Temperature-related developmental plasticity, not selection, affects offspring body size and shape in a bird of prey

Running title: Antagonistic effects of temperature on body morphology

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Abstract

Recent climate warming has led to a reduction in bird body size and a relative elongation of their appendages, consistent with Bergmann's and Allen's ecogeographical rules. These changes are generally interpreted as thermoregulatory adaptations for more efficient passive heat dissipation; however, direct evidence supporting this assumption is currently missing, and laboratory studies failed to find significant thermoregulatory benefits associated with body size or appendage length. To test whether body shrinking and shape-shifting provide a fitness advantage under climate warming, we experimentally altered nest temperatures in a lesser kestrel (*Falco naumanni*) population exposed to high temperatures during the nestling stage. We found that nest temperature was associated with nestling mortality. Among nestlings that survived to fledging, temperature was negatively correlated with their near-fledging body size (mass and tarsus length) and positively correlated with their relative bill length. Contrary to the thermoregulation hypothesis, we found that nestlings that were larger at hatching had higher survival, irrespective of the nest temperature, whereas relative bill length did not confer any significant survival advantage. Collectively, our findings suggest that temperature-related developmental plasticity, rather than selection, is a key driver of observed morphological changes in natural bird populations, and that these changes are not adaptive.

Keywords: Allen's rule, Bergmann's rule, bill length, body size, nest temperature, heatwaves

Introduction

Global climate has experienced significant warming in recent decades, accompanied by more frequent and intense temperature extremes (Lee et al., 2023). During this period, evidence has accumulated that many homeothermic animals, including birds, have progressively decreased in size and increased the relative length of their appendages, associated with rising temperatures (Gardner et al., 2011; Campbell-Tennant et al., 2015; van Gils et al., 2016; Prokosch et al., 2019; Tian and Benton, 2020; Ryding et al., 2021; Dubiner and Meiri, 2022; Youngflesh et al., 2022; Zimova et al., 2023; Romano et al., 2024). These morphological shifts align with Bergmann's and Allen's ecogeographical rules, which posit that animals in warmer climates—typically lower latitudes and altitudes—tend to have smaller body sizes and relatively longer appendages than those in colder environments (Bergmann, 1847; Allen, 1877). Smaller body size and longer appendages increase the surface-to-volume ratio, enhancing passive heat dissipation in hot climates, while lower surface-to-volume ratios are advantageous in colder climates (Mayr, 1956). Although the extent of changes in body size and appendage length (e.g., bill length; Tattersall et al., 2017) varies among species (Ryding et al., 2024; Santoro and Calzada 2022), there is extensive empirical support for a widespread avian response to warming temperatures (e.g., Campbell-Tennant et al., 2015; Gardner et al., 2016; van Gils et al., 2016; Weeks et al., 2020; Jirinec et al., 2021; Romano et al., 2024). However, the underlying mechanisms driving these rapid changes remain uncertain.

Two non-mutually exclusive explanations have been proposed to explain the observed rapid shifts in body size and relative appendage length among bird populations in response to climate warming (Campbell-Tennant et al., 2015; Cardilini et al., 2016; Youngflesh et al., 2022; Fröhlich et al., 2023). The first hypothesis suggests that these phenotypic shifts may be adaptive evolutionary responses to selection for enhanced heat dissipation capability, conferred by a higher surface-to-volume ratio (Ryding et al., 2021; Youngflesh et al., 2022). For example, relatively longer bills may offer a thermoregulatory advantage in warming climates because their vascularization improves dry heat dissipation (Tattersall et al., 2017; Schraft et al., 2019). Similarly, other non-feathered appendages, such as the tarsus, may enhance heat dissipation during heat stress in certain species (McQueen et al., 2022). Thus, individuals with smaller bodies and relatively larger appendages might increase their efficiency in dry heat dissipation, reducing the costs associated with active evaporative cooling (Greenberg et al., 2012; Song and

Beissinger, 2020). The strongest shifts in body size and shape have been observed in populations exposed to more intense climate warming, supporting the adaptive hypothesis for increased surface-to-mass ratios (Youngflesh et al., 2022; Dubiner et al., 2022; Romano et al., 2024). However, direct evidence showing that individuals with smaller size and a higher surface-to-volume ratio have increased fitness under naturally high temperatures is still lacking (Siepielski et al., 2019; Nord et al., 2024).

The second hypothesis arises from observations that in several studies, avian nestlings exposed to high temperatures during development show reduced growth rates (James, 1991; Burness et al., 2013; Andrew et al., 2017; Larson et al., 2018; Corregidor-Castro and Jones, 2021; Weeks et al., 2022; Shipley et al., 2022) and relatively longer bills by fledging (Tabh et al., 2024). It has been suggested that climate-related shifts in body size and shape observed in recent cross-sectional studies on bird populations may result from developmental plasticity rather than selection (James, 1991; Tabh and Nord, 2023). Experiments in which developmental temperature was experimentally controlled – either in the lab (e.g., Burness et al., 2013; Tabh et al., 2024; Shipley et al., 2022) or under natural conditions (Sauve et al., 2021) – provided partial support for the developmental hypothesis, possibly because the effect of temperature on bird growth may depend on whether it is experimentally raised above or lowered below the optimal range for nestling development (Shipley et al., 2022; Tabh and Nord, 2023; Nord et al., 2024). Importantly, temperature-related developmental plasticity has shown minor effects on thermoregulation, survival, and reproduction under laboratory conditions (Tabh and Nord, 2023; Hope and Angelier, 2024).

While both selection and plasticity hypotheses are plausible and may operate simultaneously, whether body size and shape shifting observed in natural populations is the consequence of a thermoregulatory advantage remains an area of ongoing debate (Nord et al., 2024; Youngflesh et al., 2024). Clarifying the roles of these mechanisms is crucial, as these changes could signify rapid adaptation to climate warming or serve as early indicators of potential population decline (Cerini et al., 2023). To address these gaps, we conducted a nest temperature manipulation experiment in a Mediterranean population of the cavity-nesting lesser kestrel (*Falco naumanni*), a small (140 g) bird of prey. Lesser kestrels readily breed in nest boxes and experience high temperatures during the breeding season, which has adverse effects on nestling survival (Catry et al., 2011; Catry et al., 2015; Campobello et al., 2017). Nest

temperature was experimentally reduced in a group of nest boxes by shading them from direct sunlight, a manipulation that reduces internal nest temperatures by approximately 4°C as compared to unshaded, control boxes and increase nestling survival and growth (Corregidor-Castro et al., 2023). Here, we expand on this approach to address two questions. First, we tested whether nest temperature affects nestling body size and bill length near fledging. Bill is considered an important heat dissipation organ in birds (Tattersall et al., 2017). Second, given that high nest temperature is linked to significant nestling mortality (Corregidor-Castro et al., 2023), we examined whether body morphology during early development is differently associated with subsequent survival to fledging in the two experimental groups. If smaller body size and relatively longer appendages confer a thermoregulatory advantage, positive selection for nestling body size, that it is typically observed in birds (Krist, 2011), should be weaker or even negative in control nests as compared to shaded ones (Siepielski et al., 2019).

Material and Methods

Study species, study area and general field procedures

Our experiment was conducted in the city of Matera, southern Italy (40°66′N, 16°61′E), home to a large population of lesser kestrels with approximately 1,000 breeding pairs (La Gioia, 2017). These kestrels nest in building cavities and artificial nest boxes (Morinay et al., 2021). Clutch size ranges from 3 to 5 eggs, which are laid from late April to early May (Ramellini et al., 2022). Both parents incubate the eggs for around 31 days and continue feeding the young for about 40 days after hatching (Podofillini et al., 2018).

The study took place over two breeding seasons (May – July 2021 and 2022) on a large roof (600 m^2), where 66 nest boxes were installed between 2008 and 2010. These nest boxes have been consistently occupied by lesser kestrels (Corregidor-Castro et al. 2023). From the start of each breeding season, we monitored nest boxes every 3-4 days to record laying and hatching dates, and both clutch and brood size, until nestlings were approx. 15 days old, after which visits ceased to minimize the risk of premature fledging (Podofillini et al., 2018). Upon hatching, individual nestlings were temporarily marked with unique dot patterns on the head and later ringed at around 10 days of age. Nestlings were ranked by hatching order, with rank 1 assigned

to the first-hatched nestling. Nestlings were blood-sampled and sexed using standard molecular markers (Corregidor-Castro et al. 2023).

Nest temperature manipulation

We performed an experimental manipulation of the nest boxes to partially decouple external environmental temperature (recorded at the Matera city meteorological station, see Corregidor-Castro et al. (2023)) from the temperature recorded inside the nest. To do so, upon hatching, we created temporally matched groups (hereafter "synchronous groups") of at least two nest boxes, paired based on hatching date, clutch size, and other nest characteristics such as orientation and sun exposure. Within each synchronous group, one randomly chosen nest box was covered on the top and sides with a 0.5 cm thick plank of plywood, forming an open box structure (41 × 36 × 45 cm; shaded nest box). The other nest box in the group was left unmanipulated (control nest box). We recorded nest box internal temperature using temperature loggers (Elitech RC-5+, Elitech, UK; accuracy 0.5°C) attached to the internal side of the wooden back panel of each nest box. To protect the panel from direct sunlight, a 40 × 40 cm tile was placed outside on the back of each nest box, shading the wall while allowing air to circulate. Temperature loggers were set to record every 15 min, from hatching of the first nestling until the end of the monitoring season, when they were retrieved. All loggers were certified as being individually calibrated by the supplier. Preliminary testing in a thermostatic chamber at constant temperature for 12 hours confirmed negligible differences between loggers.

