Journal Pre-proof

Extra food buffers thermoregulatory costs during early development but does not reduce heatwave-induced mortality in nestlings of a cavity-nesting raptor

Alejandro Corregidor-Castro, Alessandro Berlusconi, Erica Figus, Anna Kyriakopoulou, Jacopo G. Cecere, Michelangelo Morganti, Diego Rubolini, Andrea Pilastro, Andrea Romano

PII: S0306-4565(25)00318-3

DOI: https://doi.org/10.1016/j.jtherbio.2025.104361

Reference: TB 104361

To appear in: *Journal of Thermal Biology*

Received Date: 24 July 2025

Revised Date: 10 November 2025

Accepted Date: 12 December 2025

Please cite this article as: Corregidor-Castro, A., Berlusconi, A., Figus, E., Kyriakopoulou, A., Cecere, J.G., Morganti, M., Rubolini, D., Pilastro, A., Romano, A., Extra food buffers thermoregulatory costs during early development but does not reduce heatwave-induced mortality in nestlings of a cavity-nesting raptor, *Journal of Thermal Biology*, https://doi.org/10.1016/j.jtherbio.2025.104361.

This is a PDF of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability. This version will undergo additional copyediting, typesetting and review before it is published in its final form. As such, this version is no longer the Accepted Manuscript, but it is not yet the definitive Version of Record; we are providing this early version to give early visibility of the article. Please note that Elsevier's sharing policy for the Published Journal Article applies to this version, see: https://www.elsevier.com/about/policies-and-standards/sharing#4-published-journal-article. Please also note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2025 Published by Elsevier Ltd.

Journal Pre-proof

Extra food buffers thermoregulatory costs during early development but does not reduce heatwave-induced mortality in nestlings of a cavity-nesting raptor

Running title: Extra food buffers thermoregulatory costs but not heatwave-induced mortality

Alejandro Corregidor-Castro[1,2*], Alessandro Berlusconi[3,4], Erica Figus[3], Anna Kyriakopoulou[5], Jacopo G. Cecere[6], Michelangelo Morganti[2,4], Diego Rubolini[3], Andrea Pilastro[1,2], Andrea Romano[3]

[1] *Dipartimento di Biologia, Università di Padova, Via U. Bassi 58/B, I-35131 Padova, Italy*

[2] *National Biodiversity Future Centre, Piazza Marina 61, 90133, Palermo, Italy*

[3] *Dipartimento di Scienze e Politiche Ambientali, Università degli Studi di Milano, via Celoria 26, I-20133 Milano, Italy*

[4] *Consiglio Nazionale delle Ricerche – Istituto di Ricerca sulle Acque (CNR-IRSA), Via del Mulino 19, I-20861 Brugherio, Italy*

[5] *Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium*

[6] *Area Avifauna Migratrice, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), via Ca' Fornacetta 9, I-40064 Ozzano Emilia (BO), Italy*

*Corresponding author

Email: alejandro.corregidorcastro@unipd.it / alecorregidor@gmail.com

A.CC.: https://orcid.org/0000-0002-7666-2153

A.B.: https://orcid.org/0000-0001-7491-8971

E.F.: https://orcid.org/0009-0003-5621-9191

A.K: https://orcid.org/0009-0003-8283-231X

J.G.C.: https://orcid.org/0000-0002-4925-2730

M.M.: https://orcid.org/0000-0002-8047-0429

D.R.: https://orcid.org/0000-0003-2703-5783

A.P.: https://orcid.org/0000-0001-9803-6308

A.R.: https://orcid.org/0000-0002-0945-6018

Journal Pre-proof

Journal Pre-proof

Abstract

Global climate change is increasing both average temperatures and the occurrence of extreme weather events, such as heatwaves. These changes pose major challenges for wildlife, especially during vulnerable life stages. In altricial bird species, nest-bound offspring are particularly susceptible to thermal stress due to limited behavioural thermoregulation, where high nest temperatures can impair development and induce elevated mortality, particularly when exceeding critical thresholds. We experimentally manipulated nest temperature and food availability in lesser kestrels (*Falco naumanni*) rearing their nestlings in nest boxes to investigate whether compensatory feeding offsets the negative effects of high nest temperatures on offspring size and pre-fledging survival. Nestlings were reared under three conditions: control (high nest temperatures), shaded (reduced temperature), and food-supplemented (high temperature with extra food). While parental provisioning rates did not differ among experimental groups, nestlings in food-supplemented boxes showed greater body size than control nestlings, despite similar thermal exposure, and matched the size of nestlings in shaded boxes. This indicates that increased food can buffer the energetic costs of thermoregulation under elevated, but non-lethal, temperatures. Mortality during development did not differ significantly among groups, as temperatures remained below critical thresholds. However, during a naturally occurring heatwave, mortality in control and food-supplemented nests was similarly high (~40%), whereas it was very limited in shaded nest boxes (~4%). These results suggest that food supplementation cannot prevent heatwave-induced mortality, likely caused by hyperthermia rather than starvation/dehydration. Nest microclimate may thus play a key role in mitigating the negative impacts of intense heatwaves in avian species.

Keywords: climate change; *Falco naumanni*; heatwave; hyperthermia, lesser kestrel; mortality; supplementary feeding; temperature manipulation.

Acknowledgments

We are grateful to E. De Capua and E. Eletti for supporting fieldwork in Matera. Nest boxes were built and purchased under the framework of the LIFE Project "Rapaci Lucani" (LIFE05NAT/IT/00009). Monitoring of nest boxes and acquisition of equipment was carried with partial financial support from the PRIN 2022 funding scheme (grant number 2022CWMRNH to A.R., funded by the European Union, NextGenerationEU). A.CC, M.M. and A.P. were supported by the Italian Ministry of University and Research (project funded by the European Union - Next Generation EU: "PNRR Missione 4 Componente 2, "Dalla ricerca all'impresa", Investimento 1.4, Progetto CN00000033"). D.R. was also partly supported by Ecosistema MUSA (Multilayered Urban Sustainability Action) (funded by the European Union e NextGenerationEU under the NRRP M4C2 Investment Line 1.5: Strengthening of research structures and creation of R&D 'innovation ecosystems', set up of 'territorial leaders in R&D', project ECS_00000037).

Declaration of Interest statement

None

Author contributions

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

Journal Pre-proof

Journal Pre-proof

Data statement

The data that support the findings of this study are openly available in Research Data Unipd at DOI: https://researchdata.cab.unipd.it/id/eprint/1556

Ethical approval

Capture and handling was performed by the Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA) under authorization provided by Law 157/1992 [Art. 4 (1) and Art. 7 (5)]. The nest boxes, part of a long-term population monitoring project initiated in 2016, were exposed to natural sunlight and ambient temperatures. Consequently, the mortality observed in non-shaded nest boxes was expected to approach natural mortality rates. No noticeable disturbances to nestlings or adults were observed from deploying shading covers at hatching (see Corregidor-Castro et al. (2023)) or from positioning camera traps in front of the nests (see Corregidor-Castro et al. (2025)).

Journal Pre-proof

Journal Pre-proof

1. Introduction

Anthropogenic climate change is driving significant increases in global temperatures, with projections indicating an increment of 1.5–3°C in the next decades (Armstrong McKay et al., 2022; Raftery et al., 2017). Concurrently, extreme climatic events, such as heatwaves, are becoming significantly more frequent and intense, with some regions experiencing up to a sixfold increase in their occurrence and duration (Robinson et al., 2021; Stillman, 2019), and are increasingly affecting areas that have been historically unaffected by such phenomena (Perkins-Kirkpatrick & Lewis, 2020). Understanding the ecological implications of these extreme heat events is crucial, as they pose direct threats to the survival and reproductive success of wild species (Conradie et al., 2019; Corregidor-Castro et al., 2023; Ding et al., 2024; Lv et al., 2023; Murali et al., 2023).

To mitigate the physiological and fitness costs associated with exposure to extreme temperatures, animals may respond by adjusting their behaviour. They may for instance relocate to cooler microsites, or reduce their levels of activity, including parental care (Cunningham et al., 2021; Wheeler et al., 2023). However, these behavioural adaptations can incur significant costs, such as lost opportunities for foraging or reproduction (Cunningham et al., 2021; van de Ven et al., 2019), or increased predation risk (Gutiérrez et al., 2023; Ferretti et al. 2025). Moreover, the opportunity for behavioural adjustments may be severely constrained in specific contexts. For example, in altricial bird species, nestlings are confined to their natal nest sites during early development, where nest temperatures can reach critical values, leaving them limited or no opportunities to avoid thermal stress (Catry et al., 2015; Corregidor-Castro et al., 2023).

While the impact of high temperature extremes, such as those occurring during heatwaves, depends on their timing and intensity – and the temperature range within which each species is adapted (i.e. temperature increases in colder habitats may favour nestling

development and survival; e.g. Dawson et al. (2005); Pérez et al. (2018)) – exposure to these events is often associated with fitness costs, even among warm-adapted species living in extremely warm environments (e.g. desert-dwelling organisms; McKechnie & Wolf (2010); van de Ven et al. (2020)). This is especially the case when temperatures surpass critical thresholds, as documented in studies conducted under controlled (e.g. Andrew et al. (2017); Burness et al. (2013)) and natural conditions (e.g. Catry et al. (2015); Corregidor-Castro & Jones (2021); Woodruff et al. (2024)). Indeed, homeotherms lose their passive heat dissipation capability when ambient temperatures surpass the upper threshold of the thermoneutral zone (TNZ; Diehl et al., 2023; Mitchell et al., 2018). Under such circumstances, heat dissipation relies on evaporative water loss, a process that increases metabolic rates in species that rely on panting for cooling, such as most birds (McKechnie et al., 2021; Mitchell et al., 2018; Mosher, 1976). Energy devoted to thermoregulation may consequently impair growth and development.

In addition, prolonged exposure to temperatures above the TNZ may lead to even more severe consequences, such as heat-related mortality (Albright et al., 2017). This mortality can occur via two primary physiological pathways. First, lethal dehydration occurs when cumulative evaporative water loss exceeds an individual's dehydration tolerance limits by depleting water reserves necessary to sustain physiological functions (Albright et al., 2017). Second, lethal hyperthermia may arise when body temperatures approach the upper limit of the survival zone, and the maximum rate of evaporative water loss is insufficient to maintain body temperature below lethal levels, even when water and energy are available (Albright et al., 2017; Mitchell et al., 2018).

While extensive nestling die-offs have been documented in bird populations exposed to heatwaves (Catry et al., 2011; 2015; Conradie et al., 2020; Holt & Boersma, 2022; Piatt et al., 2020), the mechanisms driving such mortality events remain unclear. If dehydration is the primary cause, adverse effects of extreme heat exposure may be buffered by increased parental

effort (i.e. an increase in parentally-provisioned food, and of the water associated with it). In contrast, mortality may result from hyperthermia due to nest temperatures exceeding a critical threshold if it occurs in nests with similar high nest temperature even when food (and thus water) is present in high quantities. To tease apart these two possibilities, we experimentally manipulated nest temperature and food availability (as a proxy for energy and water acquisition) in a cavity-nesting bird of prey, the lesser kestrel (*Falco naumanni*). European lesser kestrels are concentrated in the Mediterranean region, an area which is experiencing more frequent and intense summer heatwave events in recent decades (Díaz-Poso et al., 2023). They readily breed in nest boxes (Catry et al., 2009; Morinay et al., 2021), where they may suffer extensive mortality during heatwaves (Catry et al., 2015; Corregidor-Castro et al., 2023). We assigned nest boxes to three experimental groups: 1) shading, aimed at reducing nest temperature (by 4°C on average; Corregidor-Castro et al. (2023)), limiting thermoregulatory costs; or 2) extra food provisioning, whereby nestlings received twice the food delivered by parents but were exposed to the same nest temperature as 3) control (unshaded, with no extra food). If extra food provisioning during development compensates for the thermoregulatory costs of high nest temperatures (which results in impaired growth in nestlings under heat stress; Corregidor-Castro et al. (2023)), we would expect fed nestlings to show similar size and mortality than those in shaded nest boxes, while expecting a reduced size and increased mortality among control nest boxes.

2. Material and Methods

2.1 Study species, study area and general field procedures

The lesser kestrel is a small (~140 g), long-distance Afro-Palearctic migratory raptor. European populations reach their breeding grounds between February and April (Sarà et al., 2019), with egg-laying occurring late April to early May. As a secondary cavity-nester, it does not build its

Journal Pre-proof

own nest, but relies on natural and artificial cavities such as rock crevices, ruins, roof tiles, or nest boxes (Catry et al., 2011; Negro & Hiraldo, 1993). The species exhibits sexual dimorphism in both size and plumage coloration (Cramp, 1998). Females lay a single annual clutch of 3-6 eggs. Incubation is performed by both parents, lasting approximately 30 days from laying of the last egg (Corregidor-Castro et al., 2023; Ramellini et al., 2022). Hatching of nestlings is asynchronous (Podofillini et al., 2018; Soravia et al., 2021), resulting in a strong size hierarchy that can lead to the death of the youngest one(s) during periods of food scarcity (Aparicio, 1997). Both parents feed the nestlings until they fledge at around 40 days of age. Lesser kestrels predominantly feed on invertebrates, small mammals, and lizards, which they capture in agricultural landscapes surrounding the breeding colony (Berlusconi et al. 2025; Morganti et al., 2021; Rodríguez et al., 2010).

The study was carried out during the 2024 breeding season (late April to mid-July) in the city of Matera, southern Italy (40°66′N, 16°61′E). Matera is home to one of the world's largest lesser kestrel colonies, with approximately 1,000 breeding pairs (La Gioia et al., 2017), some of which breed in nest boxes (Morinay et al., 2021). On June 22–23, the study area experienced a strong heatwave, with a June maximum temperature anomaly of up to +3.5°C compared to the 1991–2020 reference mean (ISAC, 2024). Following Catry et al. (2015), a heatwave was defined as a period during which air temperature exceeded 37°C for at least two consecutive days. This phenomenon has occurred regularly in the study area since 2021 (see Corregidor-Castro et al., 2023; 2025). During this heatwave, mean maximum air temperature was 38.3 ± 0.5°C (Table 1).

The experiment was performed on 74 nest boxes located on roof terraces (see Corregidor-Castro et al. (2023) for more details). The size of the entrance hole prevented other bird species in the study area, including feral pigeons (*Columba livia* var. *domestica*) and egg/nestling predators like the Eurasian jackdaw (*Coloeus monedula*), from accessing the nest

box. From the start of the breeding season, we monitored nest boxes every three/four day to record laying and hatching date (of the first egg), and determine clutch and brood size. At hatching, individual nestlings were temporarily marked with a unique combination of black dots on the head using a non-toxic marker and were remarked on every successive monitoring visit until they were individually ringed when ~10 days old (Corregidor-Castro et al., 2023). Nestlings were ranked based on hatching order, with rank 1 indicating the first-hatched nestlings (see Podofillini et al. (2019)). Nests were regularly checked until each individual was around 15 days old (hereafter developmental period), when we recorded nestling body mass (electronic scale, accuracy 0.1g) and tarsus length (digital calliper, accuracy 0.1 mm). By this age, nestlings reach the end of the linear growth phase (Romano et al., 2021), and their size should correlate with body size at fledging (see Braziotis et al. (2017)). Beyond 15 days, the risk of premature nest and roof abandonment increases with nestling handling (Podofillini et al., 2018), so we refrained from collecting morphological measurements of older nestlings to minimize disturbance.

In addition, we evaluated nestling infestation by the ectoparasitic fly *Carnus hemapterus* across three body regions (the interclavicular depression, and both the right and left underwings), as these parasites may affect nestlings' early growth patterns and their abundance and development can be influenced by nest box characteristics (Podofillini et al., 2018; Romano et al., 2021). Ectoparasite presence was scored based on the maximum number of flies observed in each region using a 0–3 scale (0: no visible flies, 1: 1–3 flies, 2: 4–6 flies, and 3: >6 flies). The overall ectoparasite load was calculated as the mean ectoparasite score across the three body regions (Podofillini et al., 2018; 2019; Romano et al., 2021).

Nestling mortality was determined by retrieving the corpses of marked nestlings from the nest boxes or their immediate surroundings, as parents sometimes remove corpses from the nest. Since our nest boxes are positioned on flat roof terraces with surrounding walls, the

Journal Pre-proof

126 possibility of a nestling disappearing because it fell off the roof is negligible as they are still
127 unable to fly by 15 days of age. Therefore, missing nestlings were confidently assumed to be
128 dead, as predation is negligible (Corregidor-Castro et al., 2023, 2025).
129
130 *2.2 Experimental protocol: supplementary feeding and nest temperature manipulation*
131 When the first nestling in a nest box hatched, we matched that nest box with at least two other
132 nest boxes with at least one nestling hatched on the same day, defining a 'synchronous group'.
133 One nest box per group was randomly assigned to extra food provisioning, whereas the
134 remaining ones were randomly assigned to either shading (see Corregidor-Castro et al. 2023;
135 2025) or control treatment (no shading, no extra food). Resource and logistic limitations
136 constrained the establishment of a fourth group (shaded and extra food). Nonetheless, previous
137 studies showed that differences in nestling development and survival are particularly
138 pronounced between control and shaded nest boxes (Corregidor-Castro et al. 2023), hence
139 providing additional food only to non-shaded nest boxes was relevant for addressing our
140 research questions. Overall, we established 14 synchronous groups, each consisting of one
141 food-supplemented nest box, 1–4 shaded and 1–4 control nest boxes, for a total of 74 nest boxes
142 included in the experiment (14 supplemented, 31 shaded and 29 control).
143 As extra food, we provided desert locusts (*Schistocerca gregaria*; SmartBugs, Italy),
144 which are similar to the main prey of lesser kestrels (Christakis & Sfougaris, 2021; Di Maggio
145 et al., 2018; Franco & Andrada, 1977). These locusts were kept frozen, and unfrozen overnight
146 before provisioning. Food constitutes the primary water intake for nestlings during the
147 developmental phase, as they have no direct access to water on roofs and parents do not transfer
148 water to them. The estimated water content for each individual locust provided to the nestlings
149 was ~0.6 g (Wahed et al., 2019). Based on previous studies, we observed that lesser kestrel
150 provisioning rates typically range between 0.6 and 1.4 prey items per hour (0.87 ± 0.1 prey

items/h) (Corregidor-Castro et al., 2025). Assuming a 15-h day from sunrise to sunset, this translates into about 13 prey items daily or roughly three prey per nestling, given an average brood size of four (Aparicio, 1997). Our aim was to double the available food per nestling, considering their developmental stage, and compensating for prey depletion effects (Bonal & Aparicio, 2008). To do so, we placed the locusts inside the nest three times per week over a two-week period, with a total of six extra food provisioning events per nest box. During the first week, we provided 4, 5, and 6 medium-size locusts (~0.7 g) per nestling present in the nest per day until the subsequent visit (e.g. from day 0 to day 2, the nest was provided with 8 medium-size locusts per nestling (4 locusts × 2 days); from day 4 to day 7, it was provided with 18 medium-size locusts per nestling (6 locusts × 3 days)); in the second week, we placed 6, 7, and 8 large-size locusts (~1 g) following the same procedure. This protocol resulted in an additional 36 medium-size and 50 large-size locusts per nestling in each nest (Fig. 1). Supplementation ended in all nest boxes by 18 June, before the onset of a naturally occurring heatwave, which began 6 days after the mean end of the supplementation experiment, when nestlings were ca. 21 days old (Fig. 1). During the heatwave (22-23 June), we provided an additional 10 large-size locusts per nestling per day over a two-day period (totalling 20 locusts per nestling).

To verify that the supplemented food was effectively consumed by the nestlings, we installed miniaturized cameras (Mini IP Camera, Insygrow, China) inside a subsample of nest boxes (n = 8) to obtain continuous recordings from the time of food supplementation until the subsequent monitoring visit (67 ± 0.2 h recorded per nest box). Videos were then scored by an operator, which confirmed that extra food was mostly consumed by nestlings (>85% of the locusts), the rest being consumed by parents. While extra food was not consumed immediately after provisioning, adults incorporated it into their feeding routine, distributing it alongside the prey they provided. On average, adults distributed 5.7 ± 0.4 preys per feeding event, meaning

that after 3-4 h from supplementation all supplemented food was consumed. Regardless of their rank, all nestlings consumed approximately the same number of food items (unpublished data). Additionally, to determine whether food supplementation altered parental provisioning behaviour (specifically, if adults reduced their provisioning rate in supplemented nest boxes, potentially equalizing food intake across experimental groups) we set up 27 camera traps outside the nests (Boly Scout Guard BG310-M, Shenzhen, China) to monitor provisioning frequency (following Corregidor-Castro et al. (2025)), allowing us to record 9 synchronous groups (9 shaded, 9 supplemented and 9 control nest boxes). Camera traps were equipped with a 18 MP motion activated camera with two lithium batteries and solar panels. We placed them approximately at 1.5 m from the nest box entrance, at a height of around 10 cm from the ground. Camera traps were set to record 30 s videos, and the trigger set as 'High' to detect and record as many events as possible (see Corregidor-Castro et al. (2025) for more details on camera trap positioning).

Nest boxes were shaded according to Corregidor-Castro et al. (2023), adding a plywood cover to prevent direct sunlight while allowing air to flow on both sides and top of the nest box. Both control and supplemented nest boxes were exposed to natural sunlight. To confirm temperature differences among experimental groups (control, food-supplemented, shaded) we installed miniaturized temperature loggers (Elitech RC-5+, Elitech, UK; accuracy 0.5°C) on the rear panel of each nest box. These data loggers were set to record temperature every 15 min and were individually calibrated by the supplier (see Corregidor-Castro et al. (2023)).

2.3 Statistical analyses

2.3.1 Effects of shading on nest temperature – To assess whether shading effectively reduced nest temperature, we used a linear mixed model (LMM) with daily maximum nest temperature (T_{nest}) as the response variable. Experimental treatment was included as a three-level fixed

201 factor (control, food-supplemented, shaded), with nest box and synchronous group identity as
202 random intercept effects (the latter reflecting the group structure of the experimental design).
203 We fitted separate LMMs for the developmental period and for the heatwave event (22-23
204 June).
205
206 **2.3.2 Effects of extra food and shading on nestling size** – We investigated the effects of extra
207 food and shading on nestling size (body mass and tarsus length) at the end of the developmental
208 period (around 15 d of age, varying between 13 and 17 d) (Romano et al., 2021). We relied on
209 LMMs including experimental treatment, brood size, ectoparasite load, age and rank of each
210 nestling as fixed effects. Initial models included 1) a two-way interaction between rank and
211 experimental group, to assess differential effects of rank on body size across treatments
212 (Podofillini et al., 2018; 2019; Romano et al., 2021), and 2) two-way interactions between the
213 experimental group and the other covariates (brood size and ectoparasite load). All models
214 included nest box and synchronous group identity as random intercept effects.
215
216 **2.3.3 Effects of extra food and shading on mortality** – We investigated the effect of treatment
217 on mortality separately for the developmental period and the heatwave event. During the
218 developmental period, ambient temperatures reached high but non-critical levels (air
219 temperature approximately 31°C; nest temperature 39°C in control and supplemented nest
220 boxes; Table 1), well below the 43°C critical threshold (Corregidor-Castro et al., 2023),
221 whereas during the heatwave event average air temperatures reached 38.3°C (mean nest
222 temperature around 46.5°C in control and supplemented nest boxes). We fitted binomial
223 generalized linear mixed models (GLMMs) to analyse nestling mortality as a binary response
224 variable (0 = alive; 1 = dead), including the experimental group as a fixed factor, with nest box
225 and synchronous group identity as random intercepts. Additional fixed effects included brood

Journal Pre-proof

size and nestling rank, as both can influence nestling survival (Podofillini et al., 2019), and the interaction between experimental group and each covariate. For the heatwave GLMM, we included only nestlings that were alive at the onset of the heatwave (i.e. we excluded those that died during the developmental period).

2.3.4 Effects of extra food on parental provisioning rate – To test if extra food altered parental provisioning behaviour, we examined the number of parental feeding events recorded with the camera traps. For each nest and day of recording, we calculated the hourly provisioning rate for each parent (male or female) as the number of nest visits during which a prey was delivered to the nest divided by the total daylight hours (15 h). We then fitted a LMM with provisioning rate as the response variable, including experimental group as a factor and nest box and synchronous group identity as random intercepts. Because provisioning rate may differ between sexes due to different foraging or parental nestling feeding strategies (Hernández-Pliego et al., 2017; Soravia et al., 2021), we included parent sex (0 = female, 1 = male) as an additional fixed factor, as well as the interaction between experimental group and parent sex.

2.3.5 Statistical software – All statistical analyses were carried using the R software (version 4.3.3) (R Core Team, 2024). LMMs and binomial GLMMs were fitted using the "lme4" and "glmmTMB" packages, respectively (Bates et al., 2015; Brooks et al., 2017). Collinearity and residual diