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ORIGINAL RESEARCH

Begging calls and mouth colouration as predictors of breeding success in blue tits

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Abstract

Nestlings normally exhibit a mix of traits that attract parental care, such as postural and vocal begging and carotenoid-based mouth colouration. These signals are hypothesised to be signs of nestling needs (vocal begging) and quality (mouth colouration). Therefore, we hypothesised that broods, where nestlings beg for less time and display more saturated carotenoid-based mouth colouration, would have lower nestling mortality. We tested these predictions in two wild blue tit (*Cyanistes caeruleus*) populations. The breeding success (here defined as the proportion of eggs that produced fledglings) was related to nestling mouth flanges' carotenoid-based colour saturation. This means that blue tits that raised nestlings with more coloured flanges had a higher within-population breeding success. Time spent in vocal begging, by contrast, was not associated with breeding success. Hence, our findings reveal that some communication signals displayed by nestlings (carotenoid-based colouration) predict breeding success, in our study mostly reflecting the proportion of eggs that hatched, while begging intensity does not, probably because the former reflects a better maternal pre-laying condition and nestling physiological status in the mid-term.

Introduction

In altricial birds, such as passerines, nestlings depend on parents to obtain food resources, normally exhibiting a mix of traits that attract parental care (Budden & Wright, 2001; Kilner & Johnstone, 1997). Begging can be defined as a combination of behavioural, acoustic, visual, and chemical signals displayed by the offspring that influence parental care allocation, which has been hypothesised to evolve because they mirror reliable information on offspring quality and need (Godfray, 1991; Mock et al., 2011; Royle et al., 2012). These might also be a way siblings directly compete for food (Parker et al., 2002; Royle et al., 2002). Parts of this multimodal display may contain different kinds of information, such as nestling's condition and hunger level in either the short term (vocalizations or postural cues; Jacob et al., 2011; Leonard et al., 2003; Moreno-Rueda et al., 2016) or long term (carotenoid-based mouth colouration; Saino et al., 2003).

Carotenoid-based ornaments are widespread in animals and have a dietary-based origin (Partali et al., 1987). Carotenoids are typically a limiting resource in terms of availability, play a role in diverse physiological functions (Møller et al., 2000), and signal individual conditions (McGraw & Hill, 2000; Senar & Escobar, 2002). Hence, given the close relationship between carotenoids and environmental and physiological factors, it has been proposed that avian carotenoid-based colouration could be used as an integrated measure of a multitude of diet- and health-related parameters. In many altricial bird species, carotenoid-based

colouration is commonly exhibited in the mouth as a begging signal during the nestling stage (e.g., Dugas & Rosenthal, 2010; Ewen et al., 2008; Saino et al., 2000, 2003). Nestling carotenoid-based mouth colouration is hypothesised to be a reliable signal of nestling condition, and several studies have shown that carotenoid-rich mouth colours correlate with nestling body mass (de Ayala et al., 2007; Dugas & McGraw, 2011), tarsus length (Ewen et al., 2008), immunocompetence (Saino et al., 2000, 2003), and plasma nutrient concentration (Dugas & McGraw, 2011). Carotenoid availability is typically limited by the environment (Isaksson, 2009) and carotenoid-based mouth colouration is a condition-dependent signal; therefore, one may expect lower breeding success in broods where nestlings exhibit poor-quality mouth colours, as condition-dependent traits are usually related to the probability of survival.

On the other hand, vocal and postural begging may act as a signal of nestling nutritional need (Kilner & Johnstone, 1997). Nestlings suffering from short-term food deprivation increase their begging rate (Gurguis & Duckworth, 2022; Redondo & Castro, 1992). Thus, under a low-quality rearing scenario in terms of food availability, nestlings would increase the intensity of their begging signals, with hungrier nestlings displaying more intense postural and acoustic signals. This, in turn, could provoke an increase in the parental feeding rate to maintain the nutritional status of the nestlings (Estramil et al., 2013), but this increase may be limited by food availability (Hussell, 1988), especially in poor-quality environments (Caro et al., 2016). Indeed, an increase in begging intensity linked to hunger or poor physical condition in nestlings has been reported under both natural (Budden & Wright, 2001; Gurguis & Duckworth, 2022; Henderson, 1975; Moreno-Rueda et al., 2009) and laboratory (Moreno-Rueda et al., 2016; Redondo, 1991; Redondo & Castro, 1992) conditions. Thus, it is expected that hungry nestlings and nestlings in bad condition would intensify their vocal and postural signals. Hence, we expect that broods showing high levels of begging would suffer lower breeding success.

In this study, we measured nestling time spent begging and carotenoid-based mouth colouration in blue tit (*Cyanistes caeruleus*) broods in two wild populations. Based on previous evidence, we predicted that blue tit pairs whose nestlings begged more (i.e., more time begging for food) and displayed low-quality carotenoid-based colour in their flanges (i.e., lower colour saturation) would be associated with a lower breeding success (here defined as the proportion of eggs that produced fledglings). Hence, a low breeding success would denote low egg hatching success and/or high nestling mortality. Additionally, because blue tits typically exhibit a within-brood size hierarchy, with marginal and smaller nestlings being in poorer condition (Slagsvold et al., 1995; Stenning, 2008), we predicted that blue tit pairs whose broods showed a greater difference in flange colour saturation between the largest and smallest nestling would exhibit less breeding success.

Materials and methods

Study areas and blue tit sampling

The study was carried out during the spring of 2021 using two wild populations of blue tits breeding in nest boxes. One population was located in the Sierra Nevada National Park (36°57′N, 3°24′W), southern Spain, in a typical Mediterranean oak (*Quercus pyrenaica*, *Q. ilex*) forest (hereafter, 'Sierra Nevada'). The second population was located in the Mata Nacional do Choupal (40°13′N, 8°27′W), a mixed deciduous forest peripheral to the city of Coimbra, Central Portugal (hereafter, 'Choupal'). A detailed description of Sierra Nevada and the Choupal study areas can be found in Garrido-Bautista et al. (2023) and Norte et al. (2009, 2010), respectively.

The blue tits bred in nest boxes designed for tits (Paridae), hung from tree branches using metal hooks in Sierra Nevada and attached to tree trunks in Choupal. The nest boxes were placed at heights of 2–4 m in both locations and were monitored during the breeding season to determine the laying date (the day the first egg was laid), clutch size, hatching date (the day the first egg hatched), brood size (nestlings counted at 7 days from hatching), fledgling number (nestlings counted at 13 days from hatching in Sierra Nevada and 14 days from hatching in Choupal), and the number of fledglings that successfully left the nest (successful fledging assumed if fledglings were not found dead in their nests). For each nest, and based on the results (see below), we calculated the breeding success as the proportion of eggs that produced fledglings that left the nest. In 2021, we performed experiments for different studies in Sierra Nevada and Choupal, but only unmanipulated nests were used in this study. In total, we included 26 nest boxes from Sierra Nevada and 11 nest boxes from Choupal.