To test the effect of nest temperature on nestling body size and shape near fledging, we calculated the mean of the maximum daily temperatures recorded in each nest box over the 10 days prior to the last nestling measurement (hereafter T_{nest}). This period corresponded to the minimum interval between the start of the experimental manipulation and the age when nestlings were last measured, excluding the setup day and the final measurement day. We used maximum daily temperatures because previous studies demonstrated that lesser kestrel nestlings are sensitive to high nest temperatures, which are associated with reduced survival and growth (Catry et al. 2015; Corregidor-Castro et al. 2023).

Nestling morphology

We obtained morphological measurements of nestlings during three monitoring visits. In the first visit (hereafter at-hatching), when nestlings were approximately 1 day old (± 1 day), we recorded body mass, using an electronic scale (accuracy 0.1 g), and tarsus length, using a calliper (accuracy 0.1 mm). To minimize disturbance during this sensitive stage, bill length was not measured at this time. In total, we measured body mass in 185 nestlings (control = 88; shaded = 97; 73 broods) and tarsus length in 196 nestlings (control = 93; shaded = 103; 76 broods). This visit marked the start of the experimental treatment.

Three days later, when nestlings were approximately 4 days old (± 1 day), we obtained a second set of measurements (hereafter near-hatching) for body mass and tarsus length (n = 182 nestlings: control = 85, shaded = 97; 74 broods) and the first measure of bill length (n = 179 nestlings: control = 82, shaded = 97; 73 broods). Bill length was measured as the distance from cere to bill tip using a caliper. These measurements allowed us to calculate early growth rates in body size, based on the daily increase in body mass and tarsus length from age 1 (at hatching) to age 4 (at near-hatching). By this time, nestlings had already been exposed to the experimental treatment, but no significant differences in morphology or mortality were detected between control and shaded groups (see Table S1). We limited our estimation of body growth to this initial period of development to minimize temperature-related differences in mortality and growth rate between control and shaded nestlings.

A final measurement visit was conducted when nestlings were on average 15.6 ± 1.7 days old (range 13–20 days, hereafter near-fledging). This age corresponded with the end of the linear growth phase (Romano et al., 2021) and is expected to predict body size at fledging (see Braziotis et al. 2017). We did not measure older nestlings for two reasons. First, since nestlings start to spend significant amount of time outside the nest after this age (Corregidor-Castro et al., 2024), their morphological measurements could not be related to nest manipulation and temperature. Second, capturing near-fledging individuals may have increased the risk of premature abandoning of the colony roof (Podofillini et al., 2018). Due to mortality between visits, sample size for this final visit was reduced to 147 nestlings (control = 49, shaded = 98; 55 broods). To assess fledging survival, we conducted a final check when nestlings were approximately 25 days old. Although lesser kestrel juveniles leave the colony roof at around 37

days of age, mortality between age 25 and 37 days is virtually absent (A. Corregidor-Castro, personal observations). Any nestling missing from the colony roof by age 25 days was therefore assumed to be dead, although the exact cause and date of death was occasionally unknown (Corregidor-Castro et al., 2023), and thus nestlings that were alive at age 25 days were considered to have successfully fledge from the colony.

Passive heat dissipation through the bill is expected to depend on bill surface and therefore bill area should reflect dry heat dissipation capability more closely than bill length (Tattersall et al., 2017). However, measuring bill area is a lengthy procedure which would have unduly prolonged researchers' visits at the colony and increased disturbance. In a separate sample of 26 nestlings (in 2021), we verified this proxy by correlating bill length (cere-to-tip distance) with bill surface area, obtained from digital photos taken of the left side of the head on a standardized support with a reference scale (see Fig. S1a), followed by a second photo to estimate a measurement of repeatability. Bill lateral area was calculated using ImageJ, blind of the nestling identity (Schneider et al., 2012; Fig. S1b). Nestling bill length was also measured twice following a blind procedure (i.e. one operator placed the calliper and the measure was read and transcribed by a second operator). The measurements were highly repeatable (bill length, repeatability = 0.93 ± 0.02; bill lateral area, repeatability = 0.99 ± 0.01; Lessells and Boag, 1987) and we therefore used the average of the two measurements. Upper mandible area (lateral area × 2) and bill length were significantly correlated ($r = 0.87$, $p < 0.001$, $n = 26$), supporting bill length as a reliable proxy for bill area.

Statistical analyses

Effect of shading on nest temperature - To test if shading effectively reduced T_{nest}, we used a linear mixed model (LMM) where T_{nest} was the response variable, with year and experimental treatment as two-level fixed factors (year: 2021, 2022; shading: control, shaded). To account for seasonal variation and to align with the pairwise nature of the experimental design, we included synchronous group identity as a random intercept effect (here and in all subsequent models).

Effect of shading on nestling size and shape near fledging – We examined the effect of shading on nestling morphology near fledging (body mass, tarsus length, and bill length) by fitting three separate LMMs, each with one morphological trait as the response variable. In each model, experimental treatment was included as a fixed factor, along with year, brood size, age and hatching rank of the nestling, as they could influence nestlings' final size (Aparicio, 1997; Braziotis et al. 2017; Podofillini et al. 2019). Furthermore, we included the sex of the nestling (0 = female, 1 = male) to account for sex-linked size differences. We included nest identity as a random factor to control for the non-independence of nestlings from the same brood, along with synchronous group identity. Considering that some of the nests of the two experimental groups had similar nest temperatures (caused by the variation in the external temperatures and the asynchrony between nests; Fig S2), we fitted three additional models using T_{nest} as a covariate, instead of the experimental treatment. If temperature differences are the primary driver of any morphological differences between experimental groups, we expected a stronger statistical effect of T_{nest} than experimental treatment.

To further investigate the relationship between temperature and relative bill length (accounting for body size), we included body mass and tarsus length as covariates in a model with bill length as the response variable. Fixed and random effects were as above, and an alternative model with T_{nest} instead of the experimental treatment as a covariate was also fitted. Because tarsi are naked appendages and can be related to heat dissipation (Ryeland et al., 2019; McQueen et al., 2023) we fitted two additional models with tarsus length as the response variable and body mass as a covariate, one including the experimental treatment and the other the T_{nest} as predictors. These models contained the same predictors as those stated above.

Finally, given the positive correlation between body mass, tarsus length, and bill length, we conducted a Principal Component Analysis (PCA) of these traits to generate independent indices of body size and shape. In particular, the first axis (PC1) represents a metric of body size variation (Weeks et al., 2020), while the second axis (PC2) should be regarded as a metric of the variation in the three body measures removing differences in size (see a similar approach to the analysis of bill size and shape in Darwin finches, Grant and Grant, 2008). We used the resulting PCA scores to fit two LMMs with the experimental treatment and nestling sex as fixed factors, and year, brood size, age, and hatching rank as covariates. These models were also repeated with

T_{nest} as a covariate instead of the experimental treatment to further analyze the impact of temperature on nestling morphology.

Effect of nestling size and early development on subsequent survival – We first tested whether nestlings from the two experimental groups differed in any relevant parameter at hatching (age 1) and at near-hatching (age 4). For age 1, we used LMMs to analyze differences in body mass, tarsus length, age of the nestling and brood size, with each variable included as a response variable. The experimental treatment was set as a fixed factor, with nest and synchronous group identity as random intercepts to account for group effects. For age 4, we applied similar LMMs for the same variates measured in the previous visit, with the addition of bill length (first measured at age 4) and its relative size compared to body size. Two additional LMMs tested whether growth rates in body mass and tarsus length differed between ages 1 and 4. We also evaluated differences in survival from age 1 to age 4 using a binomial generalized linear mixed model (GLMM) with a logit link function. No significant differences were found between shaded and control nestlings for any trait (see Table S1).

Given that nestlings measured at age 1 and age 4 varied in age (0-2 days for nestlings measured at hatching, and 3-5 days for nestlings measured at near-hatching), and that these age differences impacted all morphological measurements, we calculated age-corrected values for body mass and tarsus length (for both ages) and bill length (for age 4 only). These values were generated as standardized residuals from a model with age as a fixed factor (Salas et al., 2022). Next, we analyzed survival as a function of age-corrected body mass and tarsus length at hatching using a GLMM with binomial error distribution and logit link. Survival (0 = did not survive; 1 = survived) was set as the dependent variable, with the experimental treatment, age-corrected body size measurements (mass or tarsus length), and their interaction as fixed factors. A significant interaction between nestling morphology and shading would indicate that nest temperature affects selection strength and/or direction on body size and morphology. As above, we included sex, nestling rank, and brood size as fixed factors to account for their effects on survival. We repeated these analyses for age 4 nestlings, including age-corrected bill and relative bill length. Finally, we used a principal component analysis (PCA) on body mass, tarsus length, and bill length data from age 4 to derive an overall body size (PC1) and body shape index (PC2).

Using GLMMs similar to the previous analyses, we tested whether survival to fledging depended on nestling body size (PC1) and body shape (PC2).

