



More is better: predator dilution effect increases Chilean Elaenia (*Elaenia chilensis*) nest survival

Cristian A. Gorosito¹ · Diego T. Tuero² · Victor R. Cueto¹

Received: 29 December 2022 / Revised: 1 June 2023 / Accepted: 20 June 2023 / Published online: 6 July 2023
© Deutsche Ornithologen-Gesellschaft e.V. 2023

Abstract

Nest survival may be affected in several ways by predator-mediated interactions. According to the “predator dilution effect hypothesis”, the daily nest survival rate (DSR) can be density-dependent, because the probability of nest predation decreases as the number of active nests increases. Additionally, parental activity may increase with clutch size, nest age, and after low-temperature periods, while climatic components such as air humidity and moderate winds can increase odour dissipation from nests. Consequently, predators can use these cues to locate nests, reducing the DSR. Determining such predator-mediated interactions is important to understand how multiple causes can affect avian reproductive success. Thus, we evaluated the effects of predation and predator-mediated interactions of abundance of active nests, parental investment and climate on annual and seasonal variations in DSR of the Chilean Elaenia (*Elaenia chilensis*), a long-distance migratory passerine that breeds in the Andean-Patagonian Forest. We monitored nests over four breeding seasons and modelled DSR for 86 nests. The mean \pm SE DSR was 0.960 ± 0.005 , corresponding to an overall nest success of 29.5%. DSR increased with the abundance of active nests, but it did not vary among years or throughout the breeding season, nor was it affected by other variables. Hence, there was no influence of parental investment and climate on predation. Instead, the increase in abundance of active nests towards the middle of the breeding season reduces the probability of predation per nest, resulting in greater Chilean Elaenia nest survival, and providing empirical support for the “predator dilution effect hypothesis”.

Keywords Andean-Patagonian Forest · Neotropical birds · Nest survival · Predator dilution effect · Predator-mediated interactions

Zusammenfassung

Mehr ist besser: Ein Verdünnungseffekt bei der Gefahr durch Räuber erhöht beim Weißbauch-Olivtyrann (*Elaenia chilensis*) die Überlebensrate der Gelege

Das Überleben von Gelegen kann auf verschiedene Weise durch von Räufern ausgehende Wechselwirkungen beeinflusst werden. Entsprechend der Hypothese des Verdünnungseffekts bei der Gefahr durch Nesträuber könnte die tägliche

Communicated by F. Bairlein.

✉ Cristian A. Gorosito
cgorosito@conicet.gov.ar

¹ Laboratorio de Ecología de Aves, Centro de Investigación Esquel de Montaña y Estepa Patagónica (CIEMEP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de la Patagonia San Juan Bosco, Roca 780, U9200CIL Esquel, Chubut, Argentina

² Departamento de Ecología, Genética y Evolución and Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires and CONICET, Intendente Güiraldes 2160, Ciudad Universitaria, C1428EGA Buenos Aires, Argentina

Gelege-Überlebensrate (DSR) von der Dichte der Gelege abhängen, da die Wahrscheinlichkeit von Nesträuberei mit zunehmender Anzahl aktiver Gelege abnimmt. Außerdem könnte die Aktivität der Elterntiere mit der Gelegegröße, dem Alter des Nests und auch nach kühleren Perioden zunehmen, während Klimafaktoren wie Luftfeuchtigkeit und schwache Winde die Verbreitung von Gerüchen aus den Nestern möglicherweise erhöhen. Folglich könnten Fressfeinde solche Spuren nutzen, um Gelege aufzuspüren, was die DSR verringert. Das Erfassen solcher Wechselwirkungen mit Räufern ist wichtig, um zu verstehen, wie mehrere Faktoren den Fortpflanzungserfolg von Vögeln beeinflussen können. Deshalb untersuchten wir die Auswirkungen von Nesträuberei und die von Räufern initiierten Wechselwirkungen zwischen der Anzahl aktiver Nester, der Zuwendungen durch die Elterntiere und von Klimafaktoren auf die jährlichen und saisonalen Veränderungen der DSR beim chilenischen Weißbauch-Olivtyrann (*Elaenia chilensis*), einem langstreckenziehenden, im Anden-Patagonien-Wald brütenden Sperlingsvogel. Wir beobachteten Gelege über vier Brutzeiten hinweg und modellierten die DSR für 86 Gelege. Dabei betrug der mittlere \pm SE für die DSR 0.960 ± 0.005 , was einem Gesamt-Bruterfolg von 29.5% entspricht. Die DSR nahm mit der Anzahl der aktiven Gelege zu, veränderte sich jedoch weder zwischen den Jahren oder in der Brutzeit, noch wurde sie von anderen Faktoren beeinflusst. Folglich gab es keinen Einfluss der elterlichen Zuwendung oder des Klimas auf die Plünderung der Gelege durch Räuber. Stattdessen verringerte die zunehmende Anzahl aktiver Gelege zur Mitte der Brutzeit die Gefahr des Verlusts pro Gelege durch Fressfeinde, was zu einer höheren Überlebensrate von Gelegen des Weißbauch-Olivtyranns führt und die Hypothese vom Verdünnungseffekt empirisch untermauert.

Introduction

Nest survival is a crucial component of breeding output (Shaffer 2004) and as such has an impact on population size (Stahl and Oli 2006). Nest survival is mainly driven by predation, which is the main cause of nest loss (Remeš et al. 2012). As predators search for and find nests by following visual and olfactory cues (Ibáñez-Álamo et al. 2015), understanding the numerous ways they accomplish this is useful in predicting how avian population size may change over time (Sherry et al. 2015).

The daily nest survival rate (DSR) can fluctuate annually, being lower in years with a greater abundance of predators that can detect nests (Sherry et al. 2015) or during years of food shortage, when parental foraging activity is higher and consequently more visual cues about nest locations are provided to predators (Rastogi et al. 2006). Furthermore, DSR can either increase throughout the season as foliage becomes denser for nest concealment (Borgmann et al. 2013) or decrease as the breeding season progresses (Segura and Reboreda 2012). According to the “predator search image hypothesis”, predators will focus attention on the prey type most frequently encountered during recent searching, even if other prey become more abundant (Dukas 2002; Ishii and Shimada 2010). Therefore, when nest abundance increases and there is greater parental activity, nests will become more conspicuous and predators will become more efficient in finding them, reducing DSR as the season progresses (Duca et al. 2019). However, according to the “predator dilution effect hypothesis” DSR can increase with nest abundance, because the predation probability of a nest is lower when there are many nests that can be predated (Dehn 1990; Duca et al. 2019). Hence, the predator dilution effect may reduce the impact of the predator search image on avian breeding success (Duca et al. 2019).

Parental investment can also modify DSR. Daily energy expenditure of incubating birds increases with clutch size (Moreno and Sanz 1994; Nord and Williams 2015), thus they must increase food intake (Coleman and Whittall 1988), which implies increasing the number of foraging trips (Cooper and Voss 2013) and exposing their nest to a greater risk of being found by predators (Martin et al. 2000). Likewise, larger brood sizes increase the number of feeding visits to the nest (Sousa and Marini 2013), resulting in an increase of nest conspicuousness and a reduction of DSR (Martin et al. 2000).

Moreover, parental behaviour changes throughout nesting stages along with the number of cues provided to predators, and therefore DSR can vary with nest age (Grant et al. 2005). As egg laying proceeds, parental investment is greater (Verboven and Tinbergen 2002) and parents increase nest defence (Redmond et al. 2009). Then, parental activity increases during incubation, while chick begging calls (Redmond et al. 2009) and nest defence by parents intensify during the nestling stage (Cooper and Voss 2013). All these behaviours may produce a cubic relationship between DSR and nest age, when DSR increases during the laying period, decreases during incubation and finally increases again until nestlings fledge (Skagen and Yackel Adams 2012). If nest defence does not occur during the laying stage, DSR may decrease until hatching and then increase until nestlings fledge (quadratic relationship, Conrey et al. 2016). Additionally, the inverse quadratic pattern may occur, but it is very infrequent (see Weiser 2021 and references therein). If nest defence also does not increase during the nestling stage, DSR may decrease linearly with increasing nest age (Webb et al. 2012), while the inverse linear pattern is observed when nest defence increases throughout nesting stages (Segura and Reboreda 2012). Although the patterns of decreased DSR as the nest ages and as the season progresses

can be confounded, both effects can be differentiated if nests are initiated during different parts of the season (Smith and Wilson 2010).

Climatic conditions also influence the dissemination and detectability of cues used by predators to find nests. Precipitation can reduce DSR (Webb et al. 2012; Conrey et al. 2016), because high air moisture facilitates the diffusion of odours (Gutzwiller 1990), allowing predators to smell bird feathers and find nests (Ruth and Skagen 2018). Additionally, DSR may be reduced by daily minimum temperatures. After an intense cold period, parents intensify foraging activity in order to satisfy their energetic requirements to maintain both themselves and adequate nest temperatures (Reneerkens et al. 2011), increasing the probability of nest detection by predators (Rastogi et al. 2006). As wind can carry the odour of birds over longer distances, predators like mammals may more easily detect nest locations (Webb et al. 2012). During days with moderate wind speed (7.2–14.4 km/h), a greater abundance of predatory mammals can be observed (Ruzicka and Conover 2011). However, when wind speed is low, odours are concentrated in a narrow area and predators will only be able to detect their prey's odour if they are very close to it (Ruzicka and Conover 2011), while strong winds make it difficult for predators to detect nests because turbulence dissipates odours (Conover 2007).

In order to improve our understanding of the impact of predator-mediated interactions on nest survival of Neotropical birds and contribute to understand how multiple causes acting simultaneously can affect avian reproductive success, we evaluated the effects of the aforementioned variables of time (year and time of breeding), nest abundance, parental investment (clutch size and nest age) and climate (precipitation, minimum temperature and wind speed) on DSR of the Chilean Elaenia (*Elaenia chilensis*) in the Andean-Patagonian Forest.

Methods

Study area and species

We conducted our study at the Cañadón Florido Ranch (42.9253°S, 71.3628°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 is evergreen and dominated by Mayten (*Maytenus boaria*) and Laura (*Schinus patagonicus*) trees, which form a low canopy of c. 5 m in height. The understory is dominated by Box-leaved Barberry (*Berberis microphylla*) shrubs. This type of forest is common in

valleys and hill slopes in the eastern portion of the northern Patagonian Forest, and is part of the forest-steppe ecotone.

Winters are cold and wet (mean temperature = 1.8 °C) and summers are warm and dry (mean temperature = 13.4 °C). Annual mean precipitation (rain and snow) is 704 mm and 68% is concentrated in April–September (fall–winter). All climate data are from the ‘Rio Percey’ meteorological station (period: 1998–2017, 42.8583°S, 71.4297°W, 750 m.a.s.l., Hidroeléctrica Futaleufú S.A.), located 9 km NW of our study site.

The nest predator assemblage at Cañadón Florido Ranch is a mix of birds (*Milvago chimango*, Vazquez et al. 2018; *Caracara plancus*, *Curaeus curaeus*, *Falco sparverius*, *Glaucidium nana*, Menezes and Marini 2017; *Agriornis lividus*, SP Bravo, CA Gorosito and VR Cueto unpubl. data) and mammals (rodents, Vazquez et al. 2018, SP Bravo, CA Gorosito and VR Cueto unpubl. data; *Lycalopex culpaeus*, Canevari and Vaccaro 2007). The wasp *Vespula germanica* also preys on nests (CA Gorosito unpubl. data).

The Chilean Elaenia is a long-distance migratory tyrant flycatcher that breeds in the Andean-Patagonian Forest and overwinters in Brazil (Bravo et al. 2017). Males arrive in the forest from mid-October (Bravo et al. 2017; Cueto and Gorosito 2018) and females from early November (Cueto and Gorosito 2018; Gorosito 2020). Adults start fall migration between mid- and late February (Bravo et al. 2017; Cueto and Gorosito 2018), although some of them remain on the breeding grounds until early March (Cueto and Gorosito 2018; Gorosito 2020). During the spring–summer, the Chilean Elaenia is the most abundant bird species in the forest (Cueto and Gorosito 2018) and breeds between early December and late February (Gorosito et al. 2022). It builds open-cup nests, lays 1–3 eggs, incubates for 14 days, and its nestlings fledge after c. 14 days (Gorosito et al. 2022).

Nest monitoring and climatic data collection

We searched for Chilean Elaenia nests from late October to late February of the 2014–2018 breeding seasons following the method proposed by Martin and Geupel (1993). This passerine is the most abundant species of the bird assemblage in the study area (more than 35% of individual birds in the avian community are Chilean Elaenias, while the remainder belong to individuals of 24 other bird species), and the last species to initiate breeding in the Andean-Patagonian Forest (Cueto and Gorosito 2018). Because of this delay in reproduction, during the 2016/2017 and 2017/2018 breeding seasons we also monitored nests of resident and short-distance migratory species to determine the contribution of these nests to the total abundance of nests during the Chilean Elaenia breeding period (Table S1). We monitored nests following standardized protocols (Ralph et al. 1996) and visited each daily until the nest was successful (i.e., at least one

nestling left the nest) or failed. We classified causes of nest failure into predation and other causes (see Gorosito et al. 2022 for details). We considered that the nest had been predated when it was empty before the estimated fledging date and when we found all eggs broken inside or around the nest.

We used data of daily minimum temperature, daily precipitation and daily mean wind speed of the four breeding periods, recorded by the ‘Río Percey’ meteorological station.

Data analyses

We estimated DSR using program MARK (Cooch and White 2019) and quantified overall nest success as DSR^x , where x is the nesting period duration (Dinsmore et al. 2002), being 30 days for the Chilean Elaenia (Gorosito et al. 2022). We coded encounter histories following Dinsmore et al. (2002) and standardized the length of the breeding season for all years (Julian day 1 = 12 December, Julian day 82 = 3 March) according to recommendations by Dinsmore and Dinsmore (2007). We used the *sine* link function to build a constant DSR model and the *logit* link function to build models with covariates.

We used all successful and predated nests to model DSR. We built models using the following temporal covariates: year (2014/2015, 2015/2016, 2016/2017, 2017/2018), Julian day (linear relationship with DSR) and quadratic Julian day (quadratic relationship with DSR, including intercept, Julian day and Julian day²). As a nest abundance covariate, we used the abundance of active Chilean Elaenia nests. Because most nests in the bird community belonged to the Chilean Elaenia during its breeding period (~70%, Table S1), we considered its nest abundance as the main nest supply for predators and considered negligible the impact of nest abundance of other species. We calculated the daily number of active nests, considering the length of the nesting stages of the Chilean Elaenia (Gorosito et al. 2022) and backward estimating the date of the onset of egg laying in those nests found during incubation or the nestling stage. We used the following covariates of parental investment: clutch size, nest age, nest age² (quadratic relationship with DSR) and nest age³ (i.e., cubic term is added to the terms of the quadratic relationship between nest age and DSR). We considered the day of laying of the first egg as nest age = 0, following Dinsmore and Dinsmore (2007). Among climatic covariates, we used daily precipitation and precipitation of the previous day (due to the possibility of a delay in the effect of precipitation on the transmission of odours through air humidity, Webb et al. 2012). Because only precipitation events ≥ 10 mm have an impact on DSR (Skagen and Yackel Adams 2012; Conrey et al. 2016; Ruth and Skagen 2018), we transformed precipitation values into a binary scale (0 = precipitation event < 10 mm, 1 = precipitation event ≥ 10 mm). We used the daily minimum temperature, because its lowest value is

recorded before sunrise and we expected it to have an effect on DSR during that day. We used the daily mean wind speed and daily mean wind speed² in order to evaluate a quadratic relationship between this climatic variable and DSR, considering that predators are expected to follow olfactory cues more easily in moderate wind speeds (Ruzicka and Conover 2011).

We used information-theoretic procedures for model selection (Burnham and Anderson 2002). To limit the number of candidate models that may explain the variation of nest survival with the covariates mentioned above, we used a hierarchical model selection procedure (Arnold 2010; Ruth and Skagen 2018). We used Akaike’s information criterion corrected for small sample size (AICc) to identify models with the most support (Burnham and Anderson 2002). First, we correlated all predictive variables to analyse issues of collinearity and, if so, we removed the variable whose AICc was larger. The number of active nests and quadratic Julian day were highly correlated (Pearson’s $r = -0.77$, $P < 0.0001$), thus we removed the latter. Then, the model selection procedure was as follows:

1. We built models using four groups of variables: (I) year and Julian day, (II) number of active nests, (III) clutch size and nest age, and (IV) climatic variables. In each group we included a constant model (i.e., model without covariates and with constant DSR) and interactions between year and each variable to determine if there were different patterns in each year. We selected the variable in the model that had the lowest AICc (which was considered as the most supported model to explain variations in DSR) within each group for the next step. If there was a second model that had a $\Delta AICc < 0.10$ relative to the best model, the variable in the second-best model was also carried forward to the next step (Ruth and Skagen 2018).
2. We used the selected variables from the previous step to build additive models in every possible combination. Following recommendations of Rotella (2019), we kept the models in which the combination of variables produced a better AICc than that of univariate models, but if the combination of variables produced models with a higher AICc, then we removed them from the set of candidate models.
3. Finally, we added or substituted competitive variables (i.e., those variables with a $\Delta AICc \leq 1$ relative to the best model in each group from step 1, Ruth and Skagen 2018) into the best model from step 2.

We considered that the best model of the set of candidate models was the one with the lowest AICc (Burnham and Anderson 2002). Since Akaike weights < 0.90 indicate model selection uncertainty, we also considered models

with $\Delta\text{AICc} \leq 2$ to have substantial support (Burnham and Anderson 2002). We considered variables of the best model to have an effect on DSR if their 95% confidence intervals excluded zero.

Results

Characteristics of covariates

Mean daily precipitation was low during the four breeding periods (mean \pm SD = 0.84 ± 1.41 mm). There were only one (2014/2015 and 2015/2016) and four (2016/2017 and 2017/2018) precipitation events ≥ 10 mm, and no precipitation was recorded during 78% (2016/2017 and 2017/2018) and 90% (2014/2015 and 2015/2016) of the 82 days of the nesting period. Mean daily minimum temperature of the four breeding periods was 6.05 ± 0.52 °C, and there were minimum temperatures below 0 °C during 1–5 days per breeding period. Mean daily wind speed was 6.4 ± 0.4 km/h. During those days with the highest mean wind speed (> 13 km/h), gusts were ≥ 40 km/h.

Clutch size did not vary among the studied breeding seasons (zero-truncated Poisson regression: $\chi^2_{3,57} = 2.330$, $P = 0.507$). The daily number of active nests was higher towards the middle of the Chilean Elaenia breeding season (Fig. 1).

Daily survival rate of nests

Nest survival analysis was based on 86 nests, representing 1363 exposure days. Mean \pm SE DSR for the four breeding seasons was 0.960 ± 0.005 (95% CI 0.948, 0.969), corresponding to an overall nest success estimate of 29.5% (Fig. 2).

Fig. 1 Daily variation of the number of active Chilean Elaenia nests during the period of nest monitoring (12 December–3 March) in each breeding season in the forest-steppe ecotone at Cañadón Florido Ranch, Chubut Province, Argentina

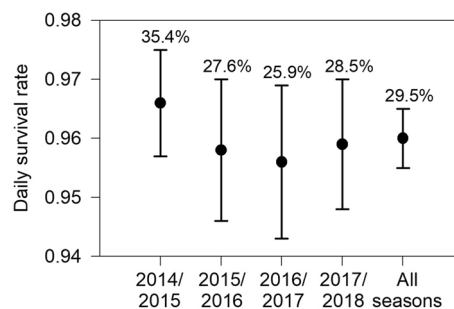
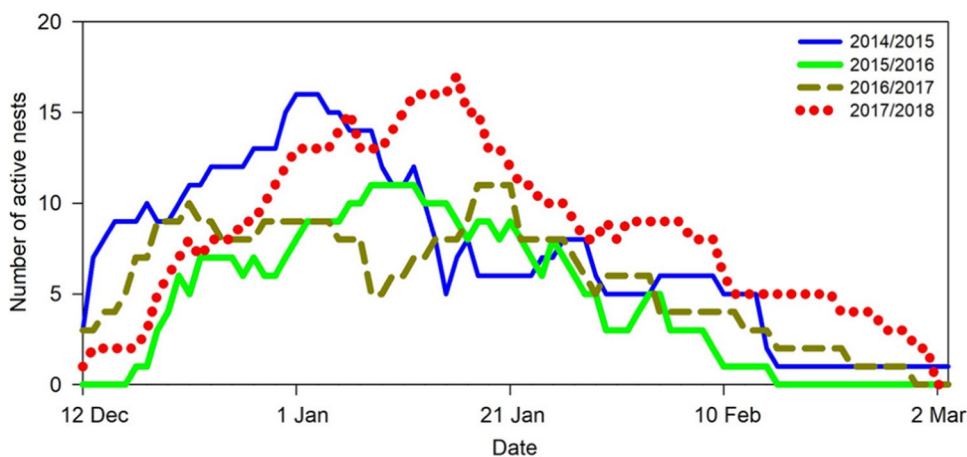


Fig. 2 Daily survival rate of Chilean Elaenia nests and overall nest success (%) during each breeding season and for all seasons pooled in the forest-steppe ecotone at Cañadón Florido Ranch, Chubut Province, Argentina

During the first step of model selection, Julian day was the variable that best explained DSR (Table S2). There were no additive or multiplicative effects of year and Julian day, nor an effect of year on DSR (Table S2). The univariate model of number of active nests was better than the constant model (Table S2). The univariate model of nest age was as supported as the constant model, while the model composed of clutch size was competitive (Table S2). Minimum temperature, a daily precipitation event of ≥ 10 mm, and a precipitation event of ≥ 10 mm on the previous day were competitive variables (Table S2).

In the second step of model selection, none of all possible additive models combining Julian day, number of active nests and nest age were better than the univariate model of number of active nests (Table 1). In the third step, only the addition of the competitive variable daily precipitation event ≥ 10 mm produced a model with a lower AICc (Table 1). DSR increased with the number of active nests ($\beta = 0.111$, SE = 0.045, 95% CI 0.022, 0.200; Fig. 3) and was not associated with the daily precipitation event of ≥ 10 mm ($\beta = -0.031$, SE = 0.018, 95% CI $-0.067, 0.004$).

Table 1 Daily nest survival models of the Chilean *Elaenia* in the forest-steppe ecotone at Cañadón Florido Ranch, Chubut Province, Argentina

Candidate models	K	ΔAICc	w_i
Number of active nests + daily precipitation event of ≥ 10 mm	3	0.000	0.293
Number of active nests	2	0.809	0.195
Julian day	2	2.752	0.074
Constant model	1	3.682	0.046
Nest age	2	3.731	0.045
Year \times number of active nests	8	3.828	0.043
Clutch size	2	4.006	0.040
Minimum temperature	2	4.044	0.039
Daily precipitation event of ≥ 10 mm	2	4.087	0.038
Precipitation event of ≥ 10 mm on the previous day	2	4.674	0.028
Nest age + nest age ²	3	4.796	0.027
Mean wind speed	2	5.120	0.023
Nest age + nest age ² + nest age ³	4	5.526	0.018
Mean wind speed + mean wind speed ²	3	6.398	0.012
Year + Julian day	5	8.265	0.005
Year	4	9.146	0.003
Year \times clutch size	5	9.924	0.002
Year \times Julian day	8	10.754	0.001
Year \times minimum temperature	8	12.954	0.000
Year \times daily precipitation event of ≥ 10 mm	8	14.267	0.000
Year \times mean wind speed	8	14.832	0.000
Year \times nest age	8	15.303	0.000
Year \times precipitation event of ≥ 10 mm on the previous day	8	15.660	0.000
Year \times (mean wind speed + mean wind speed ²)	12	21.020	0.000
Year \times (nest age + nest age ²)	12	21.977	0.000
Year \times (nest age + nest age ² + nest age ³)	16	24.025	0.000

All models include an intercept; K is the number of parameters in the model; ΔAICc is the difference between the AICc of the candidate model and the AICc of the best model, which is 442.435; w_i is the Akaike weight of the model

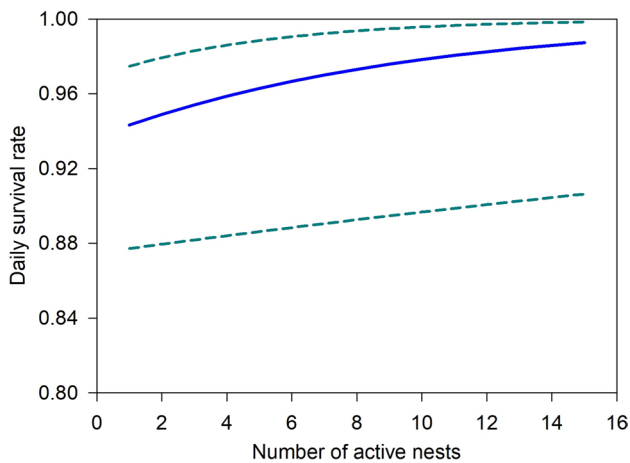


Fig. 3 Daily survival rate of Chilean *Elaenia* nests as a function of the number of active nests, using the range of nests observed daily in the forest-steppe ecotone at Cañadón Florido Ranch, Chubut Province, Argentina. Estimates were made according to the logistic-regression equation of the top model and considering days without precipitation events (Table 1). Dashed lines indicate the 95% confidence interval of the estimated daily nest survival rate

Discussion

In accordance with the “predator dilution effect hypothesis” (Dehn 1990; Duca et al. 2019), we found that DSR of Chilean *Elaenia* nests increases with the number of active nests. Conversely, we did not observe here the pattern predicted by the “predator search image hypothesis” (i.e., a reduction of DSR as the breeding season progresses, Dukas 2002). Because in our study site resident and short-distance migratory species begin breeding earlier than Chilean *Elaenia* (Cueto and Gorosito 2018), predators would already have a search image focused on eggs and nestlings before the beginning of the Chilean *Elaenia* breeding period. Consequently, nests of the Chilean *Elaenia* are immediately potential prey items, but their great increase in number towards mid-season may be producing a predator dilution effect.

Contrary to expectations, parental investment of the Chilean *Elaenia* (evaluated through clutch size and nest age) did not affect DSR. Commonly, nest survival decreases as clutch size increases due to greater parental activity around the nest

during the incubation (Nord and Williams 2015) and nestling stages (Sousa and Marini 2013). This effect on DSR is evident in species with a large clutch (e.g., > 4 eggs, Moreno and Sanz 1994) and brood size (e.g., comparing broods of 1 to 10 nestlings, Rytkönen et al. 1996). Conversely, clutch and brood sizes of the Chilean *Elaenia* are small (1–3 eggs/nestlings) and not very variable (Gorosito et al. 2022). Additionally, an effect of clutch size on DSR might be highly probable if most nest predators follow visual cues (e.g., birds). However, in our study site rodents are important nest predators (e.g., *Irenomys tarsalis*, SP Bravo and VR Cueto unpubl. data) that follow olfactory cues. Although we had not established the proportion of nests preyed by rodents, some of them use the shrub stratum for nesting and foraging (e.g., see Formoso and Sanchez 2014), and this vegetation layer is also used by Chilean *Elaenias* for breeding (Gorosito 2020). Consequently, rodents might contribute as much as birds to nest predation of this passerine.

Although intensity of parental activity differs among nestling stages (Grant et al. 2005), we did not find any effect of nest age on DSR. Predation rate is similar across nestling stages when there are active nests in both exposed and hidden sites (Martin et al. 2000). As nests in exposed sites are usually predated early during incubation, the effect of greater predation during the nestling stage is counteracted (Martin et al. 2000). Indeed, Chilean *Elaenias* built nests in places with different degrees of exposure, both in sites with high vegetation cover and in exposed sites with little vegetation (Gorosito 2020); therefore, this could have contributed to the fact that nest predation did not vary between nesting stages.

Here, we did not find any association between climatic variables and DSR. Unlike other studies (Skagen and Yackel Adams 2012; Ruth and Skagen 2018), precipitation had no effect on DSR, which may be attributable to the scarcity of rain events during the studied breeding seasons. In addition, we did not find that DSR decreases as minimum temperature decreases. Chilean *Elaenias* build thick-walled nests with abundant material and line the interior with feathers (Gorosito et al. 2022), which might maintain suitable thermal conditions for eggs and nestlings despite low environmental temperatures. Accordingly, parents would be able to make fewer and longer lasting foraging trips, reducing the detectability of the nest. Our results also showed no relationship between wind speed and DSR. At the study site, mean wind speed was outside the range of those wind speeds that are expected to have an effect on attracting predators (i.e., 7.2–14.4 km/h, Ruzicka and Conover 2011). In addition, the gusts in the area would dissipate odours and make it difficult for predators to detect nests through olfactory cues.

In this study, we provided empirical support to the “predator dilution effect hypothesis”. Such effect is a consequence of the great abundance of Chilean *Elaenia* nests

in the forest, which arises from the short breeding season of this passerine (Gorosito et al. 2022). This species begins to breed when fleshy fruits start to ripen, in such a way that the timing of egg hatching matches the timing of highest ripe fruit abundance (Gorosito et al. 2023). Consequently, the abundance of active Chilean *Elaenia* nests increases towards mid-season, increasing DSR, and thus the predator dilution effect may be a by-product of the aforementioned association between breeding and food. As shown here, by considering nest abundance it is possible to comprehensively understand a temporal pattern of variation in DSR other than seasonal decrease or increase in nest survival. Therefore, the predator dilution effect could be an important factor affecting nesting success and should be taken into account in studies that evaluate avian nest survival.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-023-02086-4>.

Acknowledgements We thank the Roberts family for allowing us to work at Cañadón Florido Ranch. We thank Alex Jahn for his comments and for improving English syntax and grammar of our paper. We also thank Will Cresswell and another anonymous reviewer for their comments and suggestions, which greatly enhanced this paper.

Author contributions All authors contributed to the study conceptualization. CAG and VRC design the study and acquired funding. Project administration was performed by CAG and VRC. Data collection, curation and analysis were performed by CAG. All authors provided resources (study materials and computing resources). CAG wrote the first draft of the manuscript. All authors revised the manuscript, contributed with writing and approved the final manuscript.

Funding This research was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET-Argentina). VRC received financial support from the National Geographic Society (GN 9289-13). CAG received the Bergstrom Award (USA, 2015) from the Association of Field Ornithologists and the François Vuilleumier Fund (USA, 2017) from the Neotropical Ornithological Society.

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Field work was conducted with permission of Dirección de Fauna y Flora Silvestre, Ministerio de Desarrollo Territorial y Sectores Productivos de la Provincia del Chubut, Argentina.

References

- Arnold TW (2010) Uninformative parameters and model selection using Akaike’s Information Criterion. *J Wildl Manag* 74:1175–1178. <https://doi.org/10.2193/2009-367>

- Borgmann KL, Conway CJ, Morrison ML (2013) Breeding phenology of birds: mechanisms underlying seasonal declines in the risk of nest predation. *PLoS ONE* 8:e65909
- Bravo SP, Cueto VR, Gorosito CA (2017) Migratory timing, rate, routes and wintering areas of White-crested Elaenia (*Elaenia albiceps chilensis*), a key seed disperser for Patagonian Forest regeneration. *PLoS ONE* 12:e0170188. <https://doi.org/10.1371/journal.pone.0170188>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Canevari M, Vaccaro O (2007) Guía de mamíferos del sur de América del Sur. L.O.L.A., Buenos Aires
- Coleman RM, Whittall RD (1988) Clutch size and the cost of incubation in the Bengalese Finch (*Lonchura striata* var. *domestica*). *Behav Ecol Sociobiol* 23:367–372
- Conover MR (2007) Predator–prey dynamics: the role of olfaction. CRC Press, Taylor & Francis Group, Boca Raton, London
- Conrey RY, Skagen SK, Yackel Adams AA, Panjabi AO (2016) Extremes of heat, drought and precipitation depress reproductive performance in shortgrass prairie passerines. *Ibis* 158:614–629. <https://doi.org/10.1111/ibi.12373>
- Cooch EG, White GC (2019) Program MARK: a gentle introduction. 19th edn. <http://www.phidot.org/software/mark/docs/book/>. Accessed 30 August 2019
- Cooper CB, Voss MA (2013) Avian incubation patterns reflect temporal changes in developing clutches. *PLoS ONE* 8:e65521. <https://doi.org/10.1371/journal.pone.0065521>
- Cueto VR, Gorosito CA (2018) Seasonal changes in bird assemblages of a forest-steppe ecotone in North Patagonia. *Ornitol Neotrop* 29:349–358
- Dehn MM (1990) Vigilance for predators: detection and dilution effects. *Behav Ecol Sociobiol* 26:337–342
- Dinsmore SJ, Dinsmore JJ (2007) Modeling avian nest survival in program MARK. *Stud Avian Biol* 34:73–83
- Dinsmore SJ, White GC, Knopf FL (2002) Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488. [https://doi.org/10.1890/0012-9658\(2002\)083\[3476:ATFMAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3476:ATFMAN]2.0.CO;2)
- Duca C, Brunelli WA, Doherty PF (2019) Predator search image and the dilution effect: When is the best time to nest? *Auk* 136:1–7. <https://doi.org/10.1093/auk/ukz009>
- Dukas R (2002) Behavioural and ecological consequences of limited attention. *Philos Trans R Soc B* 357:1539–1547. <https://doi.org/10.1098/rstb.2002.1063>
- Formoso AE, Sánchez JP (2014) First description of the breeding nest of *Irenomys tarsalis*, a sigmodontine rodent endemic to southern Andean forests. *Rev Mex Biodivers* 85:987–989. <https://doi.org/10.7550/rmb.44050>
- Gorosito CA, Tuero DT, Cueto VR (2022) Breeding biology of the Chilean Elaenia *Elaenia chilensis*, a long-distance migratory passerine in South America. *Ardea* 110:227–238. <https://doi.org/10.5253/arde.2022.a8>
- Gorosito CA, Tuero DT, Cueto VR (2023) Fruit abundance may fine-tune timing of reproduction of the Chilean Elaenia (*Elaenia chilensis*), a long-distance migratory bird in South America. *Ibis*. <https://doi.org/10.1111/ibi.13196>
- Gorosito CA (2020) Determinantes del éxito reproductivo de *Elaenia albiceps* (Aves: Tyrannidae) en bosques andino-patagónicos. PhD thesis, Universidad de Buenos Aires
- Grant TA, Shaffer TL, Madden EM, Pietz PJ (2005) Time-specific variation in passerine nest survival: new insights into old questions. *Auk* 122:661–672. <https://doi.org/10.1093/auk/122.2.661>
- Gutzwiller KJ (1990) Minimizing dog-induced biases in game bird research. *Wildl Soc Bull* 18:351–356
- Ibáñez-Álamo JD, Magrath RD, Oteyza JC, Chalfoun AD, Haff TM, Schmidt KA, Thomson RL, Martin TE (2015) Nest predation research: recent findings and future perspectives. *J Ornithol* 156(Suppl 1):247–262. <https://doi.org/10.1007/s10336-015-1207-4>
- Ishii Y, Shimada M (2010) The effect of learning and search images on predator–prey interactions. *Popul Ecol* 52:27–35. <https://doi.org/10.1007/s10144-009-0185-x>
- Martin TE, Geupel GR (1993) Nest-monitoring plots: methods for locating nests and monitoring success. *J Field Ornithol* 64:507–519
- Martin TE, Scott J, Menge C (2000) Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc Royal Soc B* 267:2287–2293. <https://doi.org/10.1098/rspb.2000.1281>
- Menezes JCT, Marini MÁ (2017) Predators of bird nests in the Neotropics: a review. *J Field Ornithol* 88:99–114. <https://doi.org/10.1111/jof.12203>
- Moreno J, Sanz JJ (1994) The relationship between the energy expenditure during incubation and clutch size in the Pied Flycatcher *Ficedula hypoleuca*. *J Avian Biol* 25:125–130. <https://doi.org/10.2307/3677030>
- Morrone JJ (2001) Biogeografía de América Latina y el Caribe. Manuales & Tesis de la Sociedad Entomológica Aragonesa, Zaragoza
- Nord A, Williams JB (2015) The energetic costs of incubation. In: Deeming DC, Reynolds SJ (eds) Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, Oxford, pp 152–170
- Ralph CJ, Geupel GR, Pyle P, Martin TE, DeSante DF, Milá B (1996) Manual de métodos de campo para el monitoreo de aves terrestres. Gen. Tech. Rep. PSW-GTR-159. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany (CA)
- Rastogi AD, Zanette L, Clinchy M (2006) Food availability affects diurnal nest predation and adult antipredator behaviour in song sparrows, *Melospiza melodia*. *Anim Behav* 72:933–940. <https://doi.org/10.1016/j.anbehav.2006.03.006>
- Redmond LJ, Murphy MT, Dolan AC, Sexton K (2009) Parental investment theory and nest defense by Eastern Kingbirds. *Wilson J Ornithol* 121:1–11. <https://doi.org/10.1676/07-166.1>
- Remeš V, Matysioková B, Cockburn A (2012) Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. *J Avian Biol* 43:435–444. <https://doi.org/10.1111/j.1600-048X.2012.05599.x>
- Reneerkens J, Grond K, Schekkerman H, Tulp I, Piersma T (2011) Do uniparental sanderlings *Calidris alba* increase egg heat input to compensate for low nest attentiveness? *PLoS ONE* 6:e16834. <https://doi.org/10.1371/journal.pone.0016834>
- Rotella J (2019) Nest survival models. In: Cooch EG, White GC (eds) Program MARK: a gentle introduction, pp 17.1–17.19
- Ruth JM, Skagen SK (2018) Reproductive response of Arizona Grasshopper Sparrows to weather patterns and habitat structure. *Condor* 120:596–616. <https://doi.org/10.1650/CONDOR-17-128.1>
- Ruzicka RE, Conover MR (2011) Influence of wind and humidity on foraging behavior of olfactory mesopredators. *Can Field Nat* 125:132–139. <https://doi.org/10.22621/cfn.v125i2.1196>
- Rytönen S, Koivula K, Orell M (1996) Patterns of per-brood and per-offspring provisioning efforts in the Willow Tit *Parus montanus*. *J Avian Biol* 27:21–30. <https://doi.org/10.2307/3676957>
- Segura LN, Reboreda JC (2012) Nest survival rates of Red-crested Cardinals increase with nest age in south-temperate forests of Argentina. *J Field Ornithol* 83:343–350. <https://doi.org/10.1111/j.1557-9263.2012.00384.x>
- Shaffer TL (2004) A unified approach to analyzing nest success. *Auk* 121:526–540. <https://doi.org/10.1093/auk/121.2.526>
- Sherry TW, Wilson S, Hunter S, Holmes RT (2015) Impacts of nest predators and weather on reproductive success and population

- limitation in a long-distance migratory songbird. *J Avian Biol* 46:559–569. <https://doi.org/10.1111/jav.00536>
- Skagen SK, Yackel Adams AA (2012) Weather effects on avian breeding performance and implications of climate change. *Ecol Appl* 22:1131–1145. <https://doi.org/10.1890/11-0291.1>
- Smith PA, Wilson S (2010) Intra-seasonal patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia* 163:613–624. <https://doi.org/10.1007/s00442-010-1644-y>
- Sousa NOM, Marini MÂ (2013) A negative trade-off between current reproductive effort and reproductive success: an experiment with clutch-size in a tropical bird. *Emu* 113:8–18. <https://doi.org/10.1071/MU111102>
- Stahl JT, Oli MK (2006) Relative importance of avian life-history variables to population growth rate. *Ecol Model* 198:23–39. <https://doi.org/10.1016/j.ecolmodel.2006.04.001>
- Vazquez MS, Rodríguez-Cabal MA, Gonzalez DV, Pacheco GS, Amico GC (2018) Different nest predator guild associated with egg size in the Patagonian temperate forest. *Bird Study* 65:478–483. <https://doi.org/10.1080/00063657.2018.1555572>
- Verboven N, Tinbergen JM (2002) Nest desertion: a trade-off between current and future reproduction. *Anim Behav* 63:951–958. <https://doi.org/10.1006/anbe.2001.1971>
- Webb SL, Olson CV, Dzialak MR, Harju SM, Winstead JB, Lockman D (2012) Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human-altered environments. *Ecol Process* 1:4. <https://doi.org/10.1186/2192-1709-1-4>
- Weiser EL (2021) Fully accounting for nest age reduces bias when quantifying nest survival. *Ornithol Appl* 123:duab030. <https://doi.org/10.1093/ornithapp/duab030>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.