Measurement and quantification of nestling mouth colour

In the blue tit, as in other passerines, nestling mouths are defined by flanges that display an intense carotenoid-based yellow colour (Dugas & McGraw, 2011; Dugas & Rosenthal, 2010; Heeb et al., 2003). When the nestlings were 7 days old (0 = hatching day), they were weighed with a portable digital scale (accuracy: 0.1 g) in Sierra Nevada and a Pesola balance (accuracy: 0.1 g) in Choupal to identify the smallest and largest nestlings in a brood. We took photographs of nestling mouth flanges from the smallest and largest nestlings within each brood using a Canon 700D camera equipped with a Canon 18–135 mm lens. Nestling mouths were photographed following the protocols and recommendations of Stevens et al. (2007) and Gómez and Liñán-Cembrano (2017). All the photographs were taken at *f*/8.0 aperture, 1/200 s exposure, ISO 200, in RAW format, between 12:00 and 14:00 h (GMT) and using an LED-based ring flash to ensure the same lighting conditions between locations. The photographs were taken zenithward (thus, mimicking the perspective of a feeding parent) and at a height of approximately 30 cm from each nestling. When taking the pictures, the nestlings were placed under a shadow, on a dark background and next to a standard grey reference scale (ColorChecker Passport Photo 2, X-Rite, Michigan). Nestling mouths were gently opened using tweezers to enable visualization and to photograph the flanges (Fig. 1a). The nestlings were manipulated for a maximum of 2–3 min, and immediately returned to their nests.

The digital images were normalised and linearised according to the grey scale using the 'SpotEgg' software (Gómez &

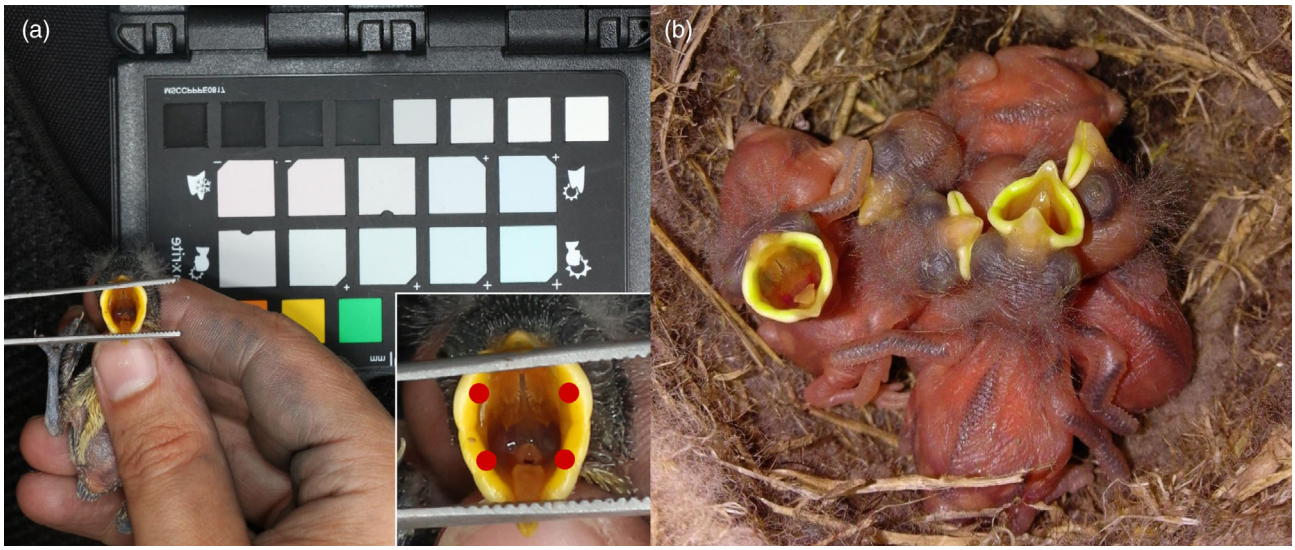

Figure 1 Photographs illustrating (a) the method for determining nestling flange colouration, and (b) a whole brood begging when the nestlings were 3-day old. The four red points in the lower-right picture indicate the flange portions (left and right maxilla, and left and right mandible) where the colour saturation was measured.

Liñán-Cembrano, 2017). This software produced TIFF format images where RGB values were linearly equivalent to the actual reflectance of the colours (Gómez & Liñán-Cembrano, 2017; Stevens et al., 2007). Although birds possess biologically functional receptors for UV light, carotenoids produce colours rich in long wavelengths via the absorption of short-wavelength light (Andersson & Prager, 2006). Therefore, meaningful variation in carotenoid-based colouration in nestling flanges can be captured even if we restrict our analysis to the human visible range provided by most digital cameras (e.g., Dugas & McGraw, 2011). We used saturation as a carotenoid quantity proxy because this colour descriptor has been empirically demonstrated to predict the carotenoid content in nestling yellow flanges when measured from digital photographs (Dugas & McGraw, 2011). Thus, from the normalised and linearised TIFF images mentioned above, we measured the mean saturation values at four points (5 × 5 pixels) on the nestling flange (left and right of the maxilla and left and right of the mandible; Fig. 1a) using Adobe Photoshop 8.0 software. Dirty flange areas were excluded when selecting the points to measure. The mean saturation of those four points per nestling flange was used for the analyses. The repeatability of saturation measurements was high ($r = 0.71$, F-ratio (d.f.) = 10.15 (69, 203), $P < 0.001$) (Lessells & Boag, 1987). We then calculated the mean brood colour saturation as the mean saturation of a brood's smallest and largest nestlings. The colour saturation range was calculated as the saturation value of the largest minus the value of the smallest nestling in a brood.

Vocal begging and feeding rate measurements

To measure feeding rates and vocal begging behaviour in Sierra Nevada and Choupal (Fig. 1b), we placed GoPro Hero 5 microcamera under the roof of the nest boxes when the nestlings were 7 days old. The microcameras were placed in the morning, at approximately 9:00 h (GMT), and recorded for approximately 2 h. A box of a similar size and appearance was installed the previous day to ensure parental habituation. We considered the recording time in a nest from the first to the last feed. Using this time, we estimated the number of feeds and standardised the feeding rate as the number of feeds per hour in each nest. We also measured the average time spent begging by nestlings in each brood using the 'JWatcher 1.0' software (Blumstein & Daniel, 2007). The average time spent begging per nestling in a brood was calculated as the sum of individual begging duration divided by the brood size, expressed as time spent begging in seconds per hour of video recording (s/h). Microcameras were recording on days without cold or rain. No nestling mortality or nest abandonment was observed during the trials.

Statistical analyses

We graphically inspected all the recorded variables for a normal distribution and for the presence of outliers following Zuur et al. (2010). The differences in standardised laying date (day 0 = day the first egg was laid in the population) between the two populations (Sierra Nevada and Choupal) were tested using the Student's t-test (Quinn & Keough, 2002). Differences in clutch size, brood size, number of fledglings, number of fledglings that successfully left the nest, and breeding success (arcsine-transformed) between the two populations were tested in separate linear models. These linear models included the population as a predictor and standardised laying date as a covariate. Variations in the mean of time spent begging (considering total time spent begging by the whole brood) and mean feeding rate between the populations were examined in separate linear models with the population as the predictor,

and the standardised laying date and brood size as covariates. The results obtained from the aforementioned models can be found in the Appendix S1.