Effect of nestling early growth on subsequent survival – We examined whether nestlings' early growth rate, calculated as the daily difference in age-corrected body mass and tarsus length between ages 1 and 4, was associated with subsequent survival to fledging, and whether this association differed between the two experimental treatments. We used GLMMs, with individual survival as the binomial response variable, and the experimental treatment, growth rate (in body mass o tarsus length), and their interaction as fixed factors. We included sex, nestling rank, and brood size as fixed factors to control for their potential effects on survival.

All statistical analyses were carried using the statistical software R, version 4.3.3 (R Core Team, 2024). We fitted LMMs and binomial GLMMs using the "lme4" and "glmmTMB" libraries (Bates et al., 2015; Brooks et al., 2017). We checked for collinearity and inspected residual diagnostics using the "performance" package (Lüdecke et al., 2021). In all our mixed models, we mean-centred the predictors. Significance of fixed predictors in LMMs and GLMMs were assessed by likelihood ratio tests (Singmann et al., 2015). For clarity in the text, we present the models including only significant predictors, where full models (with non-significant predictors) are given in the supplementary material (Tables S2-S12). In survival analyses, we retained the interaction between nestling morphology and the experimental treatment even when non-significant, to formally test if selection on morphology was influenced by nest temperature. In all survival models, nestling morphology significantly predicted survival even after excluding non-significant interactions (results not shown). Means and parameter estimates are provided with standard errors, unless noted otherwise.

Results

Effect of shading on nest temperature

Shading reduced nest temperatures during nestling growth. In particular, recorded nest temperatures (T_{nest}) were significantly higher in control nest boxes compared to shaded ones

(control: 41.9 ± 0.3°C; shaded: 39.1 ± 0.2°C; $F_{2,52} = 54.6$; $p < 0.001$), although temperatures largely overlapped between the two experimental groups (Fig. S2a). This resulted from nest temperature depending not only on our shading manipulation but also on occurrences of hot weather peaks during the breeding season and the differences in nest phenology (Fig. S2b).

Effect of shading on nestling size and shape near fledging

Control nestlings had lower body mass and shorter tarsus length near fledging compared to their shaded counterparts, indicating high maximum temperatures depressed nestling growth (Table 1a,b; Fig. 1). This conclusion was further supported by a qualitatively similar but stronger negative effect of the actual nest temperatures experienced by nestlings (T_{nest}) on nestling size (Table S3a,b). In contrast, we found no significant effect of either experimental treatment or T_{nest} on nestling bill length (Table 1c; Fig. 1; Table S3c). However, when statistically controlling for body size, bill length was positively correlated with T_{nest}. The experimental treatment effect on relative bill length followed the same positive direction, although not statistically significant (Table S4). Relative tarsus length showed no correlation with either the experimental treatment or T_{nest} (Table S5).

Similar results were obtained using principal component analysis (PCA) to describe variation in nestling morphology. PC1, accounting for 78% of variance, was positively loaded on body mass, tarsus length and bill length, representing an overall body size index. PC2, accounting for 16% of variance, was positively loaded on bill length but negatively on body mass and tarsus length. Therefore, positive PC1 scores indicated larger nestlings whereas PC2 positive scores indicated nestlings with relatively longer bills, lower body mass and shorter tarsi (Table S6). Control nestlings had significantly lower PC1 scores and higher PC2 scores than shaded counterparts (Table 2; Fig. 2). Confirming previous results, T_{nest} was negatively correlated with PC1 and positively with PC2, with T_{nest} being a stronger predictor of morphology than shading treatment (Table S8). PCA also revealed significant sexual dimorphism, with males characterized by smaller size and relatively shorter bills (lower PC1 and PC2 scores; Table 2a,b). While nestling age and year were associated with PC1 and PC2, respectively (Table 2), their interactions with treatment (or T_{nest}) were non-significant.

Effect of nestling size and early development on subsequent survival

Age-corrected body mass and tarsus length at hatching were positively correlated with survival in both experimental groups, with no significant interaction between shading and nestling size (Table 3). As expected (Corregidor-Castro et al., 2023), nestlings from shaded nests and higher-ranking nestlings had higher survival (see full models in Table S9). This positive correlation between body size and nestling survival was confirmed using measurements at near-hatching (body mass, tarsus and bill length), again with no significant interaction between the experimental treatment and the morphological traits. On the other hand, no correlations were detected between relative bill size and survival (Table 3; Table S10; Fig. 3). PCA of near-hatching nestling morphology paralleled results from near-fledging: PC1 explained 77% of variance, positively loaded on body mass, tarsus and bill length; PC2 explained 15% of variance, positively loaded on bill length but negatively on tarsus length and body mass (Table S6). As above, positive PC1 and PC2 scores corresponded to larger nestlings and nestling with relatively longer bills, respectively. Models based on PC1 and PC2 scores corroborated linear measurement results: PC1 scores positively correlated with subsequent survival, with no significant treatment group interaction, whereas PC2 scores showed no survival correlation (Table 3; Table S11). This indicates that larger nestlings had a similar survival advantage irrespective of temperature, with no measurable advantage of relatively larger bills. Growth rate, expressed as the increase in body mass and tarsus length from ages 1 to 4 days, was positively correlated with survival, irrespective of the shading treatment (Table 3; Table S12). Consistent with previous analyses, higher-ranking nestlings and those from shaded nests tended to have higher survival.

Discussion

While the phenotypic responses of birds to climate warming (Bosco et al., 2023; Ryding et al., 2024; Baldwin et al., 2023; but see Wilcox et al., 2024) match predictions from Bergmann's (body size reduction) and Allen's (relative bill length increase) ecogeographical rules, controversy remains about the proximate and ultimate drivers of such body size and shape shifts (Nord et al., 2024; Youngflesh et al., 2024). Some interpret the shape-shifting as an adaptive process resulting from enhanced survival of smaller birds with relatively longer appendages (e.g. Youngflesh et al., 2024) and/or adaptive developmental plasticity (e.g. Larson et al., 2018).

Others suggest observed shape changes largely result from neutral or non-adaptive developmental plasticity (e.g. Siepielski et al., 2019; Nord et al., 2024).

Our study is the first to simultaneously investigate, in a field experiment, how nest temperature affects nestling morphological development, and whether the link between nestling morphology and survival changes according to the temperature nestlings experience, providing answers to the above questions. First, we found that near-fledging nestlings from warm, unshaded (control) nest boxes had a smaller body size (lower body mass and shorter tarsus length – see also Corregidor-Castro et al., 2023) and a relatively longer bill, compared to nestlings from the colder, shaded nest boxes. The effect of temperature on nestling morphology was more evident when considering the maximum daily temperatures recorded in the nests during the ten days prior to morphological measurements. This is expected, as although shading significantly reduced the average nest temperature, the wide variation in environmental air temperatures and the asynchrony among nests led to some overlap in temperatures between control and shaded boxes. Second, our survival analyses confirmed that nestlings with larger body size at hatching had a greater probability of surviving until fledging (age 25 days). While control nests experienced significantly higher nestling mortality than shaded nests, the strength of positive selection on body size did not differ between control and shaded broods. In other words, nestlings with smaller body size at hatching showed no measurable survival advantage when subsequently exposed to higher temperatures during development. Third, we found that nestlings with an initially faster growth rate (i.e. larger increase in body size between ages 1 and 4 days) had better survival. Again, selection for growth rate did not differ between control and shaded broods, indicating faster-growing nestlings had a survival advantage irrespective of the temperatures experienced during later development. Fourth, nestlings with relatively longer bills at day 4 (when bill length was first measured) did not significantly differ in subsequent survival to fledging compared to those with relatively shorter bills. As above, no differences were found between control and shaded broods, indicating that nestling body shape morphology did not provide measurable thermoregulatory advantages and, indirectly, that the differences in morphology between shaded and control nestlings were due plasticity. Below we discuss how our results can contribute to interpreting the body size and shape shifts observed in bird populations responding to climate warming.

Temperature-related developmental plasticity in body size and shape

The magnitude of the temperature-related morphological shift we observed in near-fledging lesser kestrels is comparable to shifts seen in adult birds of several populations exposed to climate warming over recent decades, in both temperate (Ryding et al., 2021; Youngflesh et al., 2022; Bosco et al., 2023; Ryding et al., 2024) and tropical regions (Dubiner and Meiri, 2022; Zimova et al., 2023). For example, Ryding et al. (2024) found in a study of bird skins from 78 species collected over the past century that relative bill size increased 1.5% on average (range -20% to +19.5%). In our study, nestlings from the hottest nests (45°C) had 8.4% longer bills relative to body size compared to those from the coldest nests (35°C), corresponding to a 0.8% ± 0.4 SE increase in relative bill length per 1°C rise in maximum nest temperature. As summer (June-August) land temperatures in Europe have increased about 2°C in recent decades (Luo et al., 2023), this would correspond to a 1.6% increase in relative bill length - comparable to Ryding et al.'s (2024) findings. Our results indicate body size and shape shifts reported in bird populations may potentially be explained entirely by developmental plasticity.

