





Fruit abundance may fine-tune timing of reproduction of the Chilean Elaenia (*Elaenia chilensis*), a long-distance migratory bird in South America

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Timing of reproduction has a great impact on the breeding success of birds because a mismatch with the moment when environmental conditions are warm or when food is most plentiful can reduce nestling survival and increase the energetic cost of parental care. Consequently, birds synchronize gonadal maturation with the most favourable environmental conditions, using photoperiod changes throughout the year as an initial proximal cue. Additionally, non-photic cues, such as temperature and food abundance, may be necessary to fine-tune reproductive timing. However, the influence of non-photic cues on finely tuning reproductive timing is not yet fully understood for migratory birds. Here, we evaluate how much non-photic cues influence the reproductive timing of the Chilean Elaenia *Elaenia chilensis*, a long-distance migrant that reproduces in the Andean–Patagonian Forest. We assessed associations of mean temperature, ripe fruit and arthropod abundances with the number of nests in the laying period, and also with the number of nests with hatchlings. In both analyses we used cross-correlations and partial least squares path modelling. Mean temperature was not consistently associated with the breeding phenology of Chilean Elaenias. The increase in number of nests in the laying period was preceded by the increase in caterpillar abundance and coincided with the increase in ripe fruit abundance. The timing of nests with hatchlings matched with the timing of highest ripe fruit abundance. Both types of food could contribute to the beginning of reproduction of birds and be used as proximal cues by Chilean Elaenias. Ripe fruits would also be beneficial for nestling growth because parents feed them with fruits, and might potentially play an ultimate role in reproduction. Because ripe fruit abundance was related to the egg-laying and hatching stages, it may be the main cue used by Chilean Elaenias to fine-tune reproductive timing. These findings allow advances in our understanding of the importance of non-photic cues in the reproductive phenology of migratory birds and also generalize our knowledge among regions and taxa, as most studies on this topic focus on the Northern Hemisphere.

Keywords: Andean–Patagonian Forest, caterpillars, food availability hypothesis, Neotropical austral migrant, non-photic cues, ripe fruits.

Timing of reproduction has a great impact on breeding success (Wann *et al.* 2019). Consequently, birds

must time their gonadal growth to coincide with favourable environmental conditions, for which they use specific environmental cues (Ball & Ketterson 2008). These cues may play a proximate role by stimulating birds physiologically to initiate egg

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production and also may play an ultimate role by causing differential fitness during the breeding period (Ball & Ketterson 2008).

The lengthening of photoperiod is considered the initial predictive cue for the beginning of reproduction in many temperate zone breeding birds (Wingfield & Farner 1980). Long photoperiods activate the hypothalamic–pituitary–gonadal (HPG) axis, triggering the release of hormones and stimulating gonadal growth (Dawson *et al.* 2001). Thus, photostimulation prepares and maintains the reproductive activity of birds (Ball & Ketterson 2008). Subsequently, shortening of the photoperiod has the opposite effect, inducing an inhibitory process that causes the regression of the gonadal portion of the HPG axis, resulting in the completion of reproduction (Ball & Ketterson 2008).

However, temperate zone birds can achieve greater reproductive success by complementing the photoperiod stimulus with environmental non-photic cues (Nadolski *et al.* 2021). This allows them to fine-tune timing of reproduction (i.e. modify both the onset and termination dates of breeding determined by photostimulation; Hällfors *et al.* 2020) in step with local (Caro *et al.* 2009) and year-to-year fluctuations in environmental conditions (Wesołowski *et al.* 2021). For instance, experimental studies have shown that high temperatures can influence the growth of gonads (Wingfield *et al.* 2003), advance egg-laying (Visser *et al.* 2009) and have an effect on the regression of gonads (Wingfield *et al.* 2003). Therefore, temperature may influence fitness. Females that reproduce during warm periods experience low daily energy expenditure, which might be due to reduced thermoregulatory requirements (Stevenson & Bryant 2000). Consequently, they lay bigger eggs (Stevenson & Bryant 2000), resulting in heavier hatchlings (Whittingham *et al.* 2007). Moreover, during warm periods, nestlings experience greater growth rates and survival than during cold or hot periods (Winkler *et al.* 2013, Corregidor-Castro & Jones 2021), as they can allocate fewer energy resources to thermoregulation (Sauve *et al.* 2021). As a result, heavier fledglings showed higher recruitment rates (Monrós *et al.* 2002). Alternatively, temperature may act as a cue that indicates the approach of favourable environmental conditions, rather than being a constraint on egg formation (Visser *et al.* 2009).

Birds can also use food abundance as a reliable non-photic cue to fine-tune timing of reproduction

(Dunn & Winkler 2010). Food as a cue can have a short-term effect on the ability of adults to invest in gonadal growth and egg formation in income breeder species (i.e. birds that make their reproductive investment using the food consumed immediately before egg-laying; Drent & Daan 1980). For instance, an experimental study showed that gonadal growth of males was not noticeable during long photoperiods if food was restricted (Hahn 1995). Besides, food can act as a selective agent, because if reproduction begins when there is not enough food to raise young, offspring survival can be significantly reduced (Zhang *et al.* 2020). Additionally, a mismatch with the moment when food is most plentiful can drive breeding birds to go through a high energetic cost and workload associated with increased foraging effort to provision nestlings, consequently reducing adult survival (Thomas *et al.* 2001). In accordance with this, some studies have reported that birds synchronize timing of reproduction with the timing of maximum food abundance (Caro *et al.* 2009, Hajdasz *et al.* 2019).

How birds respond to non-photic cues would also depend on their migratory behaviour (Chmura *et al.* 2019). The responsiveness to non-photic cues is expected to be lower in long-distance migratory species than in short-distance migratory and resident species, because these last two are closer to breeding grounds and their cue-response systems may be more reactive to local environmental conditions (Chmura *et al.* 2019). In contrast, there is evidence that long-distance migrants already start gonadal development during spring migration in anticipation of the upcoming breeding period (Quay 1985, Ramenofsky & Wingfield 2006, Cueto *et al.* 2016b), and thereby they would rely primarily on photoperiodic cues and would have low gonadal response to other types of cues (Gwinner 1996). Hence, it is important to evaluate how much non-photic cues may contribute to fine-tune reproductive timing of long-distance migratory species because this knowledge allows us to make predictions about how climate change could affect their populations (Both *et al.* 2010). For example, climate change may advance the phenology of food resources on breeding grounds and, consequently, food resources required to raise young would be scarce when migratory birds are breeding, resulting in population declines (Both *et al.* 2006).

Here we studied the timing of reproduction of the Chilean Elaenia *Elaenia chilensis* (Gill *et al.* 2022), a

long-distance Neotropical austral migrant that breeds in the Andean–Patagonian Forest (Bravo *et al.* 2017). The reproductive phenology of this species makes it a good model to analyse what environmental cues may be influencing its reproduction: almost 40 days pass between the arrival of the first female to the breeding grounds and the first egg-laying date (Gorosito *et al.* 2022). Because this long period of time could allow Chilean Elaenias to track changes in climatic conditions and food abundance, similarly to short-distance migratory and resident species, non-photic cues might be influencing the breeding phenology of this long-distance migrant more than expected. Therefore, our aim was to evaluate the relative contribution of non-photic cues to fine-tune reproductive timing of the Chilean Elaenia. Considering that low temperatures are common during spring (Paruelo *et al.* 1998) and that there is a seasonality of food resources in the Patagonian forest (Dzendoletas *et al.* 2003, Gönc 2013), we hypothesized that Chilean Elaenias rely on non-photic cues to begin egg-laying. We predicted that the number of nests in the laying period would increase in response to increased mean temperature and food abundance. Furthermore, taking into account the ‘food availability hypothesis’, which indicates that birds should breed when food is abundant to raise young (Lack 1954), we also hypothesized that Chilean Elaenias rely on non-photic cues to match the timing of egg-hatching with the timing of maximum food abundance. We predicted that the increase in the number of nests with hatchlings would be associated with the timing of greatest food abundance. Finally, considering that climate in the Andean–Patagonian Forest is cool-temperate (Paruelo *et al.* 1998), and that low temperatures may reduce growth and survival of nestlings (Sauve *et al.* 2021), we hypothesized that Chilean Elaenias use non-photic cues to match the timing of egg-hatching with the timing of the most suitable thermal environmental conditions. We predicted that the increase in the number of nests with hatchlings would be associated with the timing of the highest mean temperatures.

METHODS

Study site

We carried out our study at the Cañadón Florido Ranch (42°55′35″S, 71°21′53″W, 616 m.a.s.l., Fig. S1), Chubut Province, Argentina. The vegetation of the area corresponds to the Valdivian

Forest Province of the Andean Region (Morroni 2001). The forest at the study site is dominated by *Maytenus boaria* and *Schinus patagonicus* trees. The canopy is low, averaging 5 m in height, and the understorey is dominated by *Berberis microphylla* shrubs. This forest is part of the Patagonian forest-steppe ecotone (Kitzberger 2012). Winters are cold and wet, and summers are warm and dry. Annual mean precipitation in the area is 704 mm and falls as rain and snow mainly between April and September (autumn–winter). Summer and winter mean temperatures are 13.4 and 1.8°C, respectively. 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.)

Study species

The taxonomic status of the Chilean Elaenia is complex and the species-level classification remains contentious (Pearman & Areta 2020). Therefore, we have adopted the taxonomy of the IOC World Bird List (Gill *et al.* 2022). *Elaenia chilensis* is the same species as *Elaenia albiceps chilensis* of Billerman *et al.* (2020) and Clements *et al.* (2021).

The Chilean Elaenia (Fig. S1) is the most abundant bird species during spring–summer in the Andean–Patagonian Forest (Cueto & Gorosito 2018). Males begin to arrive in the forest from mid-October (Bravo *et al.* 2017, Cueto & Gorosito 2018), and females from early November (Cueto & Gorosito 2018, Gorosito 2020). Adults begin autumn migration to Brazil between mid- and late February (Bravo *et al.* 2017, Cueto & Gorosito 2018), although occasionally some of them are present in breeding grounds until early March (Cueto & Gorosito 2018, Gorosito 2020).

The nesting period is between early December and late February (Gorosito *et al.* 2022). This species builds open-cup nests and lays 1–3 eggs (modal clutch size = 2 eggs) every other day (Gorosito *et al.* 2022). Its incubation and nestling periods last ~14 days each (Gorosito *et al.* 2022). Females do not double-brood, but lay a replacement clutch when the first reproductive attempt fails (Gorosito *et al.* 2022). Overall nest success is 29.5%, and predation is the main cause of nest failure (Gorosito *et al.* 2022). Successful nests fledge on average 1.7 chicks (Gorosito *et al.* 2022).

The Chilean *Elaenia* is an omnivorous species that consumes fruits (e.g. of *Aristotelia chilensis*, *B. microphylla*, *Drymis winteri*, Amico & Aizen 2005, Brown *et al.* 2007) and arthropods (e.g. Coleoptera, Hymenoptera, Lepidoptera, Muñoz *et al.* 2017; Araneae, Diptera, Hemiptera, Brown *et al.* 2007). The diet of nestlings in our study site consisted of *B. microphylla* fruits and arthropods (Gorosito *et al.* 2022).

Nest searching

We searched for nests daily from late November to late February during three breeding seasons (2015/2016–2017/2018) following the method proposed by Martin and Geupel (1993). Nest search effort was the same among years and throughout each breeding season. We monitored nests daily by recording dates of egg-laying, incubation onset and egg-hatching. We visited nests until nesting was successful (i.e. at least one nestling left the nest) or failed. We defined the variable ‘nests in the laying period’ as those nests when eggs were being laid. We determined the beginning of this period when the first egg in the nest was laid and its end when eggs were warm. Additionally, we estimated the dates of the laying period backwards using the mean duration of incubation and nesting stages (Gorosito *et al.* 2022) in case we had found the nest after egg-laying. We defined the variable ‘nests with hatchlings’ as those nests where eggs had just hatched (i.e. nests with 0-day-old nestlings). We determined the hatching date from daily nest monitoring or by estimating this date backwards when we found the nest after egg-hatching, considering the estimated average weight of nestlings according to their age (C. A. Gorosito unpubl. data).

Climatic and food abundance data collection

We used daily values of mean temperature recorded in the Río Percey meteorological station (Hidroeléctrica Futaleufú S.A.). Data were collected for the period October–March of each breeding season. Although precipitation may play proximate (Hidalgo Aranzamendi *et al.* 2019) and ultimate roles in reproduction (Schöll & Hille 2020), we did not consider it as a possible non-photic cue influencing breeding phenology in our study site because it is low and inconsistent throughout the breeding season (Fig. S2).

During October–March we sampled the abundance of ripe fleshy fruits (mean diameter = 9.8 ± 1.0 mm, mean weight = 0.6 ± 0.1 g, $n = 80$ fruits) of 10 individuals of *B. microphylla* distributed throughout the study area. We monitored the same individuals during all breeding seasons. We selected this shrub species because it is the only one that fructifies during the breeding period of Chilean *Elaenias* in our study area (Gorosito 2020). We considered that a fruit was ripe when at least 50% of its skin surface was purple (i.e. physiological maturity, Arena *et al.* 2013a), which also coincides with the moment when Chilean *Elaenias* began to eat *B. microphylla* fruits (C. A. Gorosito pers. obs.). Once a week we estimated ripe fruit abundance per plant using a semiquantitative scale based on Saracco *et al.* (2004), as follows: 0 = without ripe fruits, 1 = 1–10 ripe fruits, 2 = 11–50 ripe fruits, 3 = 51–100 ripe fruits, 4 = 101–500 ripe fruits, 5 = 501–1000 ripe fruits, 6 = 1001–5000 ripe fruits, 7 = 5001–10 000 ripe fruits, and 8 = >10 000 ripe fruits. Because the mean value of the categories would not be informative of the mean value of fruit abundance (i.e. it is not possible to assign a numerical value of fruit supply to a mean value of 5.3 on the scale used), we transformed the value of the abundance category of each plant into the mean value corresponding to the range of each category (e.g. an individual with an abundance category 4 was assigned a mean abundance of 300 ripe fruits, whereas an individual from category 8 was assigned a mean abundance of 10 001 ripe fruits). Then, we estimated a weekly mean value of ripe fruit abundance per plant.

We estimated arthropod abundance on the two dominant woody plant species at the study site (*B. microphylla* and *M. boaria*, Gorosito 2020) every 10 days from October to March of each breeding season. During each sampling, we randomly selected 15 individuals of each woody plant species throughout the entire study area. We used the beating method (Cooper & Whitmore 1990) to collect arthropods in a plastic tray ($60 \times 40 \times 6$ cm), which had a 5.2-cm-diameter hole in the base connected to a 100-cm³ plastic jar where arthropods were held and euthanized with an insecticide. To evaluate the abundance of arthropods eaten by Chilean *Elaenias*, we considered only those individuals that were longer than 1 mm, because this is the minimum prey size consumed by other Neotropical passerines of similar size (e.g. *Myiothlypis leucoblephara*, Manhães *et al.* 2015; *Stigmatura*

budytoides, Guerra Navarro 2016). Because the main foraging manoeuvre of Chilean *Elaenias* is sally-hovering (i.e. when a flying bird takes prey items from the surface of a substrate, Cueto *et al.* 2016a), we divided arthropod abundance into foliage arthropods (including Orders Coleoptera, Araneae, Hemiptera, Isoptera, Ortoptera, Dermaptera and Plecoptera, the Family Formicidae and the Subclass Acari) and flying arthropods (including Orders Diptera and Hymenoptera). Considering that it is common for birds to feed their nestlings with soft prey (e.g. caterpillars, García-Navas & Sanz 2011), we counted the abundance of caterpillars separately from foliage arthropod abundance. We estimated the mean abundance of each group of arthropods per plant for each sample.

Statistical analysis

We divided each month into three 10-day periods, from November (when both male and female Chilean *Elaenias* have arrived at the study area, Bravo *et al.* 2017, Cueto & Gorosito 2018) to late February (when the last active nests are found, Gorosito *et al.* 2022), according to the frequency of sampling of arthropod abundance, in such a way that sampling dates fell in the middle of these 10-day periods. We included the pre-reproductive period of 40 days (from early November to early December) because Chilean *Elaenias* might be following environmental cues during this period to fine-tune reproductive timing. We used the number of nests in the laying period and the number of nests with hatchlings in each 10-day period as response variables to identify which non-photic cues may influence each variable independently, allowing us to interpret their possible roles as proximate and ultimate factors in reproduction. We used the mean values of mean temperature, number of ripe fruits per plant, number of caterpillars per plant, number of foliage arthropods per plant and number of flying arthropods per plant during each 10-day period as predictor variables. Because ripe fruit abundance was sampled once a week, in only three cases/year was the mean of two consecutive samplings used to obtain values for those 10-day periods.

The predictor and response variables constitute time series. As a consequence, the data have an order and the use of cross-correlations allows identifying lags between a predictor and a response variable (Crawley 2007). When the lag is negative,

changes of the X series occur before changes of the Y series for as many time periods as indicated by the lag, and the opposite pattern is observed when the lag is positive (Crawley 2007). We performed cross-correlations between each predictor and response variable for each breeding season separately to find the lags between them and determine which non-photic cues were consistently correlated with the number of nests in the laying period or the number of nests with hatchlings across breeding seasons. We considered positive cross-correlations (i.e. the predictive and response variables increase or decrease together) with lags ≤ 0 because we wanted to know which environmental cues predicted the number of nests in the laying period and the number of nests with hatchlings. In this way, a predictive variable with lag = 0 reaches its maximum during the same 10-day period as the response variable. Then, a predictive variable with lag = -1 reaches its maximum during the period that includes 1–10 days before the 10-day period in which the response variable reaches its maximum, and a predictive variable with lag = -2 reaches its maximum during the period that includes 11–20 days before, and so on. We also used positive cross-correlations with lag = 1; in this case both variables begin to increase simultaneously or the predictive variable increases before the response variable, but this latter reaches its maximum first. Thus, a predictive variable with lag = 1 reaches its maximum during the period that includes 1–10 days after the 10-day period in which the response variable reaches its maximum. We discarded cross-correlations with lags > 1 because the highest values of reproductive variables would have occurred long before the highest values of predictive environmental cues. When a predictor variable was significant (i.e. $P \leq 0.05$) or approached significance (i.e. $0.05 < P \leq 0.10$) (Murtaugh 2014) through more than one lag, we selected that predictor variable with the lag which produced the highest correlation. The use of correlations approaching significance was solely as part of the predictor selection process, and in subsequent modelling we only took into account significant variables.

We used the selected predictor variables from the cross-correlation analyses to perform Partial Least Squares Path Modelling (PLS-PM, Sanchez 2013), which allowed us to assess the potential effects of the environmental cues on the number of nests in the laying period and the

number of nests with hatchlings during each breeding season. The PLS-PM approach is insensitive to heteroscedasticity and autocorrelation of the error terms and does not require that observations be independent (Wong 2019). The parameters estimated by the PLS-PM are path coefficients, which are calculated by multiplying the ordinary regression coefficients by the standard deviations of the corresponding predictor variables (Dodge 2003). Therefore, path coefficients represent the fraction of the standard deviation of the response variable that is explained by each predictor variable (Dodge 2003). Because multicollinearity can adversely affect the estimation of path coefficients (Olivoto *et al.* 2017), before running PLS-PM we conducted a multicollinearity diagnosis by observing which predictor variables were significantly highly correlated ($r \geq 0.7$, $\alpha \leq 0.05$) in a correlation matrix. Due to multiple testing, we applied the sequential Bonferroni procedure to correct the α table-wide level of significance (Rice 1989). When there were highly correlated predictive variables during a breeding season, we excluded one or more of them from the PLS-PM for that particular breeding season (Olivoto *et al.* 2017). When temperature was correlated with a food variable, we gave the latter preference. When two food variables were correlated, we selected the one that had consistently been correlated with the same lag with the number of nests in the laying period or the number of nests with hatchlings during each year.

We performed cross-correlations with software R* 4.1.0 (R Core Team 2021). We ran the PLS-PM using software R* 3.0.1 (R Core Team 2013) and the *plspm* package.

RESULTS

Seasonal variation of nests and environmental conditions

The number of nests in the laying period (2015/2016: $n = 22$, 2016/2017: $n = 26$, 2017/2018: $n = 31$) increased from mid-December and peaked during mid- and late December, depending on the breeding season (Fig. 1a). Birds laid eggs for a longer time period during the 2017/2018 breeding season than during the other two (Table S1). The number of nests with hatchlings (2015/2016: $n = 11$, 2016/2017: $n = 16$, 2017/2018: $n = 22$) increased from late December or early January and

peaked during early and mid-January, according to the breeding season (Fig. 1b). There were hatchlings for a longer time period during the 2017/2016 and 2017/2018 breeding seasons than during the 2015/2016 breeding season (Table S1). Mean temperature increased slightly throughout each breeding season (Fig. 1c). Ripe fruit abundance began to increase during the first days of December and peaked in early January during each breeding season (Fig. 1d). Caterpillar abundance peaked in mid-December during each breeding season and decreased from mid-January, maintaining very low values during the remainder of the breeding period (Fig. 1e). Foliage arthropod abundance was similar throughout each breeding season, although it showed peaks in mid-December during the 2015/2016 breeding season and in early December during the 2017/2018 breeding season (Fig. 1f). Flying arthropod abundance was similar throughout each breeding season (Fig. 1g).

Cross-correlations

Cross-correlation analyses showed that only during the 2015/2016 breeding season was the number of nests in the laying period associated with the mean temperature in a posterior 10-day period (lag = 1), reaching its maximum value 10 days earlier than the maximum mean temperature (Fig. 2). The number of nests in the laying period was correlated with ripe fruit abundance in a posterior 10-day period (lag = 1) during the three breeding seasons studied, and reached its maximum 10 days earlier than this food resource (Fig. 2). During the 2015/2016 breeding season, caterpillar abundance increased for two 10-day periods (lag = -2) before the number of nests in the laying period increased (Fig. 2). During the 2016/2017 breeding season, the increase in number of nests in the laying period was in phase (lag = 0) with the increase in caterpillar abundance (Fig. 2). During the 2017/2018 breeding season, caterpillar abundance increased for one 10-day period (lag = -1) before the number of nests in the laying period increased (Fig. 2). Foliage arthropod abundance increased for one (lag = -1) and three 10-day periods (lag = -3) before the number of nests in the laying period increased during the 2015/2016 and 2016/2017 breeding seasons, respectively (Fig. 2). During the 2017/2018 breeding season, there was a trend of increasing foliage arthropod abundance

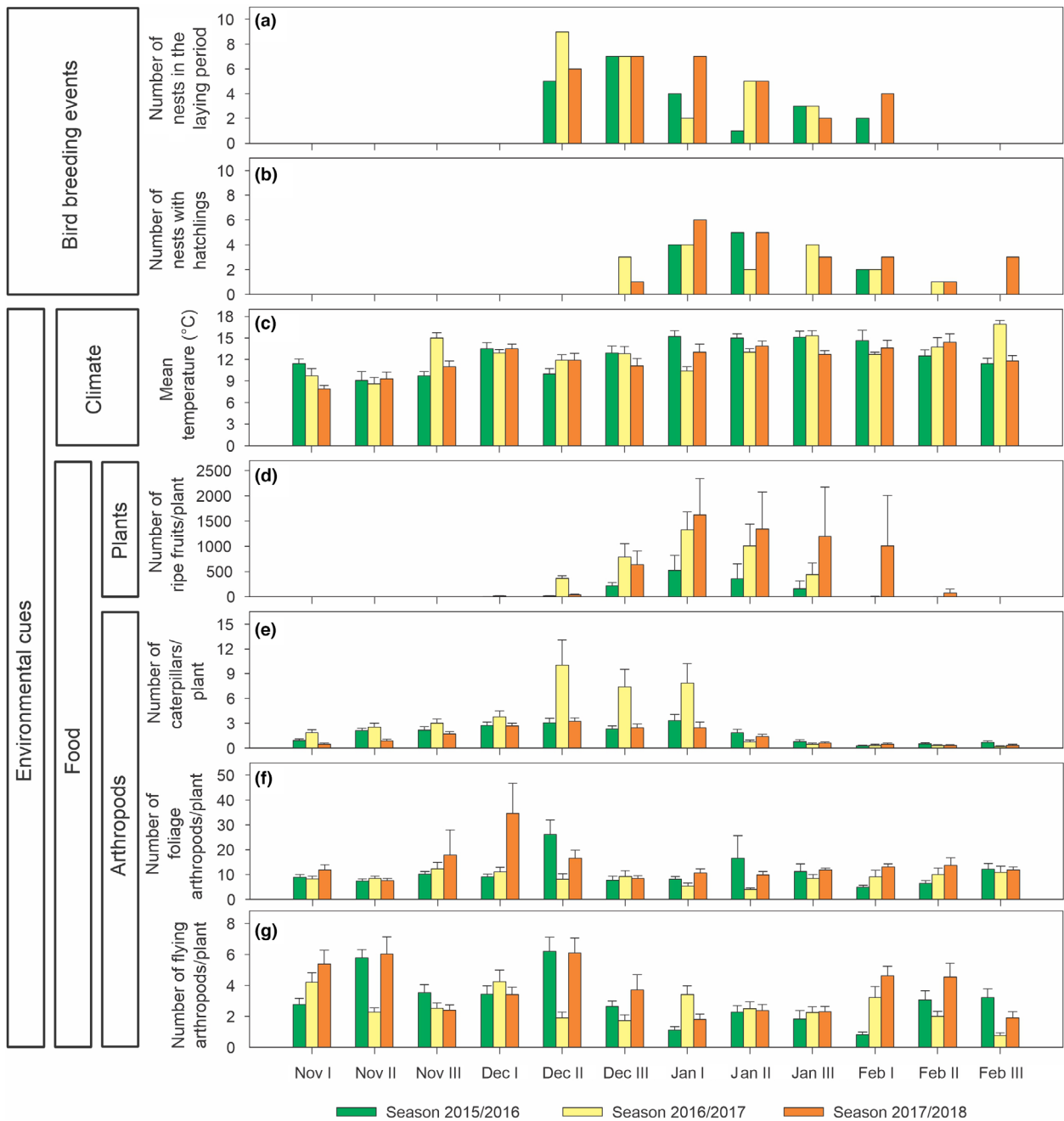


Figure 1. Temporal variation of the number of nests in the laying period (a), number of nests with hatchlings (b), mean temperature (c), ripe fruit abundance (d), caterpillar abundance (e), foliage arthropod abundance (f) and flying arthropod abundance (g) during three breeding seasons in the ecotone of the Andean–Patagonian Forest in Chubut Province, Argentina. Values correspond to the mean \pm se of each variable during each 10-day period within each breeding season.

for two 10-day periods ($\text{lag} = -2$) before the number of nests in the laying period increased (Fig. 2). There were no significant correlations or trends between flying arthropod abundance and the

number of nests in the laying period in any breeding season (Fig. 2).

The number of nests with hatchlings increased as temperature increased ($\text{lag} = 0$) during the

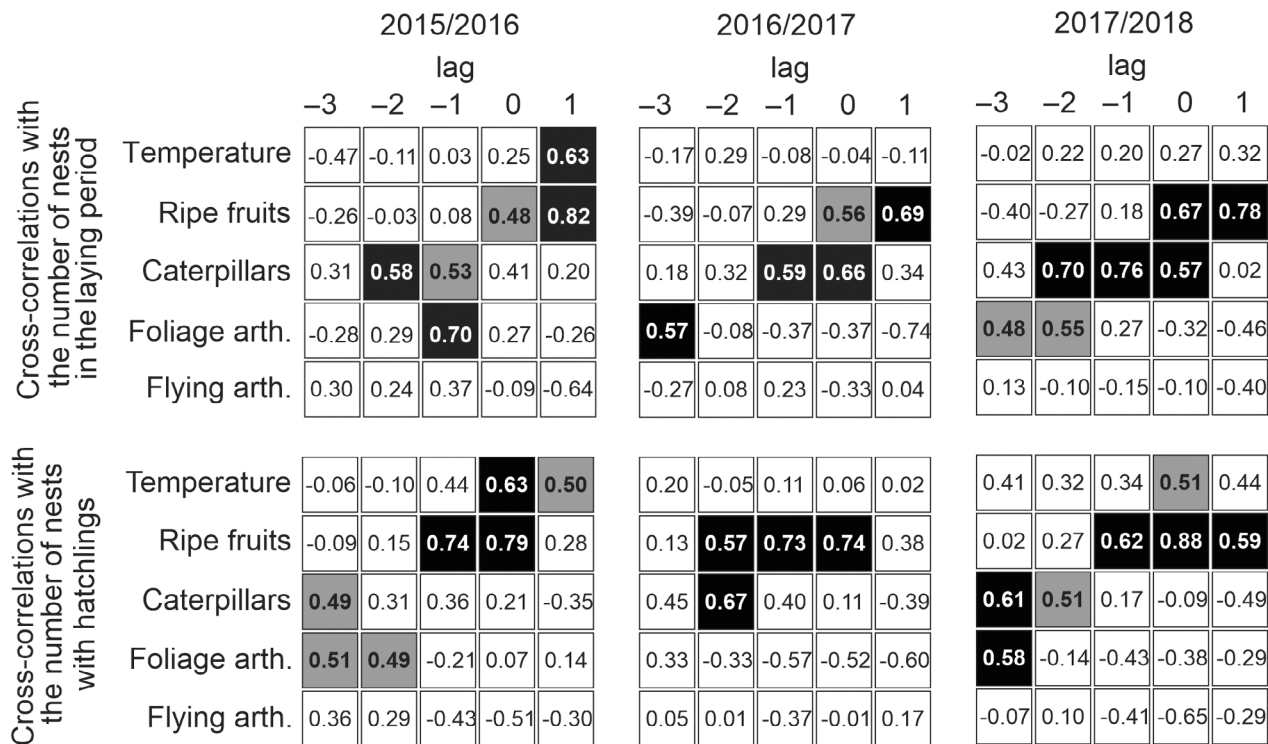


Figure 2. Cross-correlation matrixes of the number of nests in the laying period and the number of nests with hatchlings with mean temperature, the abundances of ripe fruits, caterpillars, foliage arthropods and flying arthropods during three breeding seasons in the ecotone of the Andean–Patagonian Forest in Chubut Province, Argentina. Column headings indicate the lag with which each predictor variable was correlated with each response variable. Only positive Pearson's cross-correlation coefficients were considered (see Methods). Significant cross-correlations ($P \leq 0.05$) are marked in black and cross-correlations approaching significance ($0.05 < P \leq 0.10$) are marked in grey.

2015/2016 breeding season, and the same trend was observed during the 2017/2018 breeding season (Fig. 2). During each breeding season, the increase in number of nests with hatchlings was in phase (lag = 0) with the increase in ripe fruit abundance (Fig. 2). During the 2015/2016 breeding season, there was a trend of increasing caterpillar abundance for three 10-day periods (lag = -3) before the number of nests with hatchlings increased (Fig. 2). Caterpillar abundance increased for two (lag = -2) and three 10-day periods (lag = -3) before the number of nests with hatchlings increased during the 2016/2017 and 2017/2018 breeding seasons, respectively (Fig. 2). Only during the 2017/2018 breeding season did foliage arthropod abundance increase for three 10-day periods (lag = -3) before the number of nests with hatchlings increased (Fig. 2). A similar trend can be observed in the 2015/2016 breeding season (Fig. 2). There were no significant positive correlations or trends between flying arthropod

abundance and number of nests with hatchlings in any breeding season (Fig. 2).

Multicollinearity

We found no correlations among the predictive variables selected for the PLS-PM used in the analysis of the number of nests in the laying period of the 2015/2016 breeding season (Table S2). Among the selected variables for the PLS-PM used in the analysis of the number of nests with hatchlings of the 2015/2016 breeding season, caterpillar abundance from three previous 10-day periods (lag = -3) was highly correlated with mean temperature in phase (lag = 0) (Table S2). Thus, we removed this latter variable from the final analysis. As fruit and caterpillar abundances were highly correlated during the 2016/2017 and 2017/2018 breeding seasons (Tables S3 and S4), we removed caterpillar abundance from all PLS-PM analyses of those two seasons. We additionally ran PLS-PM

after replacing caterpillar abundance with temperature, and fruit abundance with caterpillar abundance, and found similar results.

Potential effects of environmental cues

Results of the PLS-PM indicated that ripe fruit abundance in a posterior 10-day period (lag = 1) was the environmental cue that best explained the variation in the number of nests in the laying period during each breeding season (Fig. 3, Table S5). The path coefficient of caterpillar abundance was small and not significant during the 2015/2016 breeding season (Fig. 3, Table S5) but it explained as much variation as ripe fruit abundance during the 2016/2017 and 2017/2018 breeding seasons, given the high correlation between these two predictive variables (Fig. 3, Tables S3 and S4). Path coefficients of mean temperature and foliage arthropod abundance were small and not significant (Fig. 3, Table S5).

Ripe fruit abundance in phase (lag = 0) was also the environmental cue that best explained the variation in the number of nests with hatchlings during each breeding season (Fig. 3, Table S5). Caterpillar abundance explained as much variation as ripe fruit abundance (given the high correlation between these predictive variables) during the 2016/2017 and 2017/2018 breeding seasons, but there were lags of two and three 10-day periods, respectively, between the maximum caterpillar abundance and the maximum number of nests with hatchlings (Fig. 3). The other environmental cues did not explain variation of the timing of nest with hatchlings (Fig. 3, Table S5).

DISCUSSION

Long-distance migrants are thought to rely more on photic than non-photoc cues to time breeding (Chmura *et al.* 2020). However, considering the long pre-laying period of Chilean Elaenias, our results showed that this species may reliably follow a non-photoc cue to fine-tune timing of reproduction. Here, we found that the number of nests in the laying period was associated with ripe fruit abundance in a posterior 10-day period during each breeding season. This pattern arises from the fact that the maximum number of nests in the laying period occurred during a 10-day period earlier than the maximum ripe fruit abundance, despite Chilean Elaenias starting their egg-laying just as

fruits began to ripen. The timing of nests in the laying period was associated with timing of caterpillar abundance each year with different lags, but results of PLS-PM showed that this food resource explained as much variation as ripe fruit abundance in two of three breeding seasons. Therefore, these results support our prediction that the timing of nests in the laying period is associated with the timing of greatest food abundance. These results also suggest that both fruits and caterpillars may be proximate non-photoc cues in the reproduction of Chilean Elaenias because they constitute nutritious food resources used in the short term by birds to prepare their bodies for reproduction.

The daily cost of egg production is high and ranges between 86 and 230% relative to the daily protein requirements of birds (Robbins 1981). Consequently, proteins are the limiting factor for reproduction (Meijer & Drent 1999). Caterpillars have a high protein content (50–60 g of protein/100 g of dry mass, Bukkens 1997) and are an important food item in the diet of Chilean Elaenia adults (Muñoz *et al.* 2017). Hence, caterpillar abundance before and during the beginning of egg-laying of this passerine suggests that this food resource could provide the protein requirements necessary for egg production. Furthermore, *B. microphylla* fruits have important properties, such as a high carbohydrate content (Arena *et al.* 2013b) and fatty acids (Mazzuca *et al.* 2005), abundant calcium and several other minerals (Damascos *et al.* 2008), and plenty of antioxidant compounds, such as anthocyanins, polyphenols and ascorbic acid-vitamin C (Ruiz *et al.* 2010, 2013). These properties make it a food of high nutritional value (Ruiz *et al.* 2013, Arena *et al.* 2013b). For eggshell formation, females need significant calcium quantities, and they must ingest it during the laying period (Reynolds & Perrins 2010). Therefore, the synchronization found here between ripe fruit abundance and the number of nests in the laying period suggests that Chilean Elaenias could meet the nutritional requirements of egg formation through the ingestion of *B. microphylla* fruits.

In support of our prediction, we found that timing of nests with hatchlings matched with timing of ripe fruit abundance during each breeding season. Although it should be noted that the lag with fruits was shifted by only one 10-day period from the timing of egg laying to hatching, whereas incubation lasts > 10 days, this is a consequence of

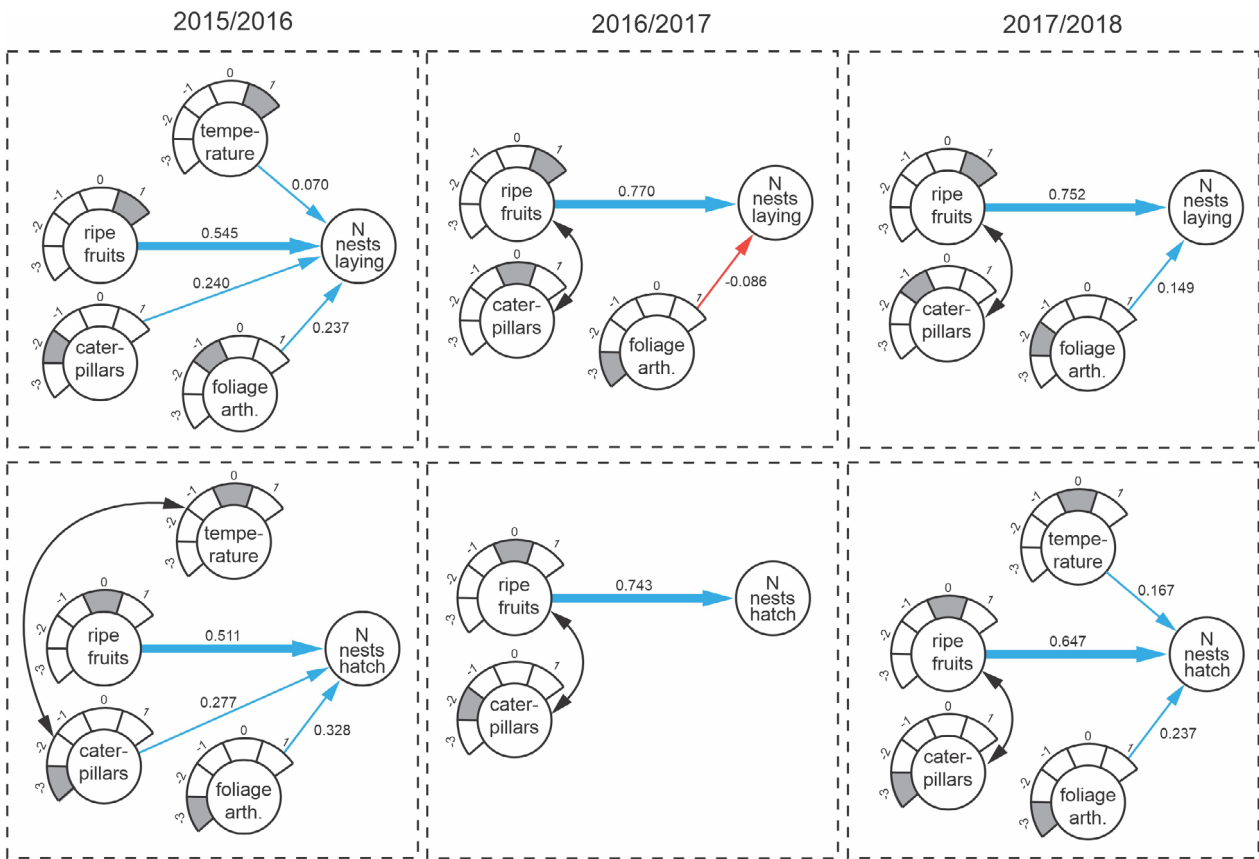


Figure 3. Results of the Partial Least Squares Path Modelling (PLS-PM), showing the path coefficients, which indicate the proportion of the standard deviation of the number of nests in the laying period and the number of nests with hatchlings that was explained by each environmental cue. Significant path coefficients are represented by thick arrows. The outer circle indicates the lag of the phenological event that explains the variation of the response variable. Double arrows indicate which pair of predictive variables were highly correlated.

the length of the periods used. If laying in most nests occurs at the beginning of the 10-day period, eggs will hatch after the middle of the next 10-day period. The use of ripe fruits may have several benefits for growing Chilean *Elaenia* nestlings, due to the high amount of antioxidant compounds and calcium content in *B. microphylla* fruits. It has been reported that a diet supplemented with antioxidant compounds allows Barn Swallow *Hirundo rustica* nestlings to attain greater weight and to experience accelerated feather growth (de Ayala *et al.* 2006). Tree Swallow *Tachycineta bicolor* nestlings fed with calcium-supplemented diets experienced faster growth rates and attained larger body size at fledging than those nestlings that did not receive calcium supplements during growth (Dawson & Bidwell 2005). In this way, ripe fruits not only contribute to the nutrition of adult breeding

birds but also represent an important resource for nestling growth. Notwithstanding these potential benefits in offspring well-being, we acknowledge that we did not analyse here the effects of ripe fruits on nestling survival or adult fitness, and thus it remains to be seen whether this non-photoc cue can actually be considered an ultimate factor in reproduction of Chilean *Elaenias*.

Caterpillars are considered the main food item in the diet of nestlings (Caro *et al.* 2009, Thomas *et al.* 2010) because of their soft consistency that facilitates digestion (Orłowski *et al.* 2015). However, we found that caterpillar abundance was high in mid-December (when Chilean *Elaenias* were just beginning reproduction) and low in January, when most eggs were hatching. Furthermore, the results of the PLS-PM indicating that caterpillar abundance from two or three previous 10-day

periods is associated with the number of nests with hatchlings reinforce the conclusion that this food resource would be important for egg formation and not for feeding nestlings. Although Chilean Elaenias have a 40-day pre-breeding period (Gorosito *et al.* 2022), they did not advance egg-laying to match timing of egg-hatching with timing of greatest caterpillar abundance. This could seem like a phenological mismatch but it actually would not be for Chilean Elaenias, because nestlings are mainly fed with ripe fruits (Gorosito *et al.* 2022). Moreover, the aforementioned potential benefits of *B. microphylla* fruits for both adult birds and chicks may help to explain why timing of nests with hatchlings does not coincide with timing of caterpillar abundance.

Our results did not support the predictions that Chilean Elaenias would use a climatic cue to fine-tune timing of reproduction, given that neither the number of nests in the laying period nor the number of nests with hatchlings were consistently associated with the timing of highest mean temperatures. Probably this species would not have to face temperature restrictions to reproduce, as its breeding period occurs during the warmest months of the year and temperature progressively increases throughout the season. Besides, this passerine shows several nesting behaviours that could ensure optimal nest temperatures for raising young, such as building a thick-walled nest, lining the nest interior with abundant feathers (Gorosito *et al.* 2022) and placing nests opposite the prevailing wind direction (Gorosito 2020). In such a way, Chilean Elaenias might be able to cope with occasional temperature challenges during the breeding period.

In this work, we have shown that a long-distance migrant, the Chilean Elaenia, may rely on a specific non-photoc cue to fine-tune timing of reproduction. The 40-day pre-breeding period (Gorosito *et al.* 2022) allows adults to track variations in local food resources and assess when to breed. Because ripe fruit phenology was consistently associated with the egg and nestling stages during each breeding season, this would be the main cue that allows Chilean Elaenias to predict the best time to breed. In addition to phenology, it is important to take into account the total abundance of food, given that this should be enough for egg formation or normal nestling growth (Durant *et al.* 2007, Dunn *et al.* 2011). Although we did not experimentally evaluate the food thresholds necessary for reproduction, our results

show that Chilean Elaenias seem to respond to increased ripe fruit abundance by initiating more nests and prolonging the duration of the nesting period (2017/2018 breeding season > 2016/2017 breeding season > 2015/2016 breeding season). In contrast, the highest caterpillar abundance during the 2016/2017 breeding season was not associated with the highest number of nests in the laying period of the three seasons. This may suggest that the influence of ripe fruit abundance on breeding decision of birds outweighs that of caterpillar abundance. Hence, caterpillars may represent a secondary proximal non-photoc cue for the reproduction of Chilean Elaenias.

Finally, the beginning of reproduction of Chilean Elaenias in Cañadón Florido (mid-December) occurred later than reported in other locations in the Andean–Patagonian Forest (late November, Escobar *et al.* 2004, Jara *et al.* 2019). This may suggest that this species responds slightly differently to the same non-photoc cues throughout its breeding range. For instance, in humid forests of Andean Patagonia some plant species produce ripe fruits in early spring (Riveros & Smith-Ramirez 1996) and thus Chilean Elaenias might respond earlier to this cue. Therefore, the replication of our study elsewhere at different latitudes in the Andean–Patagonian Forest will make it possible to determine the flexibility of the response of Chilean Elaenias to non-photoc cues to match timing of reproduction with timing of greatest food abundance. This would advance our understanding of how much non-photoc cues can influence the reproductive timing of long-distance migratory birds.

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CONFLICT OF INTEREST

The authors declare there are no conflicts of interest.

AUTHOR CONTRIBUTIONS

Cristian A. Gorosito: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (equal); project administration (equal); resources (equal); supervision (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Diego T. Tuero:** Conceptualization (supporting); resources (supporting); supervision (supporting); visualization (supporting); writing – review and editing (equal). **Victor R. Cueto:** Conceptualization (equal); funding acquisition (equal); investigation (supporting); methodology (equal); project administration (equal); resources (equal); supervision (equal); visualization (equal); writing – review and editing (equal).

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ETHICAL NOTE

None.

Data Availability Statement

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Adult Chilean Elaenia and map of the study area showing the forest patches (in green) at the Cañadón Florido Ranch, Chubut Province, Argentina.

Figure S2. Temporal variation of the accumulated precipitation in 10-day periods (data recorded in the Río Percey meteorological station, Hidroeléctrica Futaleufú S.A.) during three breeding seasons in the ecotone of the Andean–Patagonian Forest in Chubut Province, Argentina.

Table S1. Dates of commencement and completion and seasonal duration of the periods of egg-laying and egg-hatching of the Chilean Elaenia throughout three breeding seasons in the ecotone of the Andean–Patagonian Forest in Chubut Province, Argentina.

Table S2. Pearson correlations among the selected predictive variables (with lags indicated in parentheses) for the number of nests in the laying period and the number of nests with hatchlings during the 2015/2016 breeding season.

Table S3. Pearson correlations among the selected predictive variables (with lags indicated in parentheses) for the number of nests in the laying period and the number of nests with hatchlings during the 2016/2017 breeding season.

Table S4. Pearson correlations among the selected predictive variables (with lags indicated in parentheses) for the number of nests in the laying period and the number of nests with hatchlings during the 2017/2018 breeding season.

Table S5. Results of the Partial Least Squares Path Modelling (PLS-PM) performed for the number of nests in the laying period and the number of nests with hatchlings during each breeding season.