We assessed how flange saturation differed between nestling rank (smallest vs. largest), using a linear mixed-effect model of restricted maximum likelihood (REML-LMM) (Zuur et al., 2009). This model (model I) had the following structure: nestling colour saturation was the dependent variable, population and nestling rank were the predictors, standardised laying date and brood size were the covariates, and nest identity was introduced as a random factor. We used three linear models (models II.1, II.2 and II.3) to assess how feeding rate varied with begging signals: feeding rate was included as dependent variable in separate linear models, with the population as a predictor, and standardised laying date and brood size as covariates; the first model (II.1) included the mean brood mouth colour saturation as an extra covariate; the second model (II.2) included the colour saturation range as an extra covariate; and the third model (II.3) included the total time spent begging by the whole brood as an extra covariate.

To test the relationship between the breeding success and both nestling mouth saturation and vocal begging, we used three separate linear models with breeding success as the dependent variable and with the population as a predictor; one model (non-transformed breeding success) included the mean brood saturation as a covariate; another (arcsine-transformed breeding success) included saturation range as a covariate; and the last (arcsine-transformed breeding success) included time spent begging as a covariate. For every model, we visually checked the normality of residuals (distribution of the residuals and Q-Q plots) and homoscedasticity (plots of residuals vs. fitted values). No deviations from any of these assumptions were observed. The basic statistics are presented as the mean ± SE (standard error). All the statistical analyses were performed using the 'R 4.0.0' software package (R Development Core Team, 2020). The REML-LMM was fitted using the function 'lmer', in the 'lme4' package (Bates et al., 2020). The significance of linear models was evaluated with an *F*-test or Wald's χ^2 using the function Anova() in the 'car' package (Fox & Weisberg, 2019). Plots were constructed using the function ggplot() in the 'ggplot2' package (Wickman, 2016). The complete dataset is available in the Data S1.

Results

Blue tits from the Sierra Nevada population showed a higher clutch size, brood size, number of fledglings, number of fledglings that successfully left the nest, and breeding success than blue tits from the Choupal population (Appendix S1). Broods from Sierra Nevada begged for significantly less time than broods from Choupal, but mouth coloration did not differ between populations, and parents fed their nestlings at a similar frequency in both populations (Appendix S1).

Nestling rank was associated with mouth colouration, as the smallest nestlings presented flanges with less yellow saturation compared to the largest nestlings (smallest: 83.39 ± 0.61, largest: 85.21 ± 0.42; Table 1). Nestling mouth colour saturation did not vary significantly between the Sierra Nevada (83.92 ± 0.46) and Choupal populations (84.95 ± 0.79; Table 1). Neither laying date nor brood size correlated with nestling flange colour saturation (Table 1). The feeding rate showed no association with either mean mouth colour saturation or saturation range, but it increased with brood size (Table 1; also Appendix S1). By contrast, feeding rate was positively associated with time spent begging by the whole brood (estimate = 0.013, *t*-value = 3.34, $P = 0.003$; Table 1).

Of the 257 eggs recorded, 45 (Sierra Nevada: 22 out of 187; Choupal: 23 out of 70) did not either hatch or produced nestlings that died before day 7. From day 7 onwards, 28 nestlings died before fledging (Sierra Nevada: 1; Choupal: 27). Hence, breeding success mostly reflected mortality before taking the colour measurements (45 out of 73; 61.6%). The breeding success was positively associated with the mean brood colour saturation (estimate = 0.04, *t*-value = 3.51, $P = 0.001$; Fig. 2a) and negatively associated with the saturation range (estimate = −0.03, *t*-value = −2.08, $P = 0.047$; Fig. 2b). The breeding success did not show a significant association with the time spent begging by broods (estimate = 0.001, *t*-value = 1.58, $P = 0.13$; Fig. 2c).

Discussion

In this study, we explored how two different nestling begging signals, the time spent begging and the carotenoid-based mouth

Table 1 Results of the models for nestling flange colour saturation (model I) and parental feeding rate (models II.1, II.2 and II.3) for the blue tit (*Cyanistes caeruleus*) populations in Sierra Nevada, Spain, and Choupal, Portugal

Independent variables	Wald's χ^2 (d.f. = 1)	*P*-value
Model I (dependent variable = colour saturation)		
Population	0.327	0.567
Nestling rank	8.296	**0.004**
Laying date	0.021	0.883
Brood size	2.327	0.127
Independent variables	***F*-test (d.f.)**	***P*-value**
Model II.1 (dependent variable = feeding rate)		
Population	4.292 (1, 21)	0.051
Mean brood saturation	0.732 (1, 21)	0.402
Laying date	0.981 (1, 21)	0.333
Brood size	11.334 (1, 21)	**0.003**
Model II.2 (dependent variable = feeding rate)		
Population	4.273 (1, 19)	0.053
Saturation range	0.185 (1, 19)	0.672
Laying date	0.812 (1, 19)	0.379
Brood size	10.004 (1, 19)	**0.005**
Model II.3 (dependent variable = feeding rate)		
Population	0.001 (1, 22)	0.976
Time spent begging	11.125 (1, 22)	**0.003**
Laying date	0.968 (1, 22)	0.336
Brood size	0.054 (1, 22)	0.818

The laying date is standardised in all models (day 0 = day the first egg was laid in the population). The brood size was counted at 7 days from hatching. Bold values indicate when $P < 0.05$.