However, the extent to which the temperature effect on fledging morphology will influence adult body size and shape in subsequent generations depends on two assumptions. The first is that the temperature-related developmental plasticity observed in near-fledging morphology permanently affects adult morphology. While we lack direct evidence for our lesser kestrel population, high nestling temperatures have been shown to permanently impact adult morphology in other bird species (Mariette and Buchanan, 2016; Andrew et al., 2017; Shipley et al., 2022; Hope and Angelier, 2024; but see Burness et al., 2013). The second assumption is that reproductive recruitment is unaffected by near-fledging morphology, i.e. smaller lesser kestrel fledglings have equal survival and reproductive success as larger counterparts. This seems unlikely, as larger fledglings usually have higher survival to adulthood (Maness and Anderson 2013). Predicting plasticity and selection outcomes is further complicated by selection potentially varying across life stages after fledging, such as migration and reproduction, and differing between sexes (Shipley et al., 2022). An analyses of museum skins and morphometric data from live specimens (Romano et al., 2024) will allow to test our prediction.

Temperature-related selection on nestling body size and shape

We found a clear survival advantage for nestlings with higher body mass and tarsus length at hatching, an advantage further increased by faster nestling growth rates. In contrast, relative bill length at near-hatching showed no significant association with survival. Similar results were found using PC scores reflecting variation in body size and body shape. Importantly, the strength and direction of phenotypic selection on body size, growth rate, and relative bill length did not differ between shaded and control nests, despite control nestlings experiencing higher temperatures and increased mortality under high nest temperatures (Corregidor-Castro et al., 2023). This result implies that smaller size and relatively longer bills provided no measurable thermoregulatory benefits, or that any thermoregulatory benefit was outweighed by positive selection for larger body size and faster growth. Our results align with meta-analytic evidence from longitudinal bird studies and other endothermic and ectothermic vertebrates, showing consistent selection for larger individuals regardless of temperature, remaining stable over time despite observed body size declines (Siepielski et al., 2019; but see Shipley et al., 2022). We think that our results are important, as we provide experimental evidence that, in free living birds and independently from other ecological factors associated with climatic variation (e.g. Grant and Grant, 1993; Major et al., 2024), high temperatures had no effect on the strength and direction of selection for body size and shape in birds, as predicted by the thermoregulatory hypothesis. This result indirectly concurs with recent laboratory experiments (e.g. Tabh and Nord, 2023; Nord et al., 2024; Tabh et al., 2024) suggesting that thermoregulatory advantage may not be the most relevant explanation for the observed body size and shape shifting observed in bird populations exposed to climate warming. Our results were also in accord with a comparative study of 51 Panamanian bird species which found a temporal decline in body condition in most of these species, concluding nutritional stress, rather than an adaptive warming response, likely caused body size changes (Wilcox et al., 2024).

Conclusions

Climate warming is associated with increased frequency and intensity of extreme high temperature events like heatwaves (Rogers et al., 2022; Suarez-Gutierrez et al., 2023). Our results suggest that, particularly in areas where high temperatures occur during the breeding

season (e.g. Mediterranean), nestling development can be affected, resulting in reduced body size (mass and tarsus length) and increased relative bill length. We demonstrated that temperature-related developmental plasticity can produce near-fledging morphology matching predictions of Bergmann's (smaller mass and tarsus) and Allen's (longer relative bill) rules. However, we found no evidence that this plasticity may be adaptive, as larger nestlings and those with faster growth had higher survival, while relatively longer bills did not significantly affect pre-fledging survival, regardless of developmental temperatures experienced. While heatwaves during development may affect survival after fledging (Lv et al., 2023) and potentially alter the direction and strength of selection on body morphology, such effects would need to be substantial to counteract the significant impacts temperature had on nestling development and survival observed in our study. This warrants further investigation. In conclusion, despite widespread evidence of shrinking body size and relatively longer appendages in birds and other animals responding to climate warming, our results align with others concluding little empirical support for the idea that thermoregulatory adaptations drive these changes. As we approach critical thresholds in climate warming and extreme temperatures, understanding how temperature affects individual development and survival is essential for predicting climate change effects on population responses and adaptation in birds.

Declaration of Interest

None

Author contributions

Conceptualization: ACC, AP, DR, JGC; Data collection: ACC, JM, AR, MM; Formal analysis: ACC, AP; Writing - original draft: ACC, AP; Writing - review and editing: all authors contributed to the final draft of the manuscript.

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Tables and Figures

Table 1. Linear Mixed Models (LMMs) of the effect of the experimental treatment on near-fledging a) body mass, b) tarsus length and c) bill length (n = 147 nestlings, 55 nests). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Only significant effects are shown; original models, including non-significant predictors, can be found in the supplementary materials (Table S2).

Predictors	Estimate ± SE	df	χ^2	p
a) Body mass (g) (R^2 = 0.20)				
Treatment (shaded)	7.05 ± 1.73	1	12.85	< 0.001
Age of the nestling	2.93 ± 0.77	1	14.10	< 0.001
b) Tarsus length (mm) (R^2 = 0.33)				
Treatment (shaded)	0.79 ± 0.20	1	11.96	< 0.001
Year (2022)	-1.03 ± 0.27	1	12.08	< 0.001
Age of the nestling	0.20 ± 0.09	1	4.85	0.03
c) Bill length (mm) (R^2 = 0.36)				
Year (2022)	-0.19 ± 0.06	1	8.00	0.005
Age of the nestling	0.17 ± 0.03	1	28.95	< 0.001
Sex (male)	-0.19 ± 0.04	1	19.97	< 0.001

Table 2. Linear Mixed Models (LMMs) of the effect of the experimental treatment on nestling body morphology near fledging as described by a Principal Component Analysis of body mass, tarsus and bill length where PC1 represents an index of body size and PC2 and index of body shape (*n* = 147 nestlings, 55 nests). Positive PC1 scores represent larger nestlings, whereas positive PC2 scores represent nestlings with relatively longer bills (more details on the PCA are given on Table S6). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Only significant effects are shown; original models, including non-significant predictors, can be found in the supplementary materials (Table S7).

Predictors	Estimate ± SE	df	χ^2	p
a) PC1 (body size index) (R^2 = 0.34)				
Treatment (shaded)	0.51 ± 0.13	1	11.93	<0.001
Year (2022)	-1.11 ± 0.38	1	7.52	0.006
Age of the nestling	0.28 ± 0.07	1	17.46	<0.001
Sex (male)	-0.20 ± 0.08	1	6.48	0.01
b) PC2 (body shape index) (R^2 = 0.17)				
Treatment (shaded)	-0.14 ± 0.07	1	4.66	0.04
Age of the nestling	0.12 ± 0.03	1	11.70	<0.001
Sex (male)	-0.19 ± 0.05	1	15.21	<0.001

Table 3. Association between nestling morphology at hatching (age 1 day) and near hatching (age 4 days) and subsequent survival to fledging (age 25 days) in relation to the experimental treatment. As for morphology near fledging, we used measurement of body morphology (age corrected body mass, tarsus length and bill length) and their linear combination using a PCA (positive PC1 scores represented larger nestlings and positive PC2 scores represented nestlings with relatively longer bills, see Table S6 for further details). Furthermore, we calculated the association between initial nestling body mass and tarsus length growth rate (from age 1 to 4 days) and survival. Coefficients and standard errors for the association between morphological traits, experimental treatment (shading), and their interaction were obtained from Generalized Linear Mixed Models (GLMMs) where survival was entered as binomial dependent variable. Full models are presented in the supplementary material (Table S9-12). Significance effects are indicated by asterisks (* = p < 0.05; ** = p < 0.01; *** = p <0.001).

Nestling morphology			Treatment (shaded)	Morphology × treatment
Age 1	Body mass (g)	1.14 ± 0.60 *	3.75 ± 1.98 ***	-0.26 ± 0.43
	Tarsus length (mm)	0.93 ± 0.42 *	2.59 ± 0.94 ***	-0.22 ± 0.35
Age 4	Body mass (g)	4.58 ± 1.26 ***	6.79 ± 6.23 ***	1.18 ± 0.61
	Tarsus length (mm)	2.51 ± 0.84 ***	4.23 ± 1.73 ***	0.98 ± 0.64
	Bill length (mm)	1.25 ± 0.75 *	4.78 ± 3.15 ***	0.73 ± 0.47
	Relative bill length (mm)	0.32 ± 0.49	4.19 ± 2.39 ***	0.26 ± 0.37
PCA (age 4)	PC1[a] (body size index)	4.42 ± 1.41 ***	15.17 ± 5.04 ***	2.21 ± 1.89
	PC2[b] (body shape index)	-1.06 ± 0.63	5.19 ± 2.27 ***	0.39 ± 0.59
Nestling growth rate (from age 1 to 4)	Body mass growth rate (g/day)	0.83 ± 0.28 ***	2.51 ± 0.98 ***	-0.14 ± 0.22
	Tarsus length growth rate (mm/day)	2.91 ± 1.16 **	3.42 ± 2.18 ***	-0.42 ± 1.00

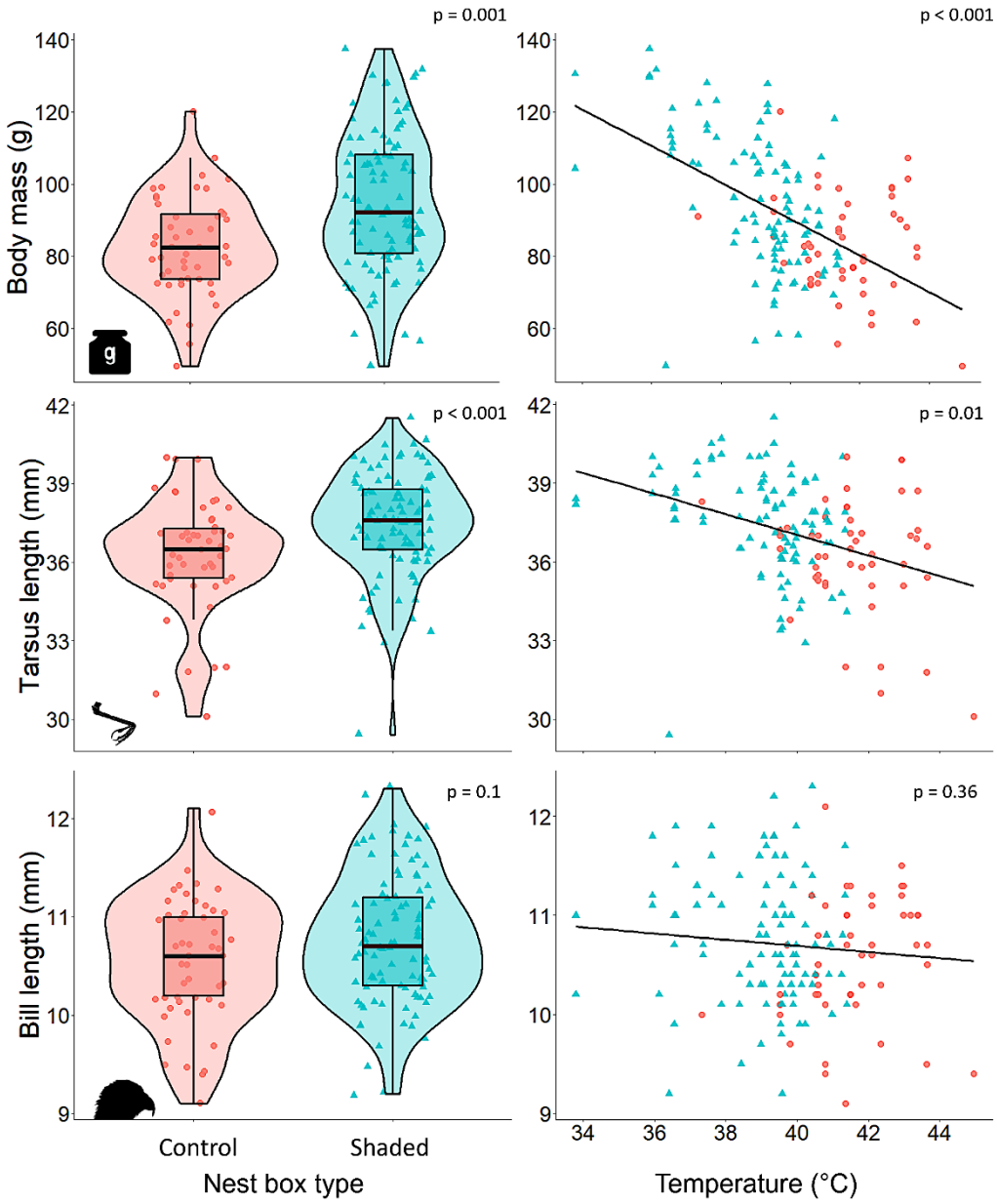

Figure 1. Body mass (g), tarsus length (mm) and bill length (mm) of control (red, circles) and shaded (blue, triangles) lesser kestrel nestlings measured near fledging (age 15.6 ± 1.7 days). Fitted lines were derived from the corresponding LMMs reported in Table S3.

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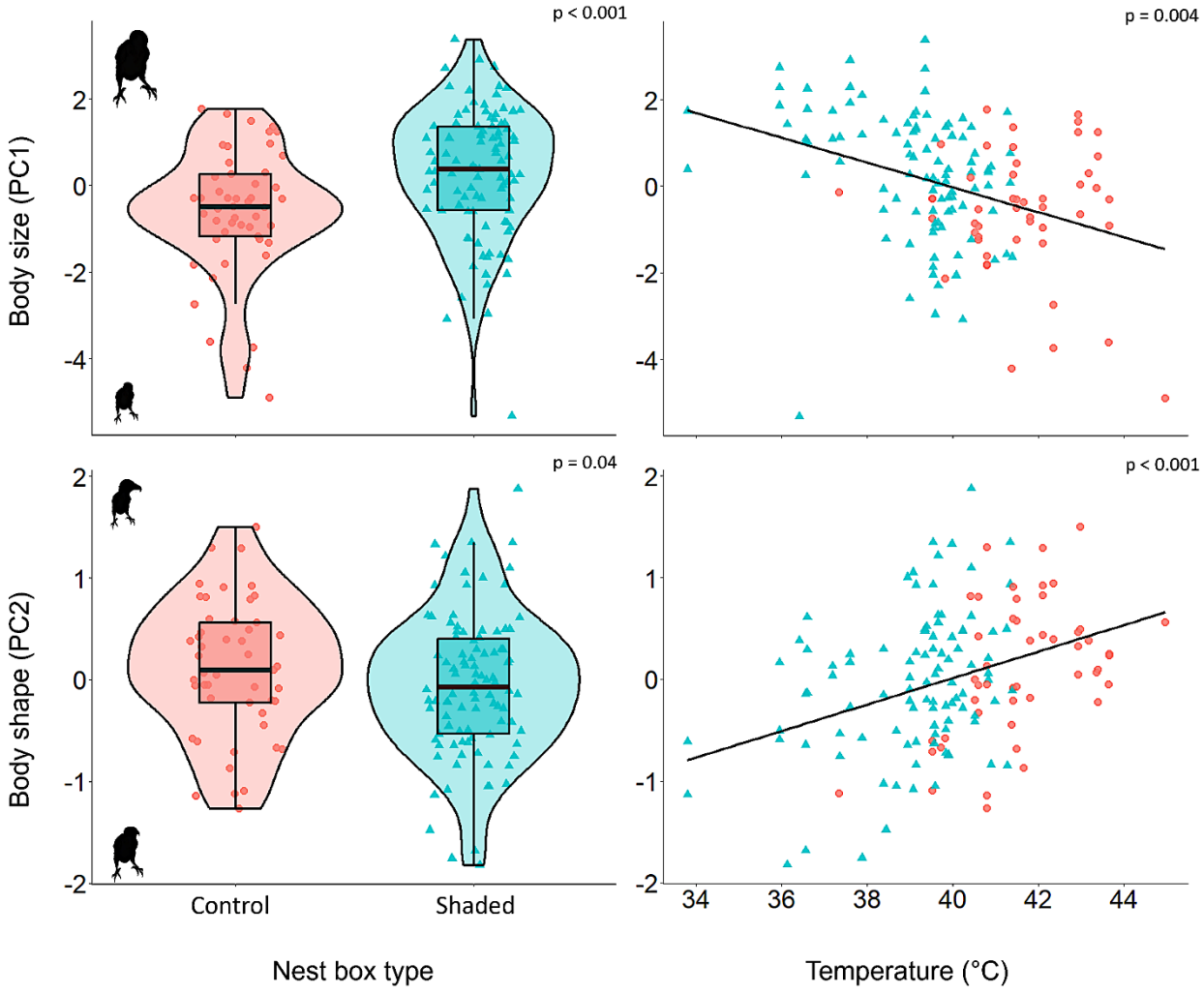

827

828 **Figure 2.** PCA scores representing body size (PC1) and body shape (PC2) in control (red,
829 circles) and shaded (blue, triangles) lesser kestrel nestlings measured near fledging (age 15.6 ±
830 1.7 days). PC1 was positively loaded to body mass, tarsus length and bill length, and positive
831 scores therefore represent larger nestlings. PC2 was positively loaded to bill length, and
832 negatively to body mass and tarsus length, and positive scores therefore represent nestlings with
833 relatively longer bill (loading factors in Table S6). Fitted lines were derived from the
834 corresponding LMMs reported in Table S8.

