

Running head: *Reproductive timing of the Chilean Elaenia*

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

CRISTIAN A. GOROSITO,^{1*} DIEGO T. TUERO² & VICTOR R. CUETO¹

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

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

*Corresponding author.

Email: cgorosito@conicet.gov.ar

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1111/ibi.13196](https://doi.org/10.1111/ibi.13196)

This article is protected by copyright. All rights reserved.

Accepted Article

ABSTRACT

Timing of reproduction has a great impact on the breeding success of birds, because a mismatch with the moment when environmental temperatures 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-photoc cues, such as temperature and food abundance, may be necessary to fine-tune reproductive timing. However, the influence of non-photoc cues on finely tuning reproductive timing is not yet fully understood for migratory birds. Here, we evaluate how much non-photoc 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 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 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-photoc 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-photoc cues, ripe fruits

El momento de la reproducción tiene un gran impacto en el éxito reproductivo de las aves, ya que un desacople con el período de temperaturas ambientales cálidas o de mayor abundancia de alimento puede reducir la supervivencia de los pichones e incrementar el costo energético del cuidado parental. En consecuencia, las aves sincronizan la maduración de sus gónadas con las condiciones ambientales más favorables, utilizando los cambios en el fotoperíodo a lo largo del año como una señal inicial próxima. Además, las señales no fóticas, como la temperatura y la abundancia de alimento, pueden ser usadas para ajustar el período reproductivo. Sin embargo, todavía no se comprende totalmente la influencia de las señales no fóticas en el ajuste del período reproductivo para las aves migratorias. Aquí evaluamos cuánto influyen las señales no fóticas a la fenología reproductiva del Fiofio Chileno *Elaenia chilensis*, un ave migratoria de larga distancia que se reproduce en el Bosque Andino Patagónico. Analizamos las asociaciones de la temperatura media, abundancia de frutos maduros y artrópodos con el número de nidos en período de puesta y con el número de nidos con huevos recién eclosionados. En ambos análisis usamos correlaciones cruzadas y Mínimos Cuadrados Parciales en Modelos de Ruta. La temperatura media no estuvo consistentemente asociada con la fenología reproductiva de los Fiofios Chilenos. El aumento del número de nidos en período de puesta fue precedido por el aumento de la abundancia de orugas y se acopló con el aumento de la abundancia de frutos maduros. El período en que hubo nidos con huevos recién eclosionados coincidió con el período de mayor abundancia de frutos maduros. Ambos tipos de alimentos podrían contribuir con el inicio de la reproducción de las aves y ser usados como señales próximas por los Fiofios Chilenos. Además, los frutos maduros serían beneficiosos para el crecimiento de los pichones, ya que los padres los alimentan con frutos, y podrían tener potencialmente un rol último en la reproducción. Debido a que la abundancia de frutos maduros estuvo relacionada con las etapas de postura de huevos y eclosión, podría

ser la principal señal usada por los Fiofios Chilenos para ajustar el período reproductivo.

Estos resultados permiten avanzar en nuestra comprensión sobre la importancia de las señales no fóticas en la fenología reproductiva de las aves migratorias y además permiten generalizar nuestro conocimiento entre regiones y taxones, ya que la mayoría de los estudios sobre este tema se centran en el hemisferio norte.

Palabras clave: Bosque Andino Patagónico, frutos maduros, hipótesis de la disponibilidad de alimento, migrante austral neotropical, orugas, señales no fóticas

INTRODUCTION

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 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 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 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-photoc 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 temperature 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 that favourable environmental conditions are approaching rather than being a constraint on egg formation (Visser *et al.* 2009)

Birds can also use food abundance as a reliable non-photoc 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 a food restriction was imposed (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 mismatching 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-photoc cues would also depend on their migratory behaviour (Chmura *et al.* 2019). The responsiveness to non-photoc 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 showing 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), 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 ground 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

Accepted Article

begin egg-laying. We predicted that the number of nests in 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-photoc 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-photoc 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 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., Supporting Online Information Fig. S1), Chubut Province, Argentina. The vegetation of the area corresponds to the Valdivian Forest Province of the Andean Region (Morrone 2001). The forest at the study site is dominated by *Maytenus boaria* and *Schinus patagonicus* trees. The canopy is low, averaging a height of 5 m, and the understory 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 (fall-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 1998–2018, 42°51’30” S, 71°25’47” W, 750 m.a.s.l., provided by Hidroeléctrica Futaleufú S.A.)

Study species

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

The Chilean *Elaenia* (Supporting Online Information Figure 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), while females from early November (Cueto & Gorosito 2018, Gorosito 2020). Adults begin fall 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 consists 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 laying period’ as those nests when eggs are 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 (Supporting Online Information 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 semi-quantitative 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 = 5001-10000 ripe fruits, and 8 = >10000 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 to 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 10001 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

Accepted Article

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 cm x 40 cm x 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 laying period and the number of nests with hatchlings in each 10-day period as response variables, in order 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 we used the mean of two consecutive samplings to obtain values for those 10-day periods.

The predictor and response variables constitute time series. As a consequence, the data has 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 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 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, while 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 laying period and the number of nest with hatchlings during each breeding season. 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 preference to the latter. 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 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 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 (Supporting Online Information 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 between late December 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 (Supporting Online Information 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 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 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 laying period increased (Fig. 2). During the 2016/2017 breeding season the increase in number of nests in 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 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 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 for two 10-day periods (lag = -2) before the number of nests in laying period increased (Fig. 2). There were no significant correlations or trends between flying arthropod abundance and the number of nests in laying period in any breeding season (Fig. 2).

The number of nests with hatchlings increased as temperature increased (lag = 0) during the 2015/2016 breeding season, and the same trend is 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 seasons (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 laying period of the 2015/2016 breeding season (Supporting Online Information 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) (Supporting Online Information 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 (Supporting Online Information Tables S3 & S4), we removed caterpillar abundance from all PLS-PM

analyses of those two seasons. We additionally ran PLS-PM 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 most explained the variation in the number of nests in laying period during each breeding season (Fig. 3, Supporting Online Information Table S5). Path coefficient of caterpillar abundance was small and not significant during the 2015/2016 breeding season (Fig. 3, Supporting Online Information 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, Supporting Online Information Tables S3 & S4). Path coefficients of mean temperature and foliage arthropod abundance were small and not significant (Fig. 3, Supporting Online Information Table S5).

Ripe fruit abundance in phase (lag = 0) was also the environmental cue that most explained the variation in the number of nests with hatchlings during each breeding season (Fig. 3, Supporting Online Information 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, Supporting Online Information Table S5).

DISCUSSION

Accepted Article

Long-distance migrants are thought to rely more on photic rather 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 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 laying period occurred during a 10-day period earlier than the maximum ripe fruit abundance, despite Chilean Elaenias started egg-laying just as fruits began to ripen. The timing of nests in 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 out of three breeding seasons. Therefore, these results support our prediction that the timing of nests in 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 would constitute nutritious food resources used in the short term by birds to prepare their bodies for reproduction.

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, like anthocyanins, polyphenols and ascorbic acid – vitamin C (Ruiz *et al.* 2010, Ruiz *et al.* 2013). These properties make it a food of high nutritional value (Arena *et al.* 2013b, Ruiz *et al.* 2013). 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 laying period suggests that Chilean Elaenias could meet nutritional requirement 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 may draw attention 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 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 was reported that a diet supplemented with antioxidant compounds allowed 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 would not only contribute to the nutrition of adult breeding birds, but would 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-photocue 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 would facilitate 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 may explain the variation of the number of nest with hatchlings reinforces 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 understand why timing of nests with hatchlings is not associated 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 laying period nor the number of nests with hatchlings were consistently associated with the timing of warmest 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 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 occasionally temperature challenges during the breeding period.

In this work, we showed 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) would allow 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 when is 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 showed 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 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 that 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 cue throughout its breeding range. For instance, in humid forests of Andean Patagonia some plant species produce ripe fruits in early spring (Riveros & Smith-Ramírez 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 allow to determine the flexibility of the response of Chilean Elaenias to non-photic cues to match timing of reproduction with timing of greatest food abundance. This will lead to advance our understanding of how much non-photic cues can influence the reproductive timing of long-distance migratory birds.

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. We also thank three anonymous reviewers and editor Ruedi Nager for their comments and suggestions, which greatly enhanced this paper. We thank the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET-Argentina) for funds to support this work. We are grateful to the National Geographic Society for funds to V. R. Cueto (GN 9289-13), the Association of Field Ornithologists for the Bergstrom Award (USA, 2015) to C. A. Gorosito and the Neotropical Ornithological Society for the François Vuilleumier Fund (USA, 2017) to C. A. Gorosito. Research was conducted under ethical and technical evaluation and authorization of Dirección de Fauna y Flora Silvestre, Ministerio de Desarrollo Territorial y Sectores Productivos de la Provincia del Chubut, Argentina.

DATA AVAILABILITY STATEMENT

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

REFERENCES

- Amico, G. C. & Aizen, M. A. 2005. Dispersión de semillas por aves en un bosque templado de Sudamérica austral: ¿quién dispersa a quién? *Ecol. Austral* 15: 89–100.
- Arena, M. E., Giordani, E. & Radice, S. 2013a. Phenological growth and development stages of the native Patagonian fruit species *Berberis buxifolia* Lam. *J. Food Agric. Environ.* 11: 1323–1327.

- Arena, M. E., Zuleta, A., Dyner, L., Constenla, D., Ceci, L. & Curvetto, N. 2013b. *Berberis buxifolia* fruit growth and ripening: evolution in carbohydrate and organic acid contents. *Sci. Hortic* 158: 52–58.
- de Ayala, R. M., Martinelli, R. & Saino, N. 2006. Vitamin E supplementation enhances growth and condition of nestling barn swallows (*Hirundo rustica*). *Behav. Ecol. Sociobiol.* 60: 619–630.
- Ball, G. F. & Ketterson, E. D. 2008. Sex differences in the response to environmental cues regulating seasonal reproduction in birds. *Philos. Trans. R. Soc. B.* 363: 231–246.
- Billerman, S. M., Keeney, B. K., Rodewald, P. G. & Schulenberg, T. S. (eds.). 2020. *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA. <https://birdsoftheworld.org/bow/home>
- Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.
- Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J. & Foppen, R. P. B. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. Royal Soc. B* 277: 1259–1266.
- Bravo, S. P., Cueto, V. R. & Gorosito, C. A. 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.
- Brown, C. E., Anderson C. B., Ippi, S., Sherriffs, M. F., Charlin, R., McGehee, S. & Rozzi, R. 2007. The Autoecology of the fio-fio (*Elaenia albiceps* Lafresnaye & d'Orbigny) in subantarctic forests of the Cape Horn Biosphere Reserve, Chile. *Anales Instituto Patagonia* 35: 29–40.
- Bukkens, S. G. F. 1997. The nutritional value of edible insects. *Ecol. Food Nutr.* 36: 287–319.

- Caro, S. P., Charmantier, A., Lambrechts, M. M., Blondel, J., Balthazart, J. and Williams, T. D. 2009. Local adaptation of timing of reproduction: females are in the driver's seat. *Funct. Ecol.* 23: 172–179.
- Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B. & Yang, L. H. 2019. The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecol. Monogr.* 89: e01337.
- Chmura, H. E., Wingfield, J. C. & Hahn, T. P. 2020. Non-photoc environmental cues and avian reproduction in an era of global change. *J. Avian Biol.* 51: e02243.
- Clements, J. F., Schulenberg, T. S., Iliff, M. J., Billerman, S. M., Fredericks, T. A., Gerbracht, J. A., Lepage, D., Sullivan, B. L. & Wood, C. L. 2021. The eBird/Clements checklist of Birds of the World: v2021. Downloaded from <https://www.birds.cornell.edu/clementschecklist/download/> on 9-September-2021.
- Cooper, R. J. & Whitmore, R. C. 1990. Arthropod sampling methods in ornithology. *Stud. Avian Biol.* 13: 29–37.
- Corregidor-Castro, A. & Jones, O. R. 2021. The effect of nest temperature on growth and survival in juvenile Great Tits *Parus major*. *Ecol. Evol.* 11: 7346–7353.
- Crawley, M. J. 2007. *The R Book*. Wiley, Chichester, UK.
- Cueto, V. R. & Gorosito, C. A. 2018. Seasonal changes in bird assemblages of a forest-steppe ecotone in North Patagonia. *Ornitol. Neotrop.* 29: 349–358.
- Cueto, V. R., Chust, L. & Bravo, S. P. 2016a. Interannual variations in foraging behavior of White-crested Elaenia (*Elaenia albiceps chilensis*) in northern Patagonian forest. *Wilson J. Ornithol.* 128: 804–810.
- Cueto, V. R., Sagario, M. C. & Lopez de Casenave, J. 2016b. Do migrating White-crested Elaenia, *Elaenia albiceps chilensis*, use stop-over sites *en route* to their breeding areas? Evidence from the central Monte desert, Argentina. *Emu* 116: 301–304.

- Damascos, M. A., Arribere, M., Svriz, M. & Bran, D. 2008. Fruit mineral contents of six wild species of the North Andean Patagonia, Argentina. *Biol. Trace Elem. Res.* 125: 72–80.
- Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. 2001. Photoperiodic Control of Seasonality in Birds. *J. Biol. Rhythms* 16: 365–380.
- Dawson, R. D. & Bidwell, M. T. 2005. Dietary calcium limits size and growth of nestling Tree swallows *Tachycineta bicolor* in a non-acidified landscape. *J. Avian Biol.* 36: 127–134.
- Dodge, Y. 2003. *The Oxford Dictionary of Statistical Terms*. Oxford University Press, Oxford, UK.
- Drent, R. H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225–252.
- Dunn, P. O. & Winkler, D. W. 2010. Effects of climate change on timing of breeding and reproductive success in birds. In Moller, A. P., Fiedler, W. & Berthold, P. (eds). *Effects of climate change on birds*. Oxford: Oxford University Press.
- Dunn, P. O., Winkler, D. W., Whittingham, L. A., Hannon, S. J. & Robertson, R. J. 2011. A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore? *Ecology* 92: 450–461.
- Durant, J. M., Hjernann, D. Ø., Ottersen, G. & Stenseth, N. C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.* 33: 271–283.
- Dzendoletas, M. A, Havrylenko, M. & Crivelli, E. 2003. Fenología de plantas en Puerto Blest, Parque Nacional Nahuel Huapi, Patagonia, Argentina. *Ecología* 17: 87–98.
- Escobar, M. A. H., Páez, M., Vukasovic, M. A. and Estades, C. F. 2004. Nidificación del migrador austral *Elaenia albiceps* en remanentes de bosque maulino y plantaciones de *Pinus radiata* en Chile central. *Bol. Chil. Ornitol.* 10: 34–36.

- García-Navas V. & Sanz J. J. 2011. The importance of a main dish: nestling diet and foraging behaviour in Mediterranean blue tits in relation to prey phenology. *Oecologia* 165: 639–649.
- Gill F., Donsker, D. and Rasmussen, P. (eds.). 2022. IOC World Bird List (v12.2). doi: 10.14344/IOC.ML.12.2. Available at <http://www.worldbirdnames.org/> [Accessed 07-October-2022].
- Gönc, R. L. (2013). Estudio de la estructura de las comunidades de artrópodos asociados a Ñirantales (*Nothofagus antarctica*) del Centro-Oeste de la provincia de Chubut, Patagonia Argentina, sometidos a diferentes tipos de impacto ambiental. – PhD thesis, Universidad Nacional de la Plata, Argentina.
- Gorosito, C. A. 2020. Determinantes del éxito reproductivo de *Elaenia albiceps* (Aves: Tyrannidae) en bosques andino-patagónicos. – PhD thesis, Universidad de Buenos Aires, Argentina.
- Gorosito, C. A., Tuero, D. T. & Cueto, V. R. 2022. Breeding biology of the Chilean *Elaenia* (*Elaenia chilensis*), a long-distance migratory passerine in South America. *Ardea* 110: 227–238.
- Guerra Navarro, C. I. 2016. Comportamiento de alimentación de las aves insectívoras del desierto del Monte central: aspectos espaciales y temporales. – PhD thesis, Universidad de Buenos Aires, Argentina.
- Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. *Ibis* 138: 47–63.
- Hahn, T. P. 1995. Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the Red Crossbill, *Loxia curvirostra* (Aves: Carduelinae). *J. Exp. Zool.* 272: 213–226.

- Hajdasz, A. C., Otter, K. A., Baldwin, L. K. & Reudink, M. W. 2019. Caterpillar phenology predicts differences in timing of mountain chickadee breeding in urban and rural habitats. *Urban Ecosyst.* 22: 1113–1122.
- Hällfors, M. H., Antão, L. H., Itter, M., Lehikoinen, A., Lindholm, T., Roslin, T. & Saastamoinen, M. 2020. Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *PNAS* 117: 18557–18565.
- Hidalgo Aranzamendi, N., Hall, M. L., Kingma, S. A., van de Pol, M. & Peters, A. 2019. Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. *J. Anim. Ecol.* 88: 1799–1811.
- Jara, R. F., Crego, R. D., Arellano, F. J., Altamirano, T. A., Ibarra, J. T., Rozzi, R. & Jiménez, J. E. 2019. Breeding strategies of open-cup-nesting birds in sub-Antarctic forests of Navarino Island, Chile. *Rev. Chil. Hist. Nat.* 92: 2.
- Kitzberger, T. 2012. Ecotones as complex arenas of disturbance, climate, and human impacts: the trans-Andean forest-steppe ecotone of northern Patagonia. In *Ecotones Between Forest and Grassland* (R. W. Myster, Editor). Springer, NY, USA.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, NY, USA.
- Manhães, M. A., Dias, M. M. & Lima, A. L. C. 2015. Feeding resource partitioning between two understory insectivorous birds in a fragment of Neotropical cloud forest. *Braz. J. Biol.* 75 (Suppl. 1): S176–S183.
- Martin, T. E. & Geupel, G. R. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *J. Field Orn.* 64: 507–519.
- Mazucca, M., Miscoria, S., Rost, E. & Balzaretto, V. 2005. Fatty acids and sterols in seeds from wild species of *Berberis* in Argentine Patagonia. *An. Asoc. Química Argentina* 93: 241–246.

- Meijer, T. & Drent, R. 1999. Re-examination of the capital and income dichotomy in breeding birds. *Ibis* 141: 399–414.
- Monrós, J. S., Belda, E. J. & Barba, E. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* 99: 481–488.
- Morrone, J. J. 2001. Biogeografía de América Latina y el Caribe. Manuales & Tesis de la Sociedad Entomológica Aragonesa, Zaragoza, España.
- Muñoz, C. E., Ippi, S., Celis-Diez, J. L., Salinas, D. & Armesto, J. J. 2017. Arthropods in the diet of the bird assemblage from a forested rural landscape in northern Chiloé island, Chile: a quantitative study. *Ornitol. Neotrop.* 28: 191–199.
- Murtaugh, P. A. 2014. In defense of *P* values. *Ecology* 95: 611–617.
- Nadolski, J., Marciniak, B., Loga, B., Michalski, M. and Bánbura, J. 2021. Long-term variation in the timing and height of annual peak abundance of caterpillars in tree canopies: Some effects on a breeding songbird. *Ecol. Indic.* 121: 107120.
- Olivoto, T., de Souza, V. Q., Nardino, M., Carvalho, I. R., Ferrari, M., de Pelegri, A. J., Szareski, V. J. & Schmidt, D. 2017. Multicollinearity in Path Analysis: a simple method to reduce its effects. *Agron. J.* 109: 131–142.
- Orłowski, G., Wuczyński, A. & Karg, J. 2015. Effect of brood age on nestling diet and prey composition in a hedgerow specialist bird, the Barred Warbler *Sylvia nisoria*. *PLoS ONE* 10: e0131100.
- Paruelo, J. M., Beltran, A., Jobbagy, E., Sala, O. E. & Golluscio, R. A. 1998. The climate of Patagonia: general patterns and controls on biotic processes. *Ecol. Austral* 8: 85–101.
- Pearman, M. and Areta, J. I. 2020. Birds of Argentina and the South-west Atlantic. Helm Field Guides. Bloomsbury Publishing, London, UK.
- Quay, W. B. 1985. Cloacal sperm in spring migrants: occurrence and interpretation. *Condor* 87: 273–280.

- Ramenofsky, M. & Wingfield, J. C. 2006. Behavioral and physiological conflicts in migrants: the transition between migration and breeding. *J. Ornithol.* 147: 135–145.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reynolds S. J. & Perrins, C. M. 2010. Dietary calcium availability and reproduction in birds. In *Current Ornithology* Volume 17 (C. F. Thomson, Editor). Springer-Verlag, NY, USA.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Riveros, M. & Smith-Ramirez, C. 1996. Patrones de floración y fructificación en bosques del sur de Chile. In *Ecología de los bosques nativos de Chile* (J. J. Armesto, C. Villagrán, and M. T. K. Arroyo, Editors). Editorial Universitaria, Santiago de Chile.
- Robbins, C. T. 1981. Estimation of the relative protein cost of reproduction in birds. *Condor* 83: 177–179.
- Ruiz, A., Hermosín-Gutiérrez, I., Mardones, C., Vergara, C., Herlitz, E., Vega, M., Dorau, C., Winterhalter, P. & Von Baer, D. 2010. Polyphenols and antioxidant activity of Calafate (*Berberis microphylla*) fruits and other native berries from Southern Chile. *J. Agric. Food Chem.* 58: 6081–6089.
- Ruiz, A., Hermosín-Gutiérrez, I., Vergara, C., von Baer, D., Zapata, M., Hirschfeld, A., Obando, L. & Mardones, C. 2013. Anthocyanin profiles in south Patagonian wild berries by HPLC-DAD-ESI-MS/MS. *Food Res. Int.* 51: 706–713.
- Sanchez, G. 2013. *PLS Path Modeling with R*. Trowchez Editions, Berkeley, CA, USA.
- Saracco, J. F., Collazo, J. A. & Groom, M. J. 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* 139: 235–245.

- Sauve, D., Friesen, V. L. & Charmantier, A. 2021. The effects of weather on avian growth and implications for adaptation to climate change. *Front. Ecol. Evol.* 9: 569741.
- Schöll, E. M. & Hille, S. M. 2020. Heavy and persistent rainfall leads to brood reduction and nest failure in a passerine bird. *J. Avian. Biol.* 51: e02418.
- Stevenson, I. R. & Bryant, D. M. 2000. Climate change and constraints on breeding. *Nature* 406: 366–367.
- Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M. & Speakman, J. R. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291: 2598–2600.
- Thomas, D. W., Bourgaud, P., Shipley, B., Perret, P. & Blondel, J. 2010. Context-dependent changes in the weighting of environmental cues that initiate breeding in a temperate passerine, the Corsican Blue Tit (*Cyanistes caeruleus*). *Auk* 127: 129–139.
- Visser, M. E., Holleman, L. J. M. & Caro, S. P. 2009. Temperature has a causal effect on avian timing of reproduction. *Proc. Royal Soc. B* 276: 2323–2331.
- Wann, G. T., Aldridge, C. M., Seglund, A. E., Oyler-McCance, S. J., Kondratieff, B. C. & Braun, C. E. 2019. Mismatches between breeding phenology and resource abundance of resident alpine ptarmigan negatively affect chick survival. *Ecol. Evol.* 9: 7200–7212.
- Wesołowski, T., Hebda, G. & Rowiński, P. 2021. Variation in timing of breeding of five woodpeckers in a primeval forest over 45 years: role of food, weather, and climate. *J. Ornithol.* 162: 89–108.
- Wingfield, J. C. & Farner, D. S. 1980. Control of seasonal reproduction in temperate-zone birds. *Prog. Reprod. Biol.* 5: 62–101.
- Wingfield, J. C., Hahn, T. P., Maney, D. L., Schoech, S. J., Wada, M. & Morton, M. L. 2003. Effects of temperature on photoperiodically induced reproductive development, circulating plasma luteinizing hormone and thyroid hormones, body mass, fat

deposition and molt in mountain white-crowned sparrows, *Zonotrichia leucophrys oriantha*. Gen. Comp. Endocrinol. 131: 143–158.

Winkler, D. W., Luo, M. K. & Rakhimberdiev, E. 2013. Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). Oecologia 173: 129–138.

Whittingham, L. A., Dunn, P. O. & Lifjeld, J. T. 2007. Egg mass influences nestling quality in Tree Swallows, but there is no differential allocation in relation to laying order or sex. Condor 109: 585–594.

Wong, K. K. 2019. Mastering Partial Least Squares Structural Equation Modeling (PLS-SEM) with SmartPLS in 38 hours. iUniverse, Bloomington, USA.

Zhang, S., Zhao, L., Zhang, X. & Liang, W. 2020. Predicting the vulnerability of birds to trophic threat posed by phenological mismatch based on nutritional and physiological status of nestlings. Conserv. Physiol. 7: coz096.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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. The dashed line square indicates the zone where nests were monitored and food resources were sampled.

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 laying period and the number of nests with hatchlings during the 2015/2016 breeding season. Significant correlation coefficients with corrected α -level of 0.05 (for each group of variables) according to the sequential Bonferroni procedure are indicated in bold.

Table S3. Pearson correlations among the selected predictive variables (with lags indicated in parentheses) for the number of nests in laying period and the number of nests with hatchlings during the 2016/2017 breeding season. Significant correlation coefficients with corrected α -level of 0.05 (for each group of variables) according to the sequential Bonferroni procedure are indicated in bold.

Table S4. Pearson correlations among the selected predictive variables (with lags indicated in parentheses) for the number of nests in laying period and the number of nests with hatchlings during the 2017/2018 breeding season. Significant correlation coefficients with corrected α -level of 0.05 (for each group of variables) according to the sequential Bonferroni procedure are indicated in bold.

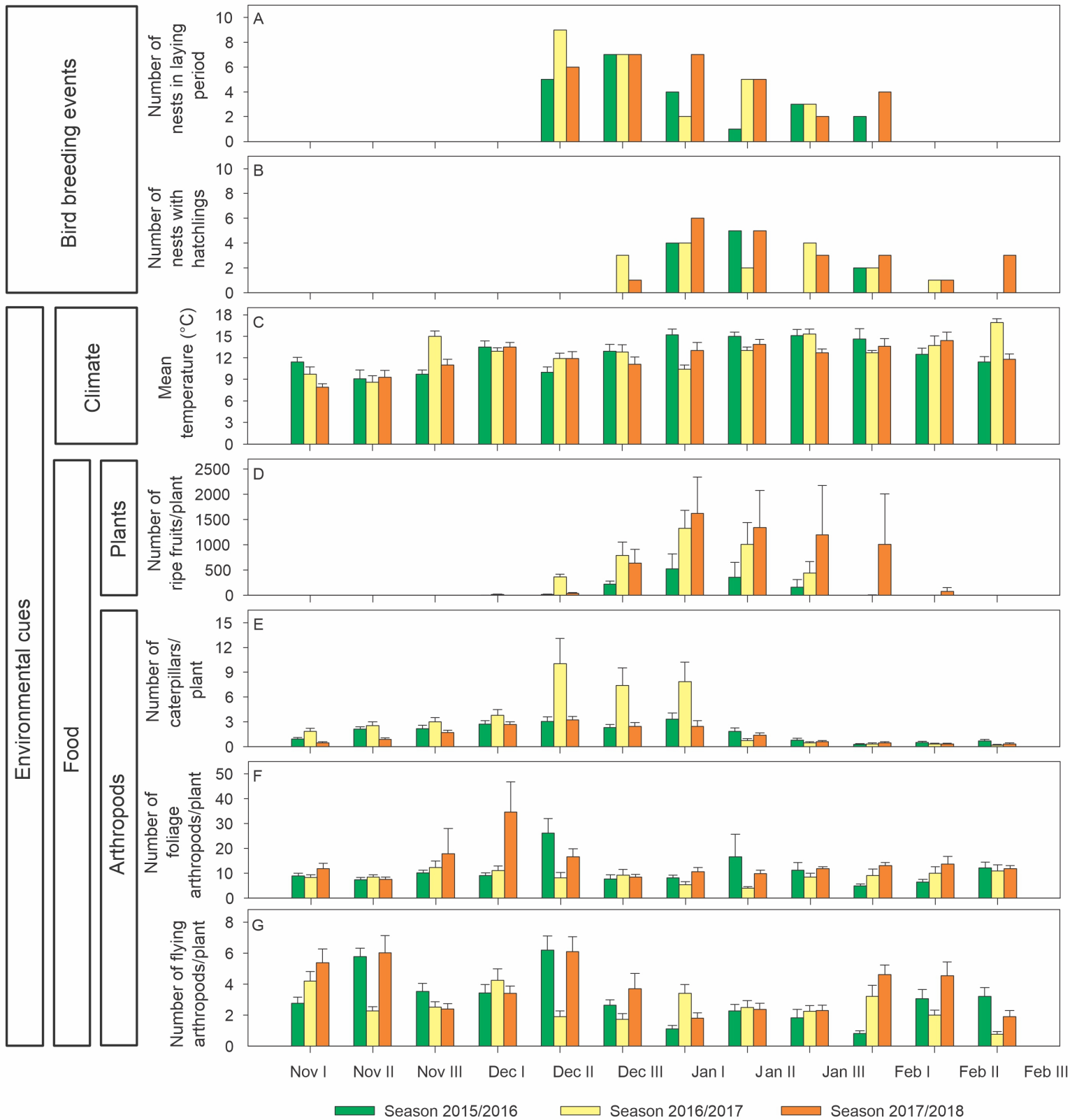
Table S5. Results of the Partial Least Squares Path Modelling (PLS-PM) performed for the number of nests in laying period and the number of nests with hatchlings during each breeding season. The lag of the selected predictive variable that explains the response variable is indicated in parentheses. Significant path coefficients (estimate \pm standard error) are indicated in bold.

FIGURE LEGENDS

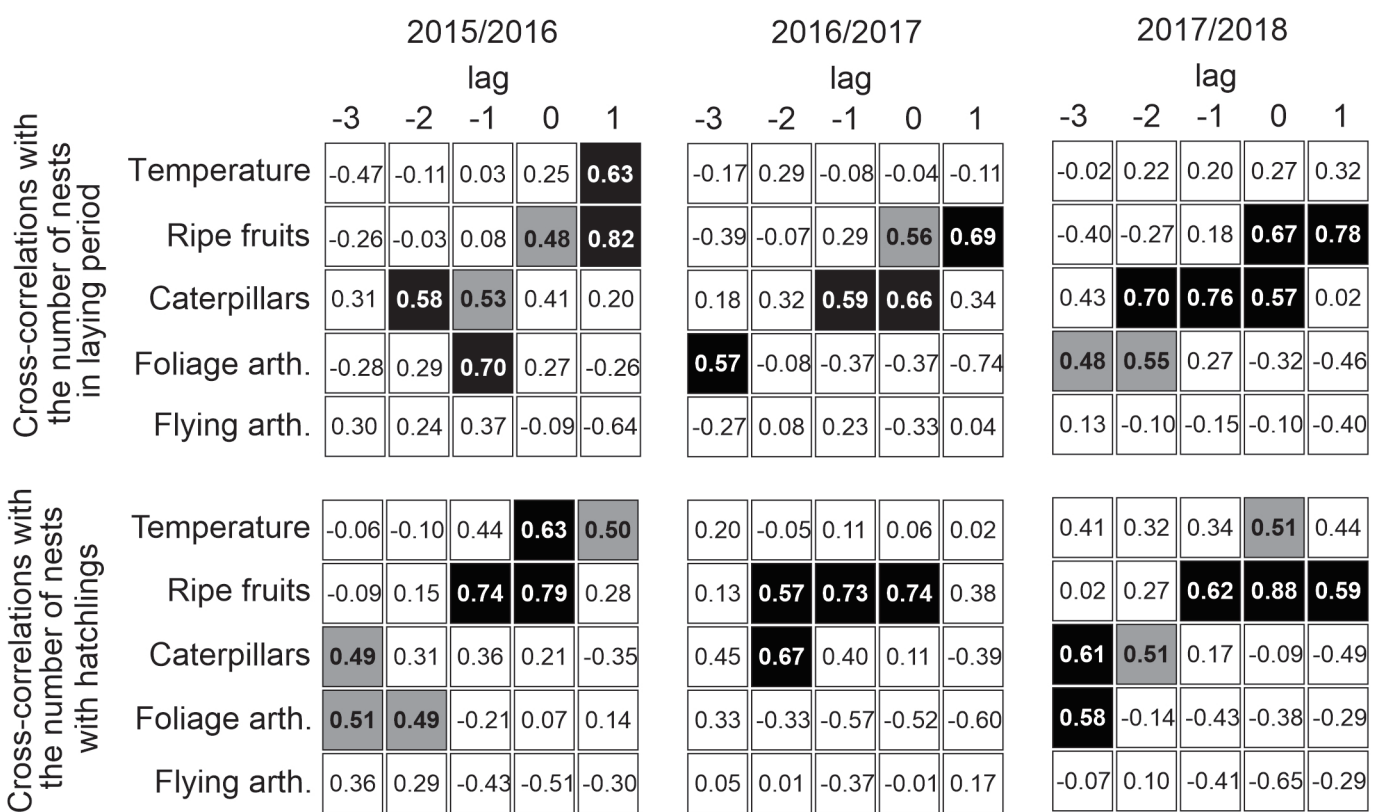
Figure 1. Temporal variation of the number of nests in laying period (A), number of nests with hatchlings (B), mean temperature (C), ripe fruit abundance (D), caterpillar abundance (E), foliage arthropod abundance (F) and flying arthropod abundance (G) during three breeding seasons in the ecotone of 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.

Figure 2. Cross-correlation matrixes of the number of nests in 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 with black and cross-correlations approaching significance ($0.05 < P \leq 0.10$) are marked with grey.

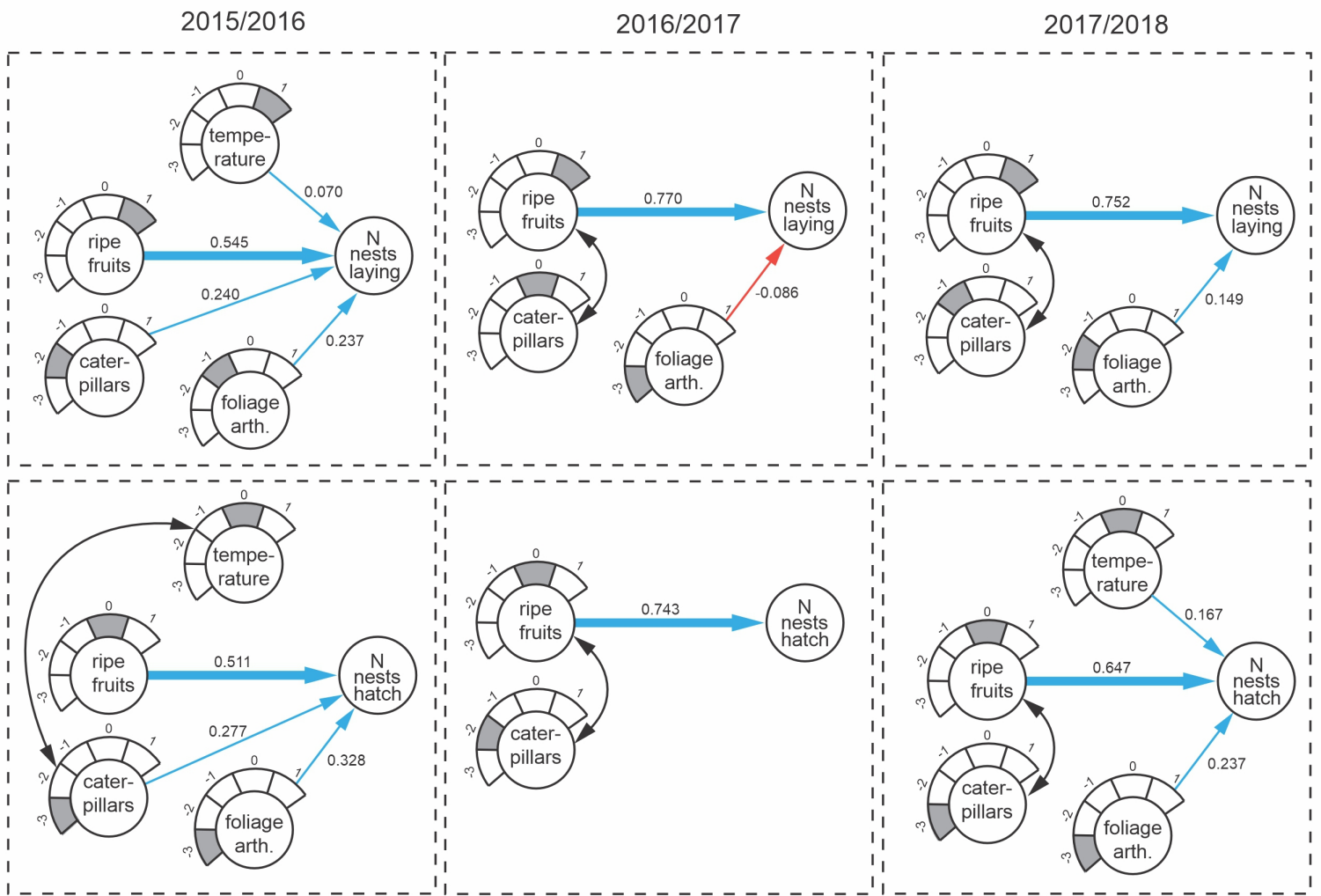
Figure 3. Results of the Partial Least Squares Path Modelling (PLS-PM), showing the path coefficients, which indicate the proportion of the standard deviation of the number of nests in laying period and the number of nests with hatchlings that was explained by each environmental cue. Significant path 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.



IBI_13196_Figure 1.jpg



IBI_13196_Figure 2.jpg



IBI_13196_Figure 3.jpg