal. Future studies could also make use of predation experiments using artificial nests and daily tracking of nest fate could provide greater power to connect predator activity and nest losses. Furthermore, investigating intra-individual variation in nest placement over time would be paramount to explore how and to which extent nest-site selection is learned and how consistent it is over time.

Conclusion

Nests are not distributed randomly within Seychelles warbler territories. Nests were placed higher than the surrounding canopy of the territory and placed in food-rich areas, especially in territories with lower mean food availability. Nests in territories with helpers were built in areas with higher food availability, while nests without helpers were in areas with fewer predators. Lastly, we found that females paired with younger males built nests closer to the territory border. Although many factors that could predict nest survival were investigated, only nest height relative to mean canopy height explained nest survival. While nest predator density seemed to influence the initial choice of nest-sites, it was not related to nest survival; this may suggest that warblers adapt their nesting behaviour in response to the perceived threat of predation. The selection of a nest-site with improved food conditions may come with the trade-off of increased predation risk from fodies, which can be counteracted by the presence of helpers, emphasizing the complex nature of nest-site selection in this system. Further research is needed to explore the underlying mechanisms and trade-offs involved in nest-site selection, as well as the long-term implications for population dynamics and breeding success.

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