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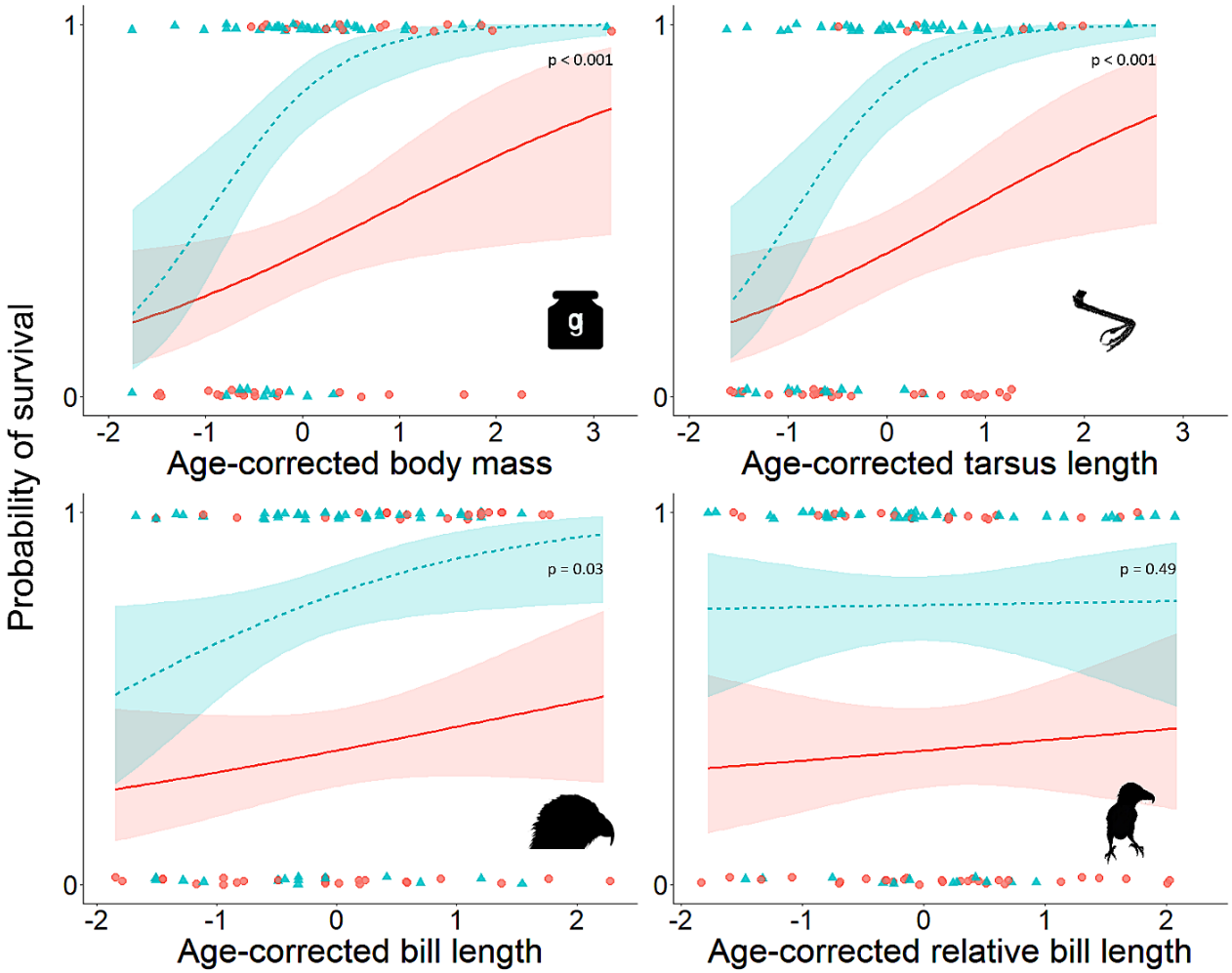

Figure 3. Association between body mass, tarsus length, bill length and relative bill length at near-hatching on subsequent survival in the two experimental treatments (control: red circles and solid line; shaded: blue triangles and dashed line). Morphological measurements were standardized for nestling age (age interval: 3-5 days). Relative bill length was calculated as the residual of the regression of bill length on body mass and tarsus length. Fitted lines (with 95% confidence bands) were derived from the corresponding GLMMs reported in Table S10. None of the interactions between the morphological trait and the experimental treatment were significant.

Supplementary Material

Supplementary Tables

Table S1. Brood size, nestling age and nestling morphology at hatching (age 0-2 days) and near-hatching (age 3-5, when bill size was measured for the first time), in the two experimental treatments (control and shaded nest boxes). Means were estimated from LMMs in which experimental treatment was entered as fixed factors and nest and dyad identity were entered as random factors.

	Control nest boxes	Shaded nest boxes	χ^2	P
a) Age 1 day (range 0-2)				
Body mass (g)	14.3 ± 0.5	13.8 ± 0.5	0.41	0.52
Tarsus length (mm)	15.1 ± 0.2	15.0 ± 0.2	0.45	0.50
Mean age of the nestling (days)	0.9 ± 0.1	1.0 ± 0.1	0.08	0.77
Brood size (number of nestlings)	3.4 ± 0.1	3.6 ± 0.1	2.40	0.23
b) Age 4 days (range 3-5)				
Body mass (g)	29.8 ± 1.3	30.2 ± 1.3	0.11	0.74
Tarsus length (mm)	20.2 ± 0.4	20.3 ± 0.4	0.01	0.93
Bill length (mm)	7.5 ± 0.9	7.4 ± 0.8	0.79	0.38
Relative bill length	0.04 ± 0.1	-0.12 ± 0.1	0.78	0.38
Growth rate body mass (g/day)	4.4 ± 0.3	4.9 ± 0.2	2.07	0.15
Growth rate tarsus length (mm/day)	1.5 ± 0.1	1.6 ± 0.1	2.56	0.11
Mean age of the nestling (days)	4.24 ± 0.1	4.21 ± 0.1	0.08	0.77
Survival (from age 1 to age 4)[a]	0.89 ± 0.1	0.95 ± 0.1	0.61	0.34

Note: [a]GLMM with binomial error distribution

Table S2. Linear Mixed Models (LMMs) of the effect of the experimental treatment on near-fledging a) body mass, b) tarsus length and c) bill length (n = 147 nestlings, 55 nests). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) Body mass (g) (R^2 = 0.23)				
Treatment (shaded)	6.60 ± 1.83	1	13.04	0.001
Year (2022)	3.57 ± 2.61	1	1.88	0.18
Age of the nestling	3.18 ± 0.78	1	16.74	< 0.001
Hatching rank	-1.29 ± 2.54	1	0.26	0.61
Sex (male)	-1.57 ± 0.91	1	2.97	0.09
Brood size	-2.02 ± 1.99	1	1.02	0.32
b) Tarsus length (mm) (R^2 = 0.35)				
Treatment (shaded)	0.75 ± 0.20	1	13.88	< 0.001
Year (2022)	-1.18± 0.28	1	17.48	< 0.001
Age of the nestling	0.23 ± 0.09	1	6.08	0.02
Hatching rank	-0.40 ± 0.28	1	2.08	0.16
Sex (male)	-0.06 ± 0.11	1	0.26	0.61
Brood size	-0.23 ± 0.22	1	1.13	0.29
c) Bill length (mm) (R^2 = 0.39)				
Treatment (shaded)	0.08 ± 0.05	1	2.99	0.10
Year (2022)	-0.22 ± 0.07	1	10.15	0.003
Age of the nestling	0.17 ± 0.03	1	32.31	< 0.001
Hatching rank	-0.11 ± 0.07	1	2.73	0.11
Sex (male)	-0.17 ± 0.04	1	17.50	< 0.001
Brood size	0.01 ± 0.06	1	0.01	0.93

Table S3. Linear Mixed Models (LMMs) of the effect of T_{nest} on near-fledging a) body mass, b) tarsus length and c) bill length (n = 147 nestlings, 55 nests). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) Body mass (g) (R^2 = 0.30)				
T_{nest}	-3.70 ± 0.68	1	20.46	< 0.001
Year (2022)	-3.24 ± 2.12	1	2.28	0.13
Age of the nestling	3.24 ± 0.75	1	17.58	< 0.001
Hatching rank	-2.36 ± 2.11	1	1.23	0.27
Sex (male)	-1.87 ± 0.91	1	4.14	0.04
Brood size	-1.72 ± 1.68	1	0.98	0.32
b) Tarsus length (mm) (R^2 = 0.35)				
T_{nest}	-0.26 ± 0.08	1	6.61	0.01
Year (2022)	-1.18 ± 0.25	1	18.13	< 0.001
Age of the nestling	0.24 ± 0.09	1	6.78	0.01
Hatching rank	-0.51 ± 0.25	1	3.87	0.05
Sex (male)	-0.09 ± 0.11	1	0.68	0.41
Brood size	-0.20 ± 0.20	1	0.94	0.33
c) Bill length (mm) (R^2 = 0.40)				
T_{nest}	-0.02 ± 0.02	1	0.83	0.36
Year (2022)	-0.22 ± 0.06	1	10.43	0.001
Age of the nestling	0.17 ± 0.03	1	31.37	< 0.001
Hatching rank	-0.12 ± 0.07	1	3.55	0.06
Sex (male)	-0.18 ± 0.04	1	17.92	< 0.001
Brood size	0.01 ± 0.05	1	0.00	0.97

Table S4. Linear Mixed Models (LMMs) of the effect of the experimental treatment and T_{nest} on near-fledging bill size relative to body mass and tarsus length (n = 147 nestlings, 55 nests). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) Relative bill length – Experimental treatment (R^2 = 0.55)				
Body mass	0.01 ± 0.01	1	1.86	0.17
Tarsus length	0.11 ± 0.03	1	10.02	0.002
Treatment (shaded)	-0.03 ± 0.05	1	0.39	0.54
Age of the nestling	0.13 ± 0.03	1	23.58	< 0.001
Sex (male)	-0.15 ± 0.04	1	17.11	< 0.001
Hatching rank	-0.06 ± 0.06	1	1.09	0.30
Year (2022)	-0.17 ± 0.12	1	1.96	0.16
b) Relative bill length – Nest temperature (T_{nest}) (R^2 = 0.57)				
Body mass	0.01 ± 0.01	1	4.32	0.04
Tarsus length	0.10 ± 0.03	1	8.68	0.003
T_{nest}	0.05 ± 0.02	1	4.68	0.03
Age of the nestling	0.12 ± 0.03	1	20.02	< 0.001
Sex (male)	-0.15 ± 0.04	1	116.43	< 0.001
Hatching rank	-0.06 ± 0.06	1	0.99	0.32
Year (2022)	-0.18 ± 0.12	1	2.29	0.13

Table S5. Linear Mixed Models (LMMs) of the effect of the experimental treatment and T_{nest} on near-fledging tarsus size relative to body mass (n = 147 nestlings, 55 nests). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) Relative tarsus length – Experimental treatment (R^2 = 0.55)				
Body mass	0.09 ± 0.01	1	109.98	<0.001
Treatment (shaded)	-0.14 ± 0.13	1	1.09	0.30
Age of the nestling	0.04 ± 0.06	1	0.38	0.54
Sex (male)	-0.07 ± 0.08	1	0.71	0.40
Hatching rank	-0.30 ± 0.15	1	3.74	0.05
Year (2022)	-1.72 ± 0.27	1	27.60	<0.001
b) Relative tarsus length – Nest temperature (T_{nest}) (R^2 = 0.83)				
Body mass	0.09 ± 0.07	1	115.31	<0.001
T_{nest}	0.08 ± 0.06	1	1.48	0.22
Age of the nestling	0.06 ± 0.06	1	0.80	0.37
Sex (male)	-0.07 ± 0.08	1	0.76	0.38
Hatching rank	-0.31 ± 0.15	1	4.03	0.05
Year (2022)	-1.74 ± 0.27	1	29.64	<0.001

Table S6. Factor loading and proportion of variance explained from PC1 (body size) and PC2 (body shape) axis regarding the morphological data (body mass, tarsus and bill length) of nestlings at near-hatching (age 4 days; n = 171 nestlings, 73 nests) and at near-fledging (age 15 days; n = 147 nestlings, 55 nests).

	PC1[a] (Body size)	PC2[b] (Body shape)
a) Near hatching (age ± 4 days)		
Body mass	0.59	-0.45
Tarsus length	0.61	-0.30
Bill length	0.53	0.84
Proportion of variance explained	0.77	0.15
b) Near fledging (age ± 15 days)		
Body mass	0.92	-0.27
Tarsus length	0.93	-0.24
Bill length	0.80	0.60
Proportion of variance explained	0.78	0.16

Note: [a]positive PC1 scores represent larger nestlings; [b]positive PC2 scores represent nestlings with relatively longer bills.

Table S7. Linear Mixed Models (LMMs) of the effect of the experimental treatment on near-fledging nestling body morphology as described by a PCA on body mass, tarsus length and bill length where PC1 represents an index of body size and PC2 a size-corrected index of body shape (n = 147 nestlings, 55 nests). Positive PC1 scores represent larger nestlings, whereas positive PC2 scores represent nestlings with relatively longer bills (more details on the PCA are given on Table S6). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) PC1 (body size index) (R^2 = 0.35)				
Treatment (shaded)	0.49 ± 0.13	1	13.72	0.001
Year (2022)	-1.31 ± 0.40	1	10.64	0.002
Age of the nestling	0.30 ± 0.07	1	20.10	<0.001
Hatching rank	-0.27 ± 0.19	1	2.01	0.16
Sex (male)	-0.20 ± 0.08	1	6.37	0.01
Brood size	-0.12 ± 0.15	1	0.64	0.42
b) PC2 (body shape index) (R^2 = 0.19)				
Treatment (shaded)	-0.16 ± 0.07	1	4.48	0.04
Year (2022)	-0.06 ± 0.16	1	0.15	0.70
Age of the nestling	0.11 ± 0.04	1	10.27	0.002
Hatching rank	-0.07 ± 0.09	1	0.65	0.42
Sex (male)	-0.18 ± 0.05	1	14.70	<0.001
Brood size	0.11 ± 0.07	1	2.07	0.16

Table S8. Linear Mixed Models (LMMs) of the effect of T_{nest} on near-fledging nestling body morphology as described by a PCA on body mass, tarsus length and bill length where PC1 represents an index of body size and PC2 a size-corrected index of body shape (*n* = 147 nestlings, 55 nests). Positive PC1 scores represent larger nestlings, whereas positive PC2 scores represent nestlings with relatively longer bills (more details on the PCA are given on Table S6). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for LMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) PC1 (body size index) (R^2 = 0.37)				
T_{nest}	-0.20 ± 0.06	1	8.22	0.004
Year (2022)	-1.30 ± 0.35	1	11.92	<0.001
Age of the nestling	0.31 ± 0.07	1	20.59	<0.001
Hatching rank	-0.34 ± 0.17	1	3.80	0.05
Sex (male)	-0.23 ± 0.08	1	7.72	0.01
Brood size	-0.11 ± 0.14	1	0.59	0.44
b) PC2 (body shape index) (R^2 = 0.28)				
T_{nest}	0.13 ± 0.03	1	16.82	<0.001
Year (2022)	-0.11 ± 0.14	1	0.60	0.44
Age of the nestling	0.11 ± 0.03	1	10.65	0.001
Hatching rank	-0.07 ± 0.08	1	0.69	0.41
Sex (male)	-0.17 ± 0.05	1	12.60	<0.001
Brood size	0.11 ± 0.06	1	2.66	0.10

Table S9. Generalized Linear Mixed Models (GLMMs) of the association between nestling morphology (body mass and tarsus length) at hatching (age 1 day) and subsequent survival to fledging (age 25 days) in relation to the experimental treatment. Body mass and tarsus length were standardized for age differences (age range: 0-2 days). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for GLMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models, with the exception of the interaction with survival, that was maintained in the models.

Predictors	Estimate ± SE	df	χ^2	p
a) Effect of body mass on survival (R^2 = 0.35; n = 185 nestlings, 73 nests)				
Body mass (age-corrected)	1.14 ± 0.60	1	7.58	0.02
Treatment (shaded)	3.75 ± 1.98	1	23.51	< 0.001
Sex (male)	-0.57 ± 0.77	1	0.55	0.46
Hatching rank	-1.45 ± 0.54	1	15.89	< 0.001
Brood size	-0.46 ± 0.82	1	0.31	0.58
Body mass (age-corrected) × Treatment (shaded)	-0.26 ± 0.43	1	0.02	0.90
b) Effect of tarsus length on survival (R^2 = 0.34; n = 196 nestlings, 76 nests)				
Tarsus length (age-corrected)	0.93 ± 0.42	1	6.32	0.01
Treatment (shaded)	2.59 ± 0.94	1	23.13	< 0.001
Sex (male)	-0.83 ± 0.90	1	0.91	0.34
Hatching rank	-1.44 ± 0.42	1	24.48	< 0.001
Brood size	0.15 ± 0.99	1	0.02	0.88
Tarsus length (age-corrected) × Treatment (shaded)	-0.22 ± 0.35	1	0.41	0.52

Table S10. Generalized Linear Mixed Models (GLMMs) of the association between nestling morphology (body mass and tarsus length) near hatching (age 4 days) and subsequent survival to fledging (age 25 days) in relation to the experimental treatment. Body mass, tarsus, bill and relative bill length were standardized for age differences (age range: 3-5 days). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for GLMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models, with the exception of the interaction with survival, that was maintained in the models.

Predictors	Estimate ± SE	df	χ^2	p
a) Effect of body mass on survival (R^2 = 0.40; n = 182 nestlings, 74 nests)				
Body mass (age-corrected)	4.58 ± 1.26	1	27.63	< 0.001
Treatment (shaded)	6.79 ± 6.23	1	30.50	< 0.001
Sex (male)	0.21 ± 1.20	1	0.04	0.84
Hatching rank	-1.35 ± 0.78	1	6.87	0.009
Brood size	-1.16 ± 1.61	1	0.74	0.39
Body mass (age-corrected) × Treatment (shaded)	1.18 ± 0.61	1	3.03	0.08
b) Effect of tarsus length on survival (R^2 = 0.45; n = 182 nestlings, 74 nests)				
Tarsus length (age-corrected)	2.51 ± 0.84	1	19.34	< 0.001
Treatment (shaded)	4.23 ± 1.73	1	26.38	< 0.001
Sex (male)	-0.10 ± 0.89	1	0.03	0.87
Hatching rank	-1.36 ± 0.56	1	11.74	< 0.001
Brood size	-1.34 ± 0.99	1	1.13	0.29
Tarsus length (age-corrected) × Treatment (shaded)	0.98 ± 0.64	1	0.63	0.43
c) Effect of bill length on survival (R^2 = 0.38; n = 179 nestlings, 73 nests)				
Bill length (age-corrected)	1.25 ± 0.75	1	5.00	0.03
Treatment (shaded)	4.78 ± 3.15	1	26.48	< 0.001
Sex (male)	-0.40 ± 0.87	1	0.22	0.64
Hatching rank	-1.45 ± 0.67	1	12.98	< 0.001

Brood size	-0.50 ± 1.09	1	0.21	0.65
Bill length (age-corrected) × Treatment (shaded)	0.73 ± 0.47	1	1.80	0.18

d) Effect of relative bill length on survival (R^2 = 0.34; n = 179 nestlings, 73 nests)

Bill length (age-corrected)	0.32 ± 0.49	1	0.48	0.49
Treatment (shaded)	4.19 ± 2.39	1	24.72	< 0.001
Sex (male)	-0.91 ± 0.85	1	1.32	0.25
Hatching rank	-1.11 ± 0.48	1	9.44	0.002
Brood size	-0.40 ± 0.91	1	0.20	0.65
Bill length (age-corrected) × Treatment (shaded)	0.26 ± 0.37	1	3.60	0.48

Table S11. Generalized Linear Mixed Models (GLMMs) of the effect of the experimental treatment on near-hatching nestling body morphology as described by a PCA on body mass, tarsus length and bill length at near hatching (age 4 days; *n* = 171 nestlings, 73 nests) on subsequent survival to fledging (age 25 days). PC1 represents an index of body size and PC2 a size-corrected index of body shape. Positive PC1 scores represent larger nestlings, whereas positive PC2 scores represent nestlings with relatively longer bills (more details on the PCA are given on Table S6). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for GLMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) PC1 (body size index) (R^2 = 0.37)				
PC1	4.42 ± 1.41	1	22.90	< 0.001
Treatment (shaded)	15.17 ± 5.04	1	31.97	< 0.001
Sex (male)	0.61 ± 1.29	1	0.16	0.69
Hatching rank	-2.00 ± 0.76	1	12.18	< 0.001
Brood size	-0.86 ± 1.34	1	1.71	0.19
PC1 × Shading	2.21 ± 1.89	1	1.24	0.27
b) PC2 (body shape index) (R^2 = 0.31)				
PC2	-1.06 ± 0.63	1	1.49	0.22
Treatment (shaded)	5.19 ± 2.27	1	25.44	< 0.001
Sex (male)	-1.22 ± 0.96	1	1.88	0.17
Hatching rank	-1.18 ± 0.49	1	8.48	0.004
Brood size	-0.40 ± 1.05	1	0.13	0.72
PC2 × Shading	0.39 ± 0.59	1	0.55	0.46

Table S12. Generalized Linear Mixed Models (GLMMs) of the effect of growth rate, i.e. body mass (g/day) and tarsus length (mm/day) from age 1 to age 4 days (n = 180 nestlings, 73 nests) on subsequent survival to fledging (age 25 days). Marginal R^2 was computed according to Nakagawa et al. (2017) coefficient of determination for GLMMs. Models include all fixed predictors; all interactions between treatment and the other fixed predictors were non-significant and were excluded from the models.

Predictors	Estimate ± SE	df	χ^2	p
a) Effect of body mass growth rate on survival (R^2 = 0.39)				
Growth rate (body mass)	0.83 ± 0.28	1	13.79	< 0.001
Treatment (shaded)	2.51 ± 0.98	1	19.59	< 0.001
Sex (male)	-0.45 ± 0.76	1	0.73	0.39
Hatching rank	-0.75 ± 0.37	1	3.68	0.06
Brood size	-0.51 ± 0.67	1	0.62	0.43
Growth rate (body mass) × Treatment (shaded)	-0.14 ± 0.22	1	0.23	0.63
b) Effect of tarsus length growth rate on survival (R^2 = 0.35)				
Growth rate (tarsus length)	2.91 ± 1.16	1	9.24	0.002
Treatment (shaded)	3.42 ± 2.18	1	18.43	< 0.001
Sex (male)	-0.91 ± 0.89	1	1.21	0.27
Hatching rank	-1.06 ± 0.49	1	7.87	0.01
Brood size	-0.77 ± 0.96	1	0.76	0.38
Growth rate (tarsus length) × Treatment (shaded)	-0.42 ± 1.00	1	0.17	0.68

Supplementary Figures

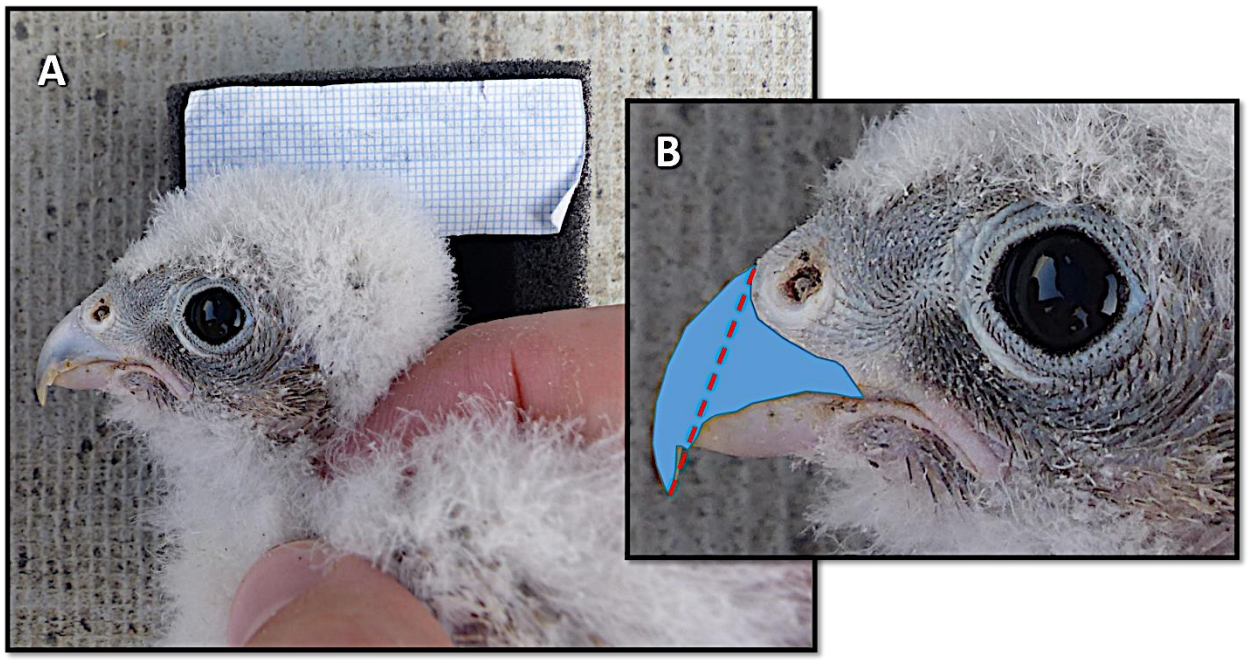

Figure S1. A) Lateral picture of a nestling on a scaled background. B) Measurement of lateral bill area (blue), obtained in ImageJ, and bill length (cere to bill tip, measured in the field; red dashed line).

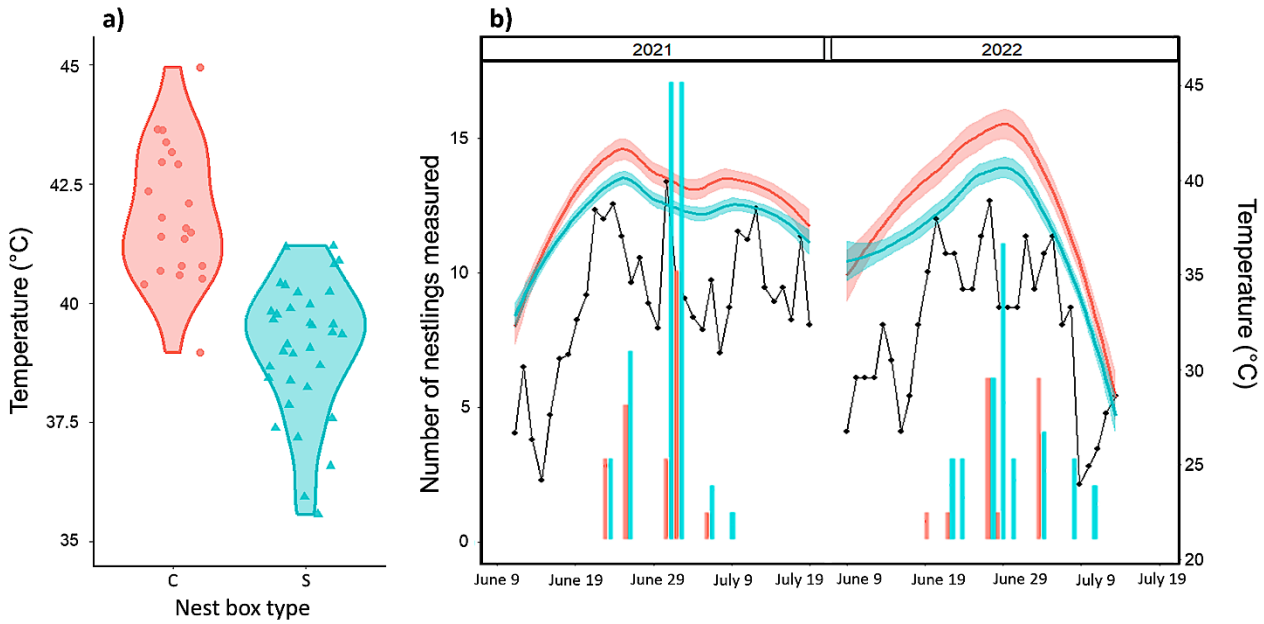

Figure S2. A) T_{nest} (average of daily maximum temperatures) in control (red circles) and shaded (blue triangles) nest boxes during the 10 days before the last biometric measurements were taken on lesser kestrel nestlings. B) Daily maximum air temperature (black dots and line) recorded in the study area during the experiment (data from Matera city whether station, https://centrofunzionale.regione.basilicata.it/) and daily mean maximum nest temperature in control (red line) and shaded (blue line) nest boxes. Vertical bars represent the number of nestlings measured per day during the last visit (red: control nestlings; blue: shaded nestlings).