ORIGINAL ARTICLE

Does predation drive Chilean Elaenia (*Elaenia chilensis*) nest-site selection in the temperate forest of southern South America?

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Abstract

Nest-site selection is a behavioral response that can provide protection for adults, eggs and nestlings, affecting fitness. Since predation is the main cause of nest loss worldwide, it has been considered as the main evolutionary driver in nest-site selection. Nevertheless, in some cases, nest microclimate may be the primary evolutionary force operating on nest-site selection. We aimed at determining at mesohabitat and microhabitat scales if Chilean Elaenia (*Elaenia chilensis*) selected the nest site and, if so, whether such selection was associated with a reduction in nest predation. Since nest orientation may influence nest microclimate, we also tested whether it affected the reproductive output. At the mesohabitat scale, the subcanopy cover (1.5–4 m from the ground) was selected by this species. At the microhabitat scale, elaenias preferred *Schinus patagonicus* to nest and oriented their nests preferentially to the north and eastern directions. These selected habitat features had no effect on nest success and reproductive output. Despite the risk of nest predation by several aerial (birds) and ground predators (rodents), both successful and predated Chilean Elaenia nests were close to the ground rather than at intermediate heights. Considering the hardness of *S. patagonicus* wood that can provide structural support to the nest against strong winds, and that nests were oriented to the opposite direction of prevailing wind, Chilean Elaenia nest-site selection might be related to microclimatic factors at nest sites rather than predation. Therefore, it is imperative to consider potential associations between nest microclimate and habitat features to advance in the understanding of bird nest-site selection.

Keywords Andean–Patagonian Forest · Nest accessibility · Nest concealment · Nest orientation · Nest survival · Predation

Zusammenfassung

Beeinflusst Prädation die Wahl des Nistplatzes des Weißbauch-Olivtyrannen (*Elaenia chilensis*) in den gemäßigten Wäldern des südlichen Südamerikas?

Nistplatzwahl ist eine Verhaltensreaktion, die Schutz für erwachsene Vögel, Eier und Nestlinge bieten kann und sich auf die Fitness auswirkt. Da Prädation weltweit die Hauptursache für den Verlust von Nestern sind, wurde sie als wichtigste evolutionäre Treibkraft für die Nistplatzwahl angesehen. Nichtsdestotrotz kann das Mikroklima des Nests in einigen Fällen die

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primäre evolutionäre Kraft bei der Nistplatzwahl sein. Wir wollten herausfinden, inwiefern Weißbauch-Olivtyrannen (*Elaenia chilensis*) auf der Ebene der Meso- und Mikrohabitate den Niststandort auswählen, und wenn ja, ob eine solche Auswahl mit einer Verringerung der Nestprädation einhergeht. Da die Ausrichtung des Nestes das Nestmikroklima beeinflussen kann, untersuchten wir auch, ob sich dieses auf den Fortpflanzungserfolg auswirkt. Auf der Ebene des Mesohabitats wurde vom Olivtyrann die Strauchschicht (1,5–4,0 m über dem Boden) ausgewählt. Auf der Ebene des Mikrohabitats bevorzugten Olivtyrannen *Schinus patagonicus* als Nistplatz und richteten ihre Nester vorranging nach Norden und Osten aus. Diese ausgewählten Habitatmerkmale hatten weder auf den Nesterfolg noch auf die Fortpflanzungsleistung einen Einfluss. Trotz des Risikos der Nestprädation durch verschiedene Luft- (Vögel) und Bodenprädatoren (Nagetiere) befanden sich sowohl die erfolgreichen als auch die prädierten Olivtyrannnester eher in Bodennähe als in mittleren Höhen. Berücksichtigt man die Holzhärte von *S. patagonicus*, die dem Nest strukturelle Unterstützung gegen starke Winde bieten kann, und der Tatsache, dass die Nester von den vorherrschenden Winden abgewandt ausgerichtet waren, könnte die Nistplatzwahl bei Weißbauch-Olivtyrannen eher mit mikroklimatischen Faktoren am Nistplatz als mit Prädation zusammenhängen. Daher ist es unerlässlich, potenzielle Zusammenhänge zwischen dem Nestmikroklima und Habitatmerkmalen zu berücksichtigen, um das Verständnis für die Nistplatzwahl von Vögeln zu verbessern.

Introduction

Habitat selection is a behavioral response of birds resulting from the disproportionate use of a part of the environment where they live (Block and Brennan 1993). Since predation is the main cause of nest failure, it would be the primary evolutionary pressure acting on nest-site selection (Martin 1993). Thus, by selecting nest sites, birds would benefit from increased survival (Miller et al. 2007) and reproductive success (Guilherme et al. 2018).

The main habitat feature selected by birds to increase their fitness would be nest concealment (Martin 1993). According to the *"total-foliage hypothesis"* (Martin 1993), predation risk decreases as vegetation around the nest increases, which inhibits transmission of visual, chemical or auditory cues by birds. Therefore, nest-site selection may depend on the type of nest predators: aerial predators (mainly birds) follow visual and auditory cues to find nests, whereas ground predators (mainly snakes and mammals) use primarily olfactory cues (Eichholz and Koenig 1992; Remeš 2005).

The selected habitat features at nest sites may vary depending on the spatial scale used for analyses (Cueto 2006). Some habitat features may not be important at one spatial scale, but crucial at another (Cueto 2006). At the mesohabitat scale (i.e., the area around the nest, which may resemble defended territory in some cases), birds place their nests in sites with high vegetation density (Crampton and Sedinger 2011), which may be concentrated in a particular stratum (e.g., in the shrub layer, Fu et al. 2016). Moreover, foliage height diversity (i.e., vegetation cover in different height strata) can influence nest location, as a greater spatial heterogeneity of vegetation (high diversity) reduces the foraging efficiency of predators (Bowman and Harris 1980). At the microhabitat scale (i.e., the area of the plant used for nesting), nest success may vary depending on the position of the nest on the plant. Nests placed near the plant periphery are more exposed to aerial predators (Remeš 2005), while those placed near the trunk are more accessible to ground predators (Alonso et al. 1991). Thus, in intermediate positions, nests are less accessible to both predator types, with a greater probability of success (Alonso et al. 1991). Furthermore, nests located higher off the ground are less vulnerable to ground predators, while nests close to the ground are less vulnerable to aerial predators (Remeš 2005). When both aerial and ground predators are present, nests at intermediate heights are more likely to be successful (Crampton and Sedinger 2011). Birds may also select plants with intermediate foliage density, which would allow them to hide their nests while still having visibility to spot predators in advance (Götmark et al. 1995). Hence, nest-site selection may result from a trade-off between visibility and concealment (Götmark et al. 1995).

Nest orientation (i.e., the position of the nest regarding the central axis of the plant) is another selected microhabitat feature (Burton 2006). Although there is no evidence that nest orientation affects the probability of predation (Nord and Williams 2015), it does have an effect on thermoregulation of nest microclimate (With and Webb 1993; Burton 2007; Schaaf et al. 2018), affecting hatching success (Burton 2006) and nestling growth rates (Lloyd and Martin 2004). In temperate latitudes, birds would orient their nests to the east to warm them up more quickly during the morning (Burton 2007). They may also orient their nests in the opposite direction of the prevailing wind to protect them from direct wind impact (Burton 2006), which in turn reduces the energetic costs of egg or chick thermoregulation in windy conditions (Heenan and Seymour 2012). Hence, the selection of nest orientation could be important for reproductive success (Heenan and Seymour 2012).

The Chilean Elaenia (*Elaenia chilensis*, Aves: Tyrannidae) is a long-distance migrant that overwinters in Brazil (Bravo et al. 2017) and breeds in the Andean–Patagonian Forest (Gorosito et al. 2022). Most of its nests fail due to predation (Gorosito et al. 2022), and the main predators in

this forest are raptors and rodents (Vazquez et al. 2018). Nest predation of this species is density-dependent, given that the probability of predation decreases as the number of active nests increases (Gorosito et al. 2024). In addition, although predators could use cues provided by parental activity and weather to find nests, the nesting success of Chilean Elaenias is not affected by these predator-mediated interactions (Gorosito et al. 2024). However, habitat features at nest sites might be expected to be associated with reduced predation. Moreover, in Patagonia, wind is frequent and strong, and freezing temperatures can occur during the breeding season (Paruelo et al. 1998). Chilean Elaenias build nests with thick walls and the interior lined with abundant feathers (Gorosito et al. 2022), suggesting they have to cope with harsh microclimatic conditions during incubation and nestling periods. We aimed at determining at different spatial scales if Chilean Elaenias selected particular nest sites. We analyzed if vegetation density and foliage height differed between selected and random mesohabitat sites, and if the increase of these mesohabitat features reduced nest predation (*total-foliage hypothesis*, Martin 1993). At the microhabitat scale, we evaluated if Chilean Elaenias selected the plant species for nesting and, if so, whether such selection had an effect on nest success. In addition, we assessed if nest survival was increased in microhabitats where nest concealment was intermediate (trade-off between visibility and concealment, Götmark et al. 1995) and when nests were placed in intermediate positions on the plant (Alonso et al. 1991). Finally, we examined if nest orientation was opposite to the prevailing wind direction and faced directions of optimal solar radiation, and if such orientations affected hatching success, nestling survival, length of incubation and nestling periods, and nest wall thickness.

Methods

Study site

We conducted our research at the Cañadón Florido Ranch (42°55′35″ S, 71°21′53″ W, 616 m.a.s.l.), Chubut Province, Argentina. The vegetation of the area belongs to the Valdivian Forest Province of the Andean Region (Morrone 2001). The forest at the study site (Fig. S1) is dominated by *Maytenus boaria* and *Schinus patagonicus* trees and the understory is composed mainly of *Berberis microphylla* shrubs. The canopy is on average 5 m in height. This forest is part of the Patagonian forest-steppe ecotone. Winters are cold (mean temperature = 1.8 ℃) and wet, while summers are warm (mean temperature = 13.4 ℃, Fig. S2) and dry. Nonetheless, freezing temperatures can occur on average between 1 and 12 nights during spring–summer (October–March, Fig. S2). Annual mean precipitation in the area is 704 mm and falls

as rain and snow mainly during fall–winter (April–September). Wind is frequent throughout the year (annual mean speed = 5.7 km/h) and intensifies during spring–summer (mean speed = 6.6 km/h, Fig. S3A) with gusts exceeding 40 km/h and blowing mostly from the west (Fig. S3B). All climate data are from the Río Percey meteorological station, located 9 km NW of our study site (period 1998–2017, 42°51′30″ S, 71°25′47″ W, 750 m.a.s.l., provided by Hidroeléctrica Futaleufú S.A.).

Among nest predators at Cañadón Florido Ranch, there are birds such as Chimango Caracara (*Milvago chimango*) (Vazquez et al. 2018), Great Shrike-Tyrant (*Agriornis lividus*), Austral Blackbird (*Curaeus curaeus*) (SP Bravo, CA Gorosito and VR Cueto unpubl. data), Crested Caracara (*Caracara plancus*), American Kestrel (*Falco sparverius*) and Austral Pygmy Owl (*Glaucidium nana*) (Menezes and Marini 2017). In the area, we identified one rodent species that preys on nests, the Chilean Climbing Mouse (*Irenomys tarsalis*) (SP Bravo, CA Gorosito and VR Cueto unpubl. data). However, other potential rodent predators were also present in the study site (e.g., Long-tailed Pygmy Rice Rat *Olygoryzomys longicaudatus*, Pearson 1983). Other nest predators present in the Andean–Patagonian Forest are mammals such as Culpeo (*Lycalopex culpaeus*) (Canevari and Vaccaro 2007), South American Gray Fox (*Lycalopex griseus*), American Mink (*Neovison vison*), Colocolo Opossum (*Dromiciops gliroides*) (Menezes and Marini 2017) and Patagonian Opossum (*Lestodelphys halli*) (Martin and Udrizar 2011), snakes like Patagonia Green Racer (*Philodryas patagoniensis*) (Menezes and Marini 2017) and insects like German Yellowjacket (*Vespula germanica*) (Gorosito and Cueto 2024).

Study species

Chilean Elaenia (Fig. S4) is the most abundant bird species during spring–summer in the Andean–Patagonian Forest (Cueto and Gorosito 2018). Males arrive to the forest during mid-October (Bravo et al. 2017; Cueto and Gorosito 2018) and females in early November (Cueto and Gorosito 2018; Gorosito 2020). Adults start fall migration at mid or late February (Bravo et al. 2017; Cueto and Gorosito 2018), but occasionally some of them stay in breeding areas until early March (Cueto and Gorosito 2018; Gorosito 2020).

Chilean Elaenia is an omnivore that consumes fruits and arthropods (Brown et al. 2007). Nestlings are fed with *B. microphylla* fruits and arthropods (Gorosito et al. 2022). Chilean Elaenia breeds between early December and late February, builds open-cup nests, lays 1–3 eggs, incubates for 14 days and its nestlings fledge after about 14 days (Gorosito et al. 2022). Nest survival is 29.5% and successful nests fledge on average 1.7 chicks (Gorosito et al. 2022). This species can renest after nest failure, raising only one

successful brood per season, and frequently mates with a different partner from one season to the next due to a high rate of divorce (Gorosito 2020).

Nest search

We searched for nests daily between late November and late February during four breeding seasons (2014/2015–2017/2018) following the method proposed by Martin and Geupel (1993). We monitored nests daily, marked each egg laid with an indelible ink marker according to the laying order, and recorded the clutch size, the number of hatched and unhatched eggs due to causes other than predation and the number of nestlings that fledged or died from causes other than predation (see Gorosito et al. 2022). We determined the duration of incubation as the time difference between the dates of laying and hatching of the last egg, excluding those nests where the last egg laid did not hatch. We estimated the length of the nestling period as the time difference between the dates of hatching of the first egg and fledging of the last nestling, ruling out those nests where the first egg laid did not hatch. We considered that a nesting attempt was successful when at least one nestling fledged. We inferred that predation occurred if a nest was empty before the estimated fledgling date and when all eggs were broken inside or around the nest. After each nesting attempt, we estimated the width of the nest wall as the difference between the internal and external diameter of the nest.

If parents of the nest were not previously ringed during the systematic mist-net samplings in the study area (see Gorosito et al. 2022), we put a 6-m net in front of the nest during the nestling period to capture parents and ring them with one numbered aluminum and three color bands.

Vegetation sampling

We recorded mesohabitat vegetation features during the post-breeding period (i.e., from March), in order to avoid interference during renesting attempts (Gorosito et al. 2022). Since the dominant plant species in our study area are evergreen, vegetation structure remained unchanged between the breeding and post-breeding periods.

We characterized the mesohabitat of each nest with four 10-m-long transects oriented in the main cardinal directions, using the nest as origin. On each transect at 20 random points, separated by at least 20 cm from one another, we recorded species and height of the plants that contacted an erected 6-m-rod marked at 0.25 m intervals (from 0 to 4 m) and at 1 m intervals (from 4 to 6 m). Overall, we sampled 80 random points in the mesohabitat of each nest. We used the same sampling procedure to characterize the mesohabitat of 112 randomly selected sites within the forest area of the study plot. In these sites, the origin of the transects was

the tree or shrub closest to the randomly selected site. We calculated for each nest and random site the horizontal cover of each plant species as the percentage of the 80 random points in which the species contacted the rod. We also calculated for each nest and random site the vegetation cover in each height category of the graduated rod as the percentage of the 80 random points in which vegetation contacted the rod in each height category. Then, we estimated the Shannon–Weaver diversity index of foliage height for each sampled mesohabitat. We used this variable as an indicator of the vertical heterogeneity of vegetation.

Based on the profile of vegetation heights (i.e., vegetation cover in each height category) of random sites and according to those heights in which a reduction in vegetation cover was observed (Fig. S5), we defined three strata: I) shrub layer: 0–1.5 m from the ground composed mainly of *B. microphylla*; II) subcanopy: 1.5–4 m from the ground represented by *S. patagonicus* and *M. boaria*; and III) canopy: > 4 m from the ground, composed primarily of *M. boaria*. Then, we calculated for each nest and random site, the horizontal cover of each of the three strata as the percentage of the 80 random points in which vegetation of the stratum contacted the rod. We used these cover data to evaluate if vegetation density in any of the strata was selected by Chilean Elaenias.

We recorded the following microhabitat features immediately after a nesting attempt ended: plant species, nest height (from the ground to the top of the nest), and distance from the nest to both, the plant edge and the trunk or central axis of the plant (both measurements were taken at the same height where the nest was located). Following Lazo and Anabalón (1991), we estimated the degree of nest periphery (relative distance of the nest from the center of the plant) as "distance between nest and plant central axis"/("distance between nest and plant edge" + "distance between nest and plant central axis"). Nests placed in the center of the plant had a periphery degree = 0 and fully exposed nests = 1. We measured vegetation density around the nest with a 50-cm-long rod graduated every 10 cm (Mezquida 2004). We took the nest as starting point and recorded the vegetation contacts in each of the five intervals of the rod, placing it vertically above and below the nest and transversely in each of the four cardinal directions (Mezquida 2004). We estimated nest concealment as the percentage of the total number of possible contacts (30) in which vegetation contacted the rod. We determined nest orientation with a compass, based on an imaginary line that went from the center of the plant to the nest.

Statistical analysis

We managed to band 30% of pairs from nests in our study site, and never observed the same pair with more than one nest. Chilean Elaenia renests close to its previous failed nest

(Gorosito 2020), but we did not have two nests very close to each other during the same breeding season in our dataset. Considering this information and interannual divorce in Chilean Elaenias (Gorosito 2020), the probability of using more than one nest from the same pair in our analysis is negligible.

We used a logistic regression to analyze the probability of finding nests at the mesohabitat scale according to vegetation features. We used the site (nest site = 1, random site = 0) as response variable, and the cover percentages of shrub layer, subcanopy and canopy, and foliage height diversity as predictor variables. We performed model selection based on the Akaike's information criterion corrected for small sample size (AIC$_c$) (Burnham and Anderson 2002). First, we evaluated multicollinearity and if two variables were highly correlated (*Pearson's r* ≥ 0.70, *P* ≤ 0.05), we removed the one whose AICc was larger. Then, we built univariate and additive models. Following recommendations of Rotella (2019), we dropped from the set of candidate models those additive models whose AICc were higher than those of univariate models. We considered as the best model the one that had the lowest AIC$_c$ and the highest Akaike weight w_i (Burnham and Anderson 2002). We also considered that models with ΔAICc ≤ 2 had substantial support (Burnham and Anderson 2002). In case of model uncertainty (i.e., w_i of top model < 0.90), we proceeded to model averaging with the package *MuMIn* (Barton 2022), using all candidate models (Burnham and Anderson 2002). We assessed the parameter likelihood by summing w_i across all models that contained the parameter being considered (Burnham and Anderson 2002). We considered that model parameters had an effect on mesohabitat selection if their 95% confidence intervals excluded zero.

At the microhabitat scale, we evaluated if Chilean Elaenias selected the plant species for nesting using the Manly's Selectivity Index W_i (Manly et al. 2002) with the widesI function in package *adehabitatHS* (Calenge 2006). We excluded from this analysis those plants species with low covers (< 3%) in the study area and very few nests (< 5) concentrated in only one or two seasons of the four studied (12 nests distributed among *Ochetophila trinervis* [4], *Adesmia volckmannii* [3], *Sambucus nigra* [2], *Ribes cucullatum* [1], *Nothofagus antarctica* [1] and *Baccharis rhomboidalis* [1]). The expected frequency of nests for each plant species was estimated as the product between the total number of nests and the cover proportion of a particular plant species in random sites (Manly et al. 2002). We determined significant selection or avoidance if 95% confidence intervals were > 1 or < 1, respectively (Manly et al. 2002). Confidence intervals overlapping one indicate that plants are used according to availability (Manly et al. 2002).

We estimated daily nest survival rate (DSR) with the package *RMark* (Laake 2013) using all predated and successful nests to identify if any habitat feature reduced Chilean Elaenia nest predation. We standardized the breeding season length for all years (Standardized day 1 = 12 December, Standardized day 82 = 3 March). We used as predictor variables the selected mesohabitat features, the plant species used for nesting, nest height, nest periphery and nest concealment, including the quadratic terms of these last three variables to assess whether DSR was higher in microhabitats with intermediate values. We did not include commonly used variables such as year, date and nest age in our analysis, because they have no effect on Chilean Elaenia DSR in the study area (Gorosito et al. 2024). Therefore, we pooled data from the four breeding seasons. Predictor variables were not highly correlated and we performed model selection using information-theoretic procedures in the same way as mentioned above for the mesohabitat selection analysis.

We analyzed nest orientation following circular statistical procedures and using the Rayleigh test (*circular* package, Agostinelli and Lund 2022) to determine if Chilean Elaenias preferentially oriented their nests in a particular cardinal direction. We calculated the mean angle and the angle deviation, and grouped nests into two categories: I) nests in optimal orientations: those that receive early morning solar radiation (SE, E, NE) and even the highest solar radiation at noon (N), all of them in the opposite prevailing wind direction (between 338° and 158°); and II) nests in non-optimal orientations: those facing wind directions (SW, W, NW) and oriented away from solar radiation (S), encompassing the remaining semicircle.

To evaluate the effect of nest orientation on hatching success, we calculated for each nest (those in which some of the eggs survived until the chick stage) the percentage of eggs at the end of incubation that finally hatched. To evaluate if nest orientation had an effect on nestling survival, we calculated for each non-predated nest the percentage of hatched eggs that became fledglings. We used *t*-tests to assess differences between nests in optimal and non-optimal orientations regarding percentages of egg hatching and nestling survival, length of incubation and nestling periods, and thickness of nest wall. We performed all statistical analyses in software R 4.2.2 (R Core Team 2022). Reported values are means ± SE.

Results

Selection of mesohabitat and microhabitat features

The vegetation profiles of nest (*n* = 112) and random sites (*n* = 112) were similar (Fig. S5). Since subcanopy cover (AIC$_c$ = 307.12) and foliage height diversity (AIC$_c$ = 309.90) were highly correlated (*r* = 0.75, *P* < 0.001), we removed the latter variable from the analysis. The best model to

explain features of used mesohabitats indicated that Chilean Elaenias nested in sites with greater subcanopy cover

Table 1 Model-selection results for models explaining features of Chilean Elaenia mesohabitats in relation to shrub, subcanopy and canopy covers

Candidate models	k	AIC_c	ΔAIC_c	w_i
Subcanopy	2	307.12	0.00	0.74
Shrub + canopy	3	311.06	3.94	0.10
Canopy	2	311.22	4.10	0.09
Null model	1	312.55	5.43	0.05
Shrub	2	314.42	7.31	0.02

Models are ranked according to AIC_c and include an intercept. k is the number of estimated parameters. w_i is the Akaike weight of the model

(Table 1, Fig. 1). The effect of this variable was corroborated after model averaging ($\beta = 0.02 \pm 0.01$, parameter likelihood = 0.74, 95% CI: 0.0060, 0.0405). Shrub cover ($\beta = 0.01 \pm 0.01$, parameter likelihood = 0.12, 95% CI: -0.0088, 0.0376) and canopy cover ($\beta = 0.01 \pm 0.01$, parameter likelihood = 0.19, 95% CI: -0.0003, 0.0326) had no effect on mesohabitat selection.

At the microhabitat scale, Chilean Elaenias used more frequently *S. patagonicus* for nesting, avoided *M. boaria* and used the other plant species according to their availabilities (Table 2, Fig. 2). They built their nests at a height of 1.04 ± 0.07 m from the ground ($n = 116$, range = 0.25–4.55 m), with a periphery degree of 0.63 ± 0.03 ($n = 116$, range = 0–1) and a concealment of $39.95 \pm 1.49\%$ ($n = 112$, range = 6.66–83.33%).
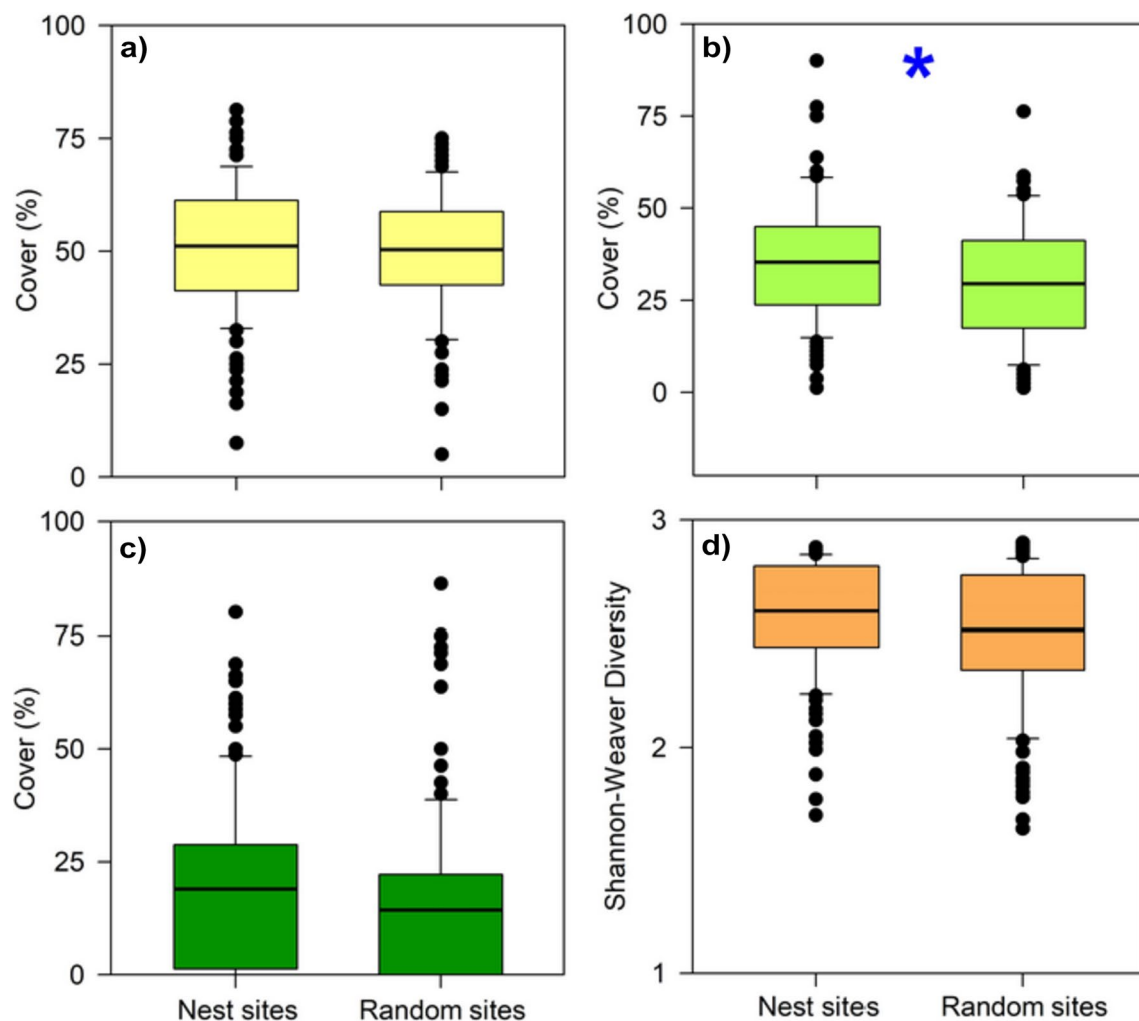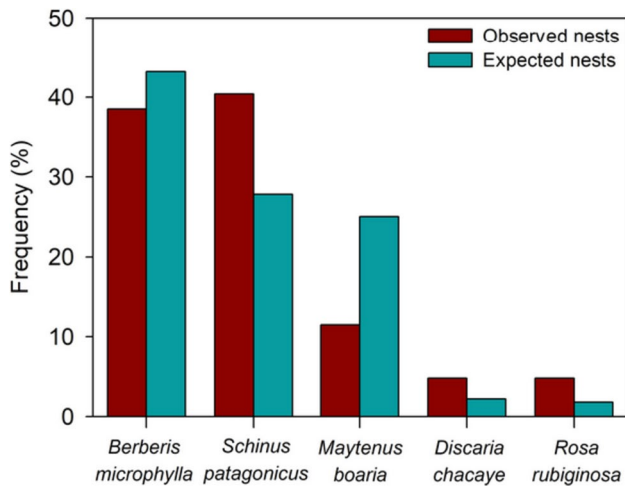

Fig. 1 Box-and-whisker plot showing comparisons of cover percentages of (**a**) shrub layer, (**b**) subcanopy and (**c**) canopy, and (**d**) foliage height diversity between nest sites of Chilean Elaenia and random sites in the forest-steppe ecotone at Cañadón Florido Ranch, Chubut Province, Argentina. Shown in each boxplot, the mean (middle solid line), the 25th and 75th percentile (lower and upper hinge), 10th and 90th percentiles (whiskers), and outliers (points). The mesohabitat feature selected by elaenias is indicated with an asterisk

Table 2 Manly's selectivity index (W_i) for each plant species used by Chilean Elaenias for nesting

Plant species	W_i	95% CI	P
Berberis microphylla	0.89	0.67–1.11	0.32
Schinus patagonicus	1.45	1.11–1.79	< 0.01
Maytenus boaria	0.46	0.21–0.70	< 0.01
Discaria chacaye	2.19	0.31–4.05	0.21
Rosa rubiginosa	2.67	0.39–4.95	0.15

Confidence intervals overlapping 1 indicate use according to availability, > 1 selection and < 1 avoidance

Table 3 Model-selection results for models explaining variations in Chilean Elaenia DSR in relation to subcanopy cover, plant species used for nesting, nest height, nest periphery and nest concealment

Candidate models	k	AIC_c	ΔAIC_c	w_i
Null model	1	479.91	0.00	0.36
Nest periphery	2	481.16	1.25	0.19
Subcanopy	2	481.53	1.62	0.16
Nest concealment	2	481.62	1.71	0.15
Nest height	2	481.90	1.99	0.13
Plant species	5	486.28	6.37	0.01

Models are ranked according to AICc and include an intercept. k is the number of estimated parameters. w_i is the Akaike weight of the model

Fig. 2 Frequency distribution of Chilean Elaenia nests placed on different plant species in the forest-steppe ecotone at Cañadón Florido Ranch, Chubut Province, Argentina

Meso- and microhabitat feature effects on nest survival

Nest survival analysis was based on 87 nests, representing 1110 exposure days. We only kept univariate models, which were better than the additive ones. The best model to explain DSR was the null model of constant DSR (Table 3). Subcanopy cover ($\beta = 0.01 \pm 0.01$, 95% CI: − 0.01, 0.02), nest concealment ($\beta = 0.01 \pm 0.01$, 95% CI: − 0.01, 0.02), nest periphery ($\beta = 0.38 \pm 0.44$, 95% CI: − 0.48, 1.26), nest height ($\beta = 3.29xe^{-4} \pm 2.39xe^{-3}$, 95% CI: − 0.01, 0.01) and plant species used for nesting (all with confidence intervals spanning zero) had no effect on DSR.
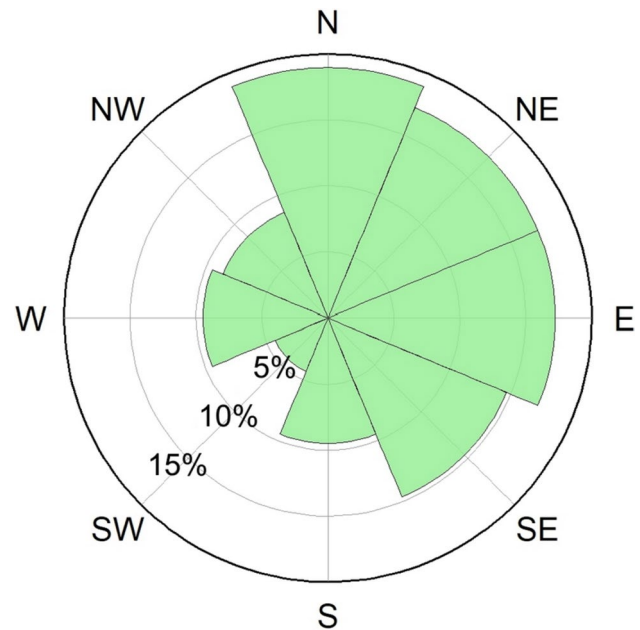
Nest orientation

Chilean Elaenias oriented their nests ($n = 116$) preferentially to the N, NE, E and SE (mean angle = 59.6°, angular deviation = 70.6°; Rayleigh test: $Z = 6.68$, $P = 0.001$; Fig. 3). Some

Fig. 3 Percentage of Chilean Elaenia nests oriented in each cardinal direction in the forest-steppe ecotone at Cañadón Florido Ranch, Chubut Province, Argentina

nests were oriented towards the S, W and NW, and very few towards the SW (Fig. 3).

Considering those nests that reach the nestling period ($n = 56$), 17.9% of them contained unhatched eggs. On average, in these nests 46.7% of the eggs did not hatch. However, nest orientation was not associated with greater egg hatching success (in optimal orientations: $91 \pm 3\%$, $n = 42$, in non-optimal orientations: $93 \pm 5\%$, $n = 14$; $t_{54,0.05} = -0.28$, $P = 0.78$). Also, there were no associations of nest orientation with higher nestling survival (in optimal orientations: $90 \pm 4\%$, $n = 21$, in non-optimal orientations: $92 \pm 6\%$, $n = 10$; $t_{29,0.05} = -0.27$, $P = 0.79$), shorter incubation (in optimal orientations: 14.08 ± 0.23 days, $n = 12$, in non-optimal orientations: 14.00 ± 0.29 days, $n = 9$; $t_{19,0.05} = 0.23$,

$P = 0.82$), shorter nestling period (in optimal orientations: 13.94 ± 0.26 days, $n = 18$, in non-optimal orientations: 13.73 ± 0.47 days, $n = 11$; $t_{27,0.05} = 0.44$, $P = 0.66$) or thinner nest wall (in optimal orientations: 1.82 ± 0.05 cm, $n = 65$, in non-optimal orientations: 1.79 ± 0.09 cm, $n = 37$; $t_{100,0.05} = 0.28$, $P = 0.78$).

Discussion

We found that at the mesohabitat scale, Chilean Elaenia nested in sites with greater subcanopy cover than in random sites, and at the microhabitat scale, elaenias selected specific plant substrates for nesting. Nonetheless, neither mesohabitat nor microhabitat variables were associated with nest survival, and thus our results did not support the hypotheses indicating that nest-site selection reduces nest predation rates (e.g., Alonso et al. 1991; Martin 1993; Götmark et al. 1995).

The lack of association between mesohabitat features and nest success has already been reported (Howlett and Stutchbury 1996; Fu et al. 2016). This result may be consequence of random predation, produced by generalist predators (Howlett and Stutchbury 1996), or the existence of a diverse predator assemblage with different search methods that could preclude the possibility of safe nest sites (Fu et al. 2016). Patagonian rodents are one of the main nest predators in the Andean–Patagonian Forest (Vazquez et al. 2018). They are generalists that feed on fruits, seeds, plant materials, and insects (Polop et al. 2015), and move in shrubby areas (Lozada et al. 2000). Thus, they forage in the same forest strata where Chilean Elaenia builds its nests. Furthermore, nests at the study site are exposed to aerial predators like Chimango Caracara, a generalist raptor with opportunistic hunting methods (Biondi et al. 2005), which is the main nest predator in the Andean–Patagonian Forest (Vazquez et al. 2018). Crested Caracara is also a generalist predator that feeds on nestlings and uses them to feed its chicks (Travaini et al. 2001). Therefore, Chilean Elaenia nests are exposed to aerial and ground generalist predators and, consequently, selected nest sites at the mesohabitat scale may not affect nest predation probability.

At the microhabitat scale, our results did not support the hypothesis that nest-site selection is driven by a trade-off between nest visibility and nest concealment (Götmark et al. 1995), as there was no relationship of DSRs with intermediate values of nest concealment, periphery and height. Both successful and predated nests were found closer to the ground than to the canopy, therefore, they were easily accessible to ground predators, even for those unable to climb through vegetation.

Nest microclimate may be an important selective agent in nest-site selection (Wiebe and Martin 1998) and Chilean Elaenia may be selecting nest sites with adequate microclimatic conditions. First, wind had an effect on the preference of elaenias regarding nest orientation, as most nests were oriented to eastern directions, contrary to prevailing winds in Patagonia (Paruelo et al. 1998). Therefore, the preference of Chilean Elaenia for nesting in a plant substrate (*S. patagonicus*) that was not associated with DSR might rather be related to protection against wind impact, as this plant species has hard wood and its branches are difficult to break (Bischeimer and Fernández 2009), which may provide good structural support for nests. Second, most nests (83.6%) were built on the shrub layer. Chilean Elaenia rarely nests below 0.5 m from the ground (Altamirano et al. 2012), but in our study site, 14% of nests were placed below such a height and the lowest nest height was 0.25 m. Thus, Chilean Elaenia might reduce heat loss from nests due to wind by building nests at low heights. Finally, the tendency to select mesohabitats with greater subcanopy cover (composed mainly of *S. patagonicus*) may also be associated with wind effects on nests. We might expect less wind impact in mesohabitats with high *S. patagonicus* covers than in mesohabitats with high cover of other species, such as *M. boaria*, which has both soft branches and foliage that may not greatly reduce the wind impact on nest structure and microclimate.

Temperature may also influence nest orientation, as low temperatures occur frequently during summer nights in the Andean–Patagonian Forest. By orienting nests to eastern directions and even to the north, birds could take advantage of early morning warming and until noon to improve egg or nestling viability while they are foraging (Nelson and Martin 1999). Furthermore, these directions allow birds in our study area to protect their nests from maximum northwestern and western solar radiation between 16:00 and 18:00 h during the hottest days of the summer. In this way, they could obtain an energetic benefit with such selection, as they can reduce the energetic cost of nest thermoregulation (Reid et al. 2000). Yet, we did not find that Chilean Elaenia nests oriented to the north and eastern directions had greater hatching success or nestling survival. Bearing in mind that we did not control other causes of hatching failure, such as infertility or embryonic mortality due to causes unrelated to weather, the lack of association between nest orientation and hatching success found here might be masked by the aforementioned causes or nest orientation might have effects on other breeding parameters. While we did not find associations of nest orientation with thickness of nest wall or length of incubation and nestling periods, those nests facing the wind and opposite to the sunrise should have a thicker lining layer to increase thermal insulation (Deeming et al. 2020). Moreover, adults might increase feeding or brooding effort to compensate for a colder microclimate. Hence, further studies are needed to evaluate the hypothesis that Chilean Elaenia adults orient their nests to north and eastern directions to reduce

the energetic cost of nest thermoregulation. This evaluation, along with the analysis of potential associations of Chilean Elaenia nest microclimate with microhabitat and mesohabitat features, will lead to advance in the understanding of nest-site selection patterns in passerines.

Declarations

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