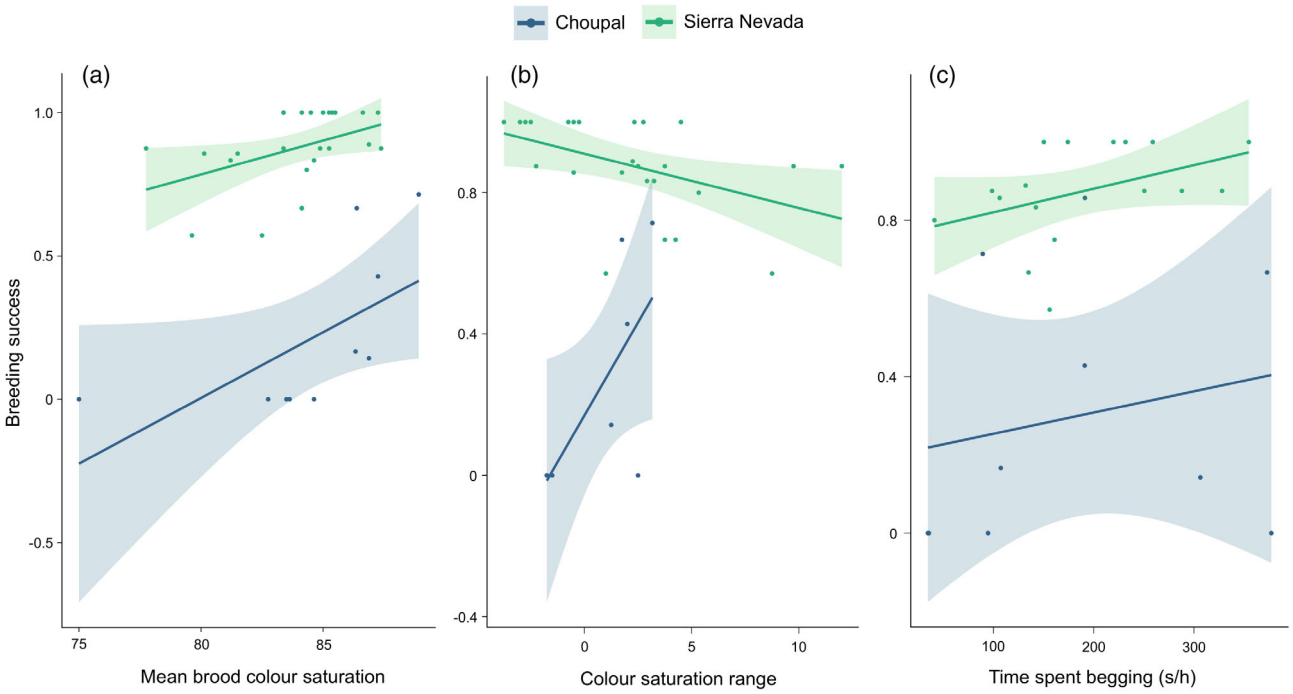

Figure 2 Relationships between the breeding success (proportion of nestlings that successfully left the nest) of blue tits (*Cyanistes caeruleus*) and (a) the mean mouth colour saturation of the brood (mean of the smallest and largest nestling); (b) the colour saturation range (values of the largest nestling minus those of the smallest); and (c) the time spent begging by nestlings. Regression lines are shown with a 95% confidence interval.

flange colouration, are related to breeding success. Vocal and postural begging is a typical indicator of the nutritional needs of nestlings (Kilner & Johnstone, 1997; Mock et al., 2011). Several studies have shown that vocal and postural begging is a reliable signal of nestling state (Cotton et al., 1996; Gurguis & Duckworth, 2022), and could reflect their health status (Saino & Møller, 2002). Also, it has been found that begging effort positively correlates with the level of nest-dwelling ectoparasite infestation (Cantarero et al., 2013; Christe et al., 1996; but see Moreno-Rueda et al., 2016), although this relationship may invert when nestling physical condition deteriorates to a point where they no longer have the energy to beg (O'Connor et al., 2014). Meanwhile, the carotenoid-based flange colouration indirectly advertises the availability of carotenoids in the local environment (Isaksson, 2009), and therefore the nestling nutritional condition (Dugas & McGraw, 2011; Saino et al., 2000, 2003). It also reliably reflects nestling health status, as parasitised chicks commonly exhibit less saturated mouth colouration (Dugas & Doumas, 2014). We predicted that higher breeding success would be related to a higher carotenoid-based colouration in nestling flanges and to a lower vocal begging effort in the brood.

Our results support the former prediction, as nestling mouth colour saturation –which reflects the carotenoid content in nestling flanges (Dugas & McGraw, 2011) – was positively related to breeding success in both populations: blue tits that raised nestlings with more intensely coloured flanges had a breeding success above the median of their population. Nestling carotenoid-based mouth colouration is known to act as a signal of nestling condition since this trait correlates with several condition parameters (de Ayala et al., 2007; Dugas & McGraw, 2011; Ewen et al., 2008; Saino et al., 2000, 2003), and indeed we confirmed that larger nestlings showed a higher colour saturation in their flanges than smallest nestlings. Therefore, higher breeding success was expected to be related to a higher nestling flange colour saturation, since nestlings in better condition normally have higher survival prospects (Merilä et al., 1999; Nur, 1984; Stjernman et al., 2008). However, in our study, most of variation in breeding success was observed before the colour measurements were taken, meaning that broods with high-quality nestlings had higher hatching success rather than lower fledgling mortality than broods with low-quality nestlings. This implies that nestling flange colouration may reflect the maternal pre-laying condition, rather than predicting nestling survival until fledging (Pirrello et al., 2017). In fact, the experimentally increasing carotenoid availability to mothers during the pre-laying stage resulted in enhanced carotenoid content in their offspring's flanges (Ewen et al., 2008), probably through maternal carotenoid investment in the egg yolk (Biard et al., 2005; Ewen et al., 2006).

Furthermore, the breeding success was negatively associated with carotenoid-based colouration range (i.e., the difference in colour saturation between the largest and the smallest nestlings within a brood), meaning that the greater the colour difference

between the smallest and largest nestlings in a brood, the lower the relative breeding success. In the blue tit, the eggs generally hatch asynchronously (Slagsvold et al., 1995; Stenning, 2008), leading to a within-brood size hierarchy and to an unequal distribution of food by the parents according to nestling reproductive value, usually benefiting core nestlings to the detriment of smaller, marginal nestlings (Dickens & Hartley, 2007; García-Navas et al., 2014). Accordingly, smaller nestlings are expected to receive fewer food resources (stimulated by their carotenoid-poor flanges; Border et al., 2023), including carotenoid pigments, which would be reflected in their plasma nutrient concentrations (Sternalski et al., 2012) or their carotenoid-based mouth colouration (this study). Moreover, poor breeding conditions in terms of food availability would exacerbate differences in nestling size since hatching, making nestlings in poorer condition display less coloured mouths (Hõrak et al., 2000). Thus, once a size hierarchy is established in a brood, when food availability is suboptimal, a greater difference in colouration between the largest and smallest nestlings is expected because of the poorer condition of the latter, which often results in partial mortality. Consequently, a decrease in breeding success would be preceded by a greater saturation range. However, we cannot discard the possibility that the greater saturation range would be also a consequence of lower egg hatching success.

In contrast to our prediction that breeding success would be related to vocal begging effort in the brood, the time nestlings spent begging was not significantly associated with breeding success. This result may have emerged because vocal and postural begging typically reflects the hunger level, with nestlings suffering from short-term food deprivation increasing their begging rate (Redondo & Castro, 1992), and hunger may be quickly satiated with the parental response (e.g., Kilner et al., 1999; Leonard & Horn, 2001; Ottosson et al., 1997). In fact, vocal begging appeared to signal current nestling needs, since we found that parents increased their feeding effort in broods where nestlings beg for more time. However, vocal and postural begging could indirectly mirror the quality of the rearing environment, as nestlings from the Choupal population (with low breeding success) begged for significantly longer than those of the Sierra Nevada population (see below). This situation may occur when food availability or quality is so low that parents cannot satisfactorily respond to begging demands.

Despite the large difference in breeding success between the Sierra Nevada and Choupal populations (87% vs. 27% respectively; Appendix S1), nestling mouth colouration did not differ between the two locations but vocal and postural begging did. Urbanization often negatively impacts avian reproductive success and nestling development and condition (Grabarczyk et al., 2022; Redondo et al., 2021; Seress et al., 2012). Caterpillars, the main component of the blue tit nestling diet (García-Navas et al., 2014), show lower biomass and availability in urban and suburban habitats than in forests (Narango et al., 2018; Senar et al., 2021; Seress et al., 2018), which might imply that Choupal blue tit parents cannot adjust their feeding rate to nestling begging rate, making that hungry nestlings beg for longer and, ultimately, leading to reduced breeding success. However, carotenoid-based mouth colouration was similar between the two populations, suggesting that caterpillar abundance was similar. Moreover, the feeding rate was about 33% higher in Choupal than in the Sierra Nevada (albeit the difference was marginally non-significant; Table 1). Therefore, it seems improbable that differences in food availability explain the differences found between the two populations. Alternatively, it may be that filming only on climatologically benign days affected the results, as unfavourable weather was more common in Choupal, the abundance of these days in Choupal perhaps being the cause of the elevated breeding failure.

In conclusion, our findings suggest that differences in carotenoid-based mouth colouration of nestlings within a blue tit population mirror the parents' breeding success during laying and breeding events. Concretely, clutches and broods with nestlings showing more saturated mouth colouration presented higher hatching success and lower fledging survival. On the other hand, vocal and postural begging was unrelated to breeding success probably because it reflected short-term rearing conditions (i.e., parents increased their feeding effort when broods beg for more time). Therefore, morphological begging traits, such as mouth colour, seem to be more integrative than behavioural components of begging since the former probably reflects nestling physiological status in the mid-term (see, for example, Gil et al., 2008), while the latter is more sensitive to the short-term (i.e., reflecting the hunger levels; see, for example, Gurguis & Duckworth, 2022). Consequently, mouth colour rather than behavioural begging display would better reflect the mother pre-laying condition, given the definition of breeding success adopted here and that most of variation in breeding success occurred during the egg incubation stage.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

GMR, JGB and ACN conceived the ideas and designed the study. LPR designed the method for measuring mouth colour. JGB, GMR and ACN performed the fieldwork. PMR obtained the data from the photos. JGB developed the statistical analyses. PMR and JGB wrote the first draft of the manuscript, with input from the other authors. GMR, JR and ACN secured the funding and supervised the project. All authors read and approved the final version of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Dataset.

Appendix S1. Supplementary results.

Table S1. Reproductive parameters of blue tits (*Cyanistes caeruleus*) from the Choupal (Portugal) and Sierra Nevada (Spain) populations.

Figure S1. Relationships between the clutch size of blue tits (*Cyanistes caeruleus*) and the laying date from Choupal (blue) and Sierra Nevada (green) populations.

Figure S2. Relationships between the brood size and the laying date from Choupal (blue) and Sierra Nevada (green) populations.

Figure S3. Relationships between the number of nestlings and the laying date from Choupal (blue) and Sierra Nevada (green) populations.

Figure S4. Relationships between the number of nestlings that successfully left the nest and the laying date from Choupal (blue) and Sierra Nevada (green) populations.

Figure S5. Histograms representing the frequency distribution of breeding success of blue tits (*Cyanistes caeruleus*) in the Choupal (blue) and Sierra Nevada (green) populations.

Figure S6. Relationships between the breeding success, arcsine-transformed, of blue tits (*Cyanistes caeruleus*) and the laying date from Choupal (blue) and Sierra Nevada (green) populations.

Figure S7. Relationships between the total time spent begging by broods from Choupal (blue) and Sierra Nevada (green) populations and the brood size when nestlings were 7 days old (a), and the laying date (b).

Figure S8. Relationships between the feeding rate from Choupal (blue) and Sierra Nevada (green) populations and the brood size when nestlings were 7 days old (a), and the laying date (b).

Supporting information

Journal of Zoology

Begging calls and mouth colouration as predictors of breeding success in blue tits

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Appendix S1

Supplementary results

Reproductive parameters between the two populations

Laying date was an average of one month earlier in the Choupal population (13 April ± 1.78 days) than in the Sierra Nevada population (12 May ± 1.07; $t_{35} = 14.34$, $p < 0.001$). Clutch size was smaller in Choupal than in Sierra Nevada ($F_{1, 34} = 11.12$, $p = 0.002$; Table S1), and in both regions clutch size was negatively related to laying date ($F_{1, 34} = 7.32$, $p = 0.011$; Fig. S1). Brood size, number of nestlings and number of nestlings that successfully left the nest were also lower in Choupal than in Sierra Nevada (in all cases, $F_{1, 37} < 19.92$, $p < 0.001$; Table S1). Brood size was negatively related to the laying date ($F_{1, 34} = 5.12$, $p = 0.030$; Fig. S2), whilst the number of nestlings and the number of nestlings that successfully left the nest showed no significant relationship with the laying date (Fig. S3 and S4).

In Sierra Nevada, all the nests produced at least one nestling (26 out of 26), while in Choupal 8 out of 11 nests (72.73%) produced at least one nestling. When considering nestlings that left the nest at 18-20 days old, in Choupal only 6 out of 11 nests (54.55%) produced at least one nestling, while in Sierra Nevada all the nests produced at least one (26 out of 26). Overall, the breeding success was significantly higher in Sierra Nevada than in Choupal ($F_{1, 34} = 8.11$, $p = 0.007$; Fig. S5; Table S1), but breeding success did not vary with laying date in either of the two regions ($F_{1, 34} = 0.13$, $p = 0.72$; Fig. S6).

Begging and feeding rate between the two populations

Broods from Sierra Nevada begged for significantly less time than broods from Choupal (Sierra Nevada = 491 ± 240 s/h, Choupal: 2173 ± 388 s/h; $F_{1, 23} = 7.89$, $p = 0.010$). In the two populations, the time spent begging increased with both brood size ($F_{1, 23} = 30.86$, $p < 0.001$) and laying date ($F_{1, 23} = 6.26$, $p = 0.019$; Fig. S7). However, parents fed their nestlings at a similar frequency in both populations (Sierra Nevada: 30.57 ± 1.76, Choupal: 39.90 ± 5.84 feeds/h; $F_{1, 24} = 2.19$, $p = 0.15$). In both populations, the feeding rate increased with brood size ($F_{1, 24} = 12.39$, $p = 0.002$), but the feeding rate did not vary significantly with the laying date ($F_{1, 24} = 0.10$, $p = 0.75$; Fig. S8).

Supplementary tables

Table S1. Reproductive parameters of blue tits (*Cyanistes caeruleus*) from the Choupal (Portugal) and Sierra Nevada (Spain) populations. The table presents the mean values and the standard error (± SE).

Parameter	Population	
	Choupal	Sierra Nevada
Laying date [a]	8.55 ± 1.78	38.31 ± 1.07
Clutch size	6.36 ± 0.31	7.19 ± 0.23
Brood size	4.27 ± 0.66	6.35 ± 0.31
Number of nestlings [b]	2.55 ± 0.69	6.31 ± 0.31
Number of nestlings that successfully left the nest	1.82 ± 0.68	6.31 ± 0.31
Breeding success (%)	27.06 ± 0.10	87.20 ± 0.03

[a] 0 = day the first egg was laid.

[b] Number of nestlings was measured when nestlings were 14 days old in Choupal and 13 days old in Sierra Nevada.

Supplementary figures

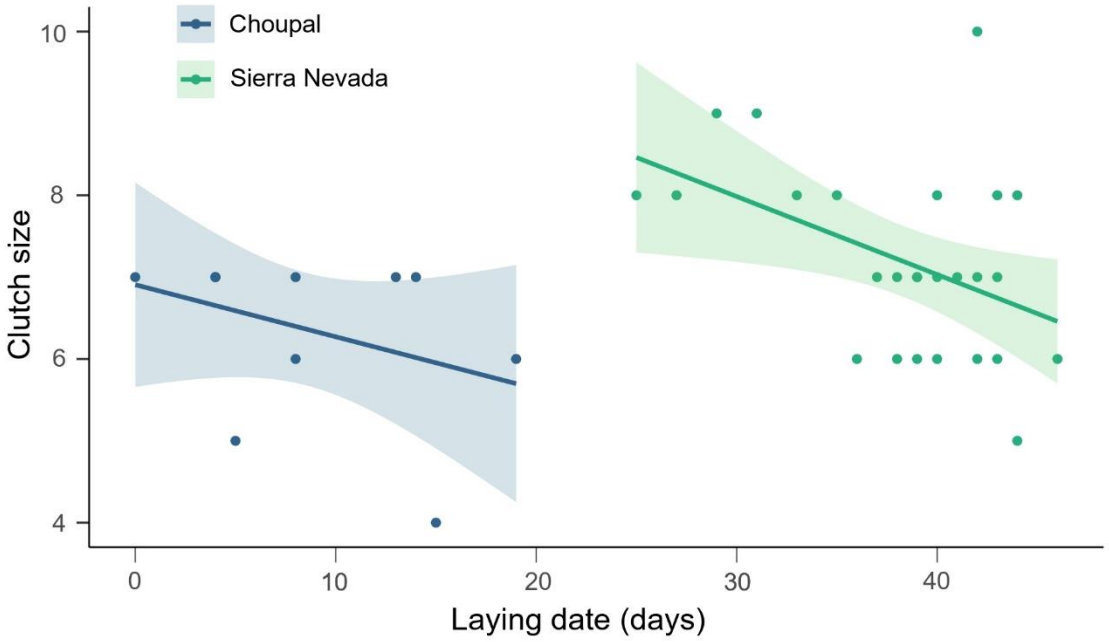

Figure S1. Relationships between the clutch size of blue tits (*Cyanistes caeruleus*) and the laying date from Choupal (blue) and Sierra Nevada (green) populations. Regression lines are shown with 95% confidence interval. Laying date is standardized (0 = day the first egg was laid).

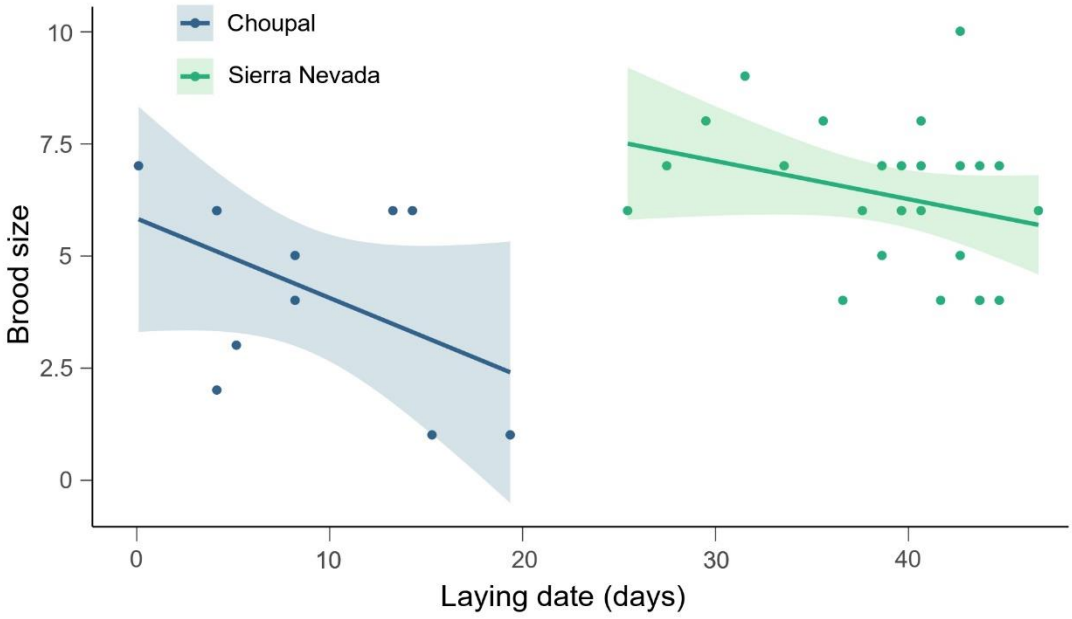

Figure S2. Relationships between the brood size and the laying date from Choupal (blue) and Sierra Nevada (green) populations. Brood size is measured when nestlings were 7 days old. Regression lines are shown with 95% confidence interval. Laying date is standardized (0 = day the first egg was laid).

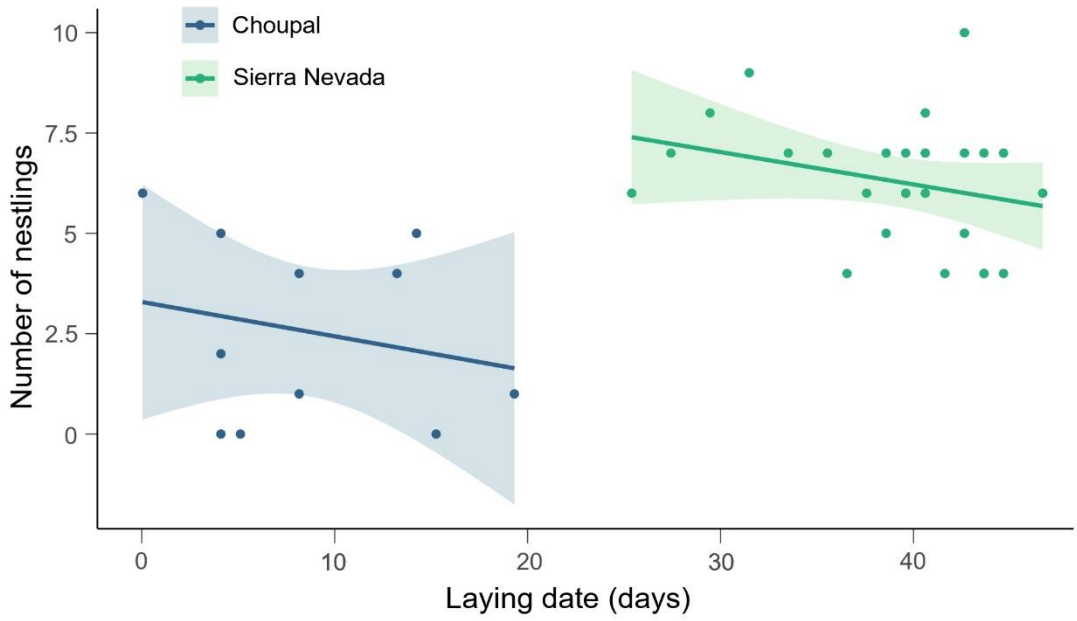

Figure S3. Relationships between the number of nestlings and the laying date from Choupal (blue) and Sierra Nevada (green) populations. Number of nestlings was measured when nestlings were 13 days old in Sierra Nevada and 14 days old in Choupal. Regression lines are shown with 95% confidence interval. Laying date is standardized (0 = day the first egg was laid).

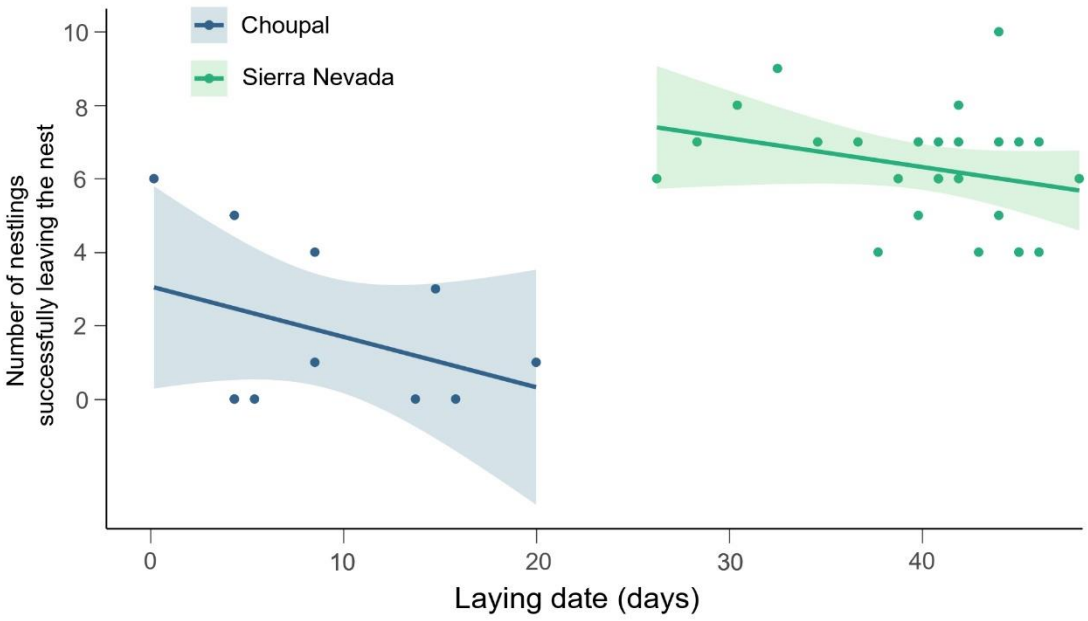

Figure S4. Relationships between the number of nestlings that successfully left the nest and the laying date from Choupal (blue) and Sierra Nevada (green) populations. Number of nestlings was measured when nestlings left their nests, approximately when 18-20 days old. Regression lines are shown with 95% confidence interval. Laying date is standardized (0 = day the first egg was laid).

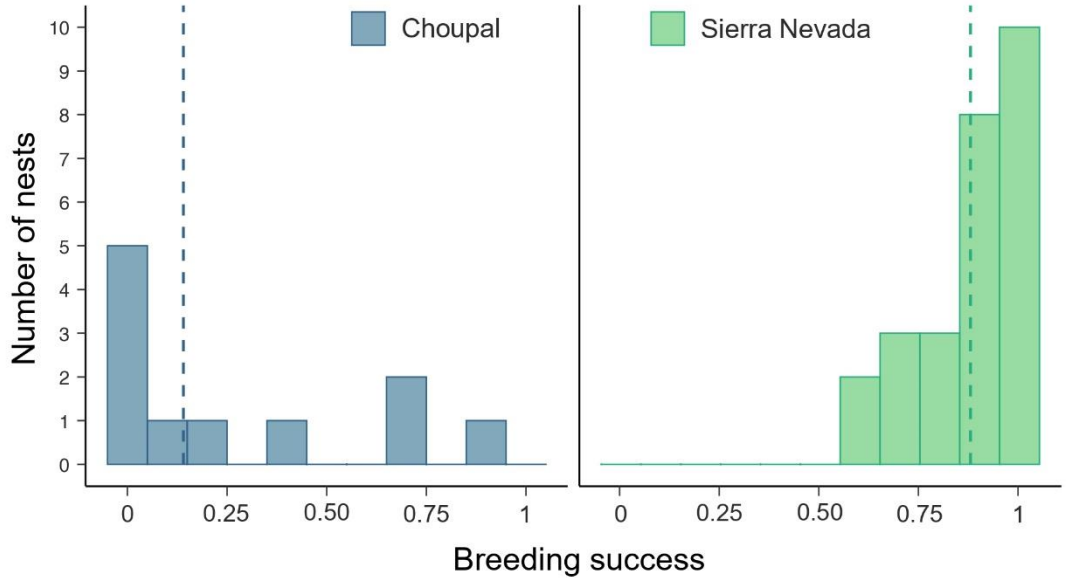

Figure S5. Histograms representing the frequency distribution of breeding success of blue tits (*Cyanistes caeruleus*) in the Choupal (blue) and Sierra Nevada (green) populations. The dashed lines indicate the median breeding success in each population.

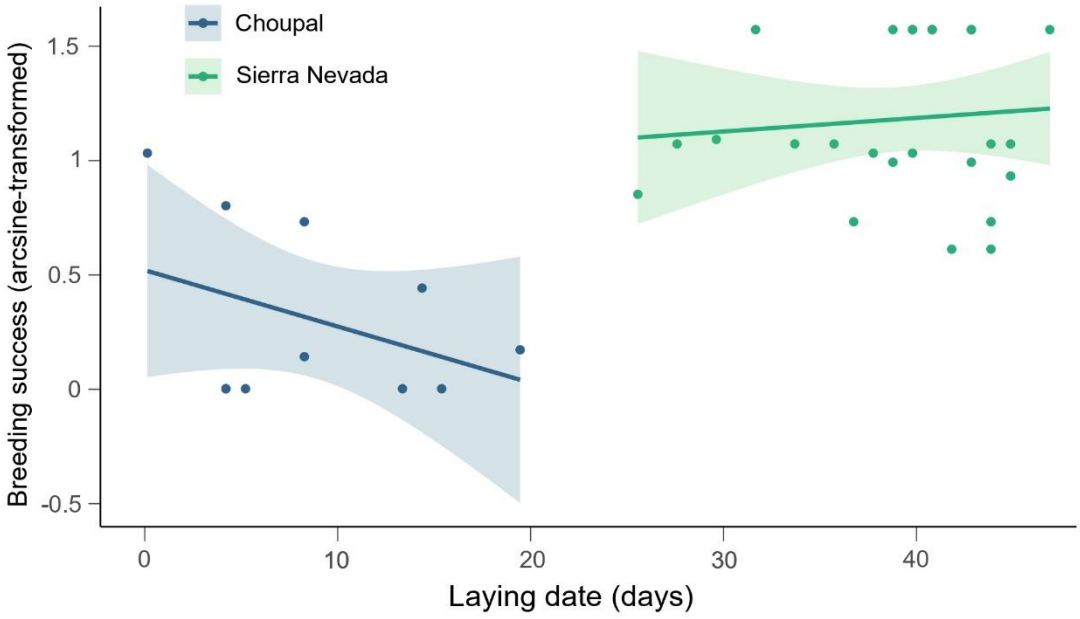

Figure S6. Relationships between the breeding success, arcsine-transformed, of blue tits (*Cyanistes caeruleus*) and the laying date from Choupal (blue) and Sierra Nevada (green) populations. Regression lines are shown with 95% confidence interval. Laying date is standardized (0 = day the first egg was laid).

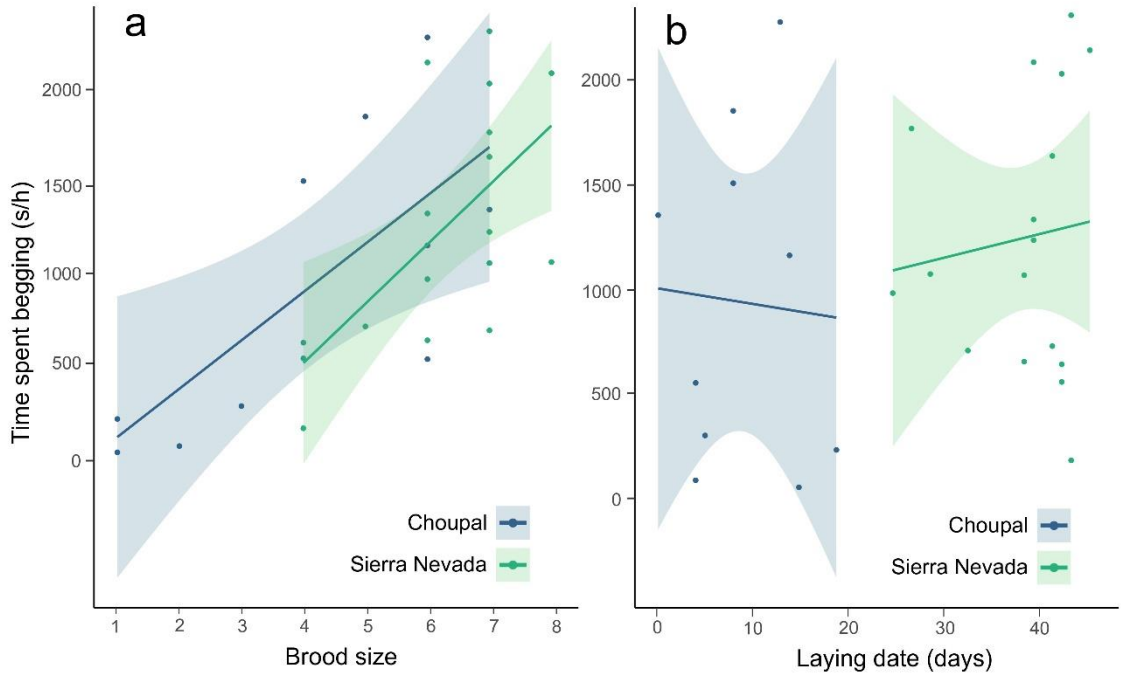

Figure S7. Relationships between the total time spent begging by broods from Choupal (blue) and Sierra Nevada (green) populations and the brood size when nestlings were 7 days old (a), and the laying date (b). Time spent begging refers to seconds spent begging by the whole brood per hour of video recording. Regression lines are shown with 95% confidence interval. Laying date is standardized (0 = day the first egg was laid).

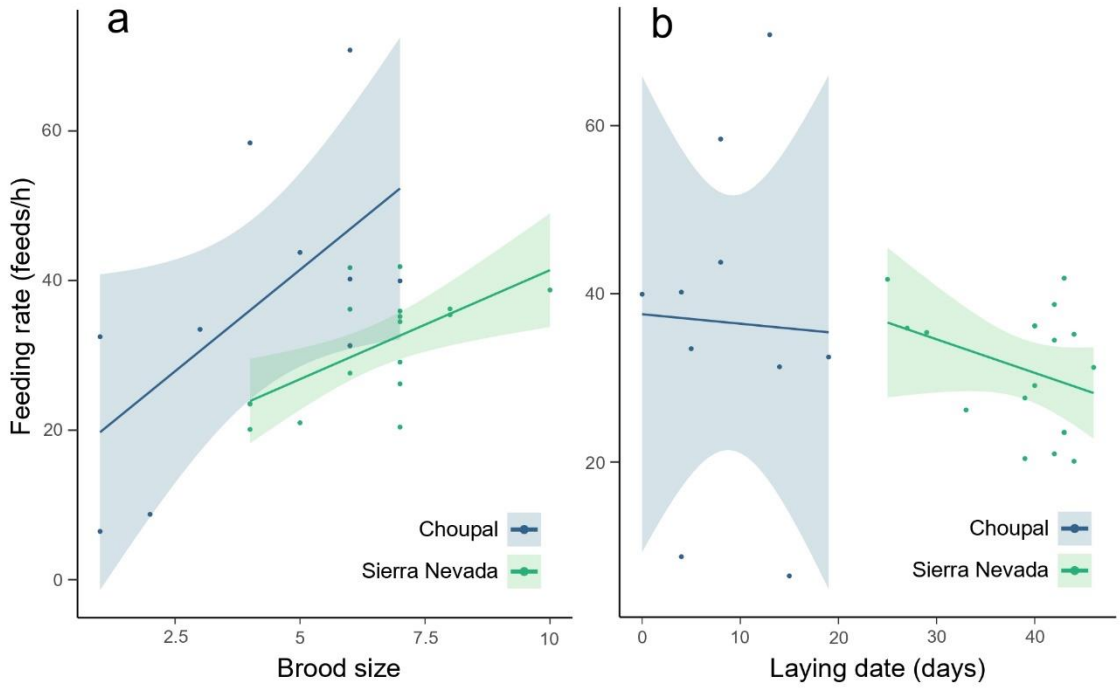

Figure S8. Relationships between the feeding rate from Choupal (blue) and Sierra Nevada (green) populations and the brood size when nestlings were 7 days old (a), and the laying date (b). Feeding rate refers to the number of feeds in a nest per hour of video recording. Regression lines are shown with 95% confidence interval. Laying date is standardized (0 = day the first egg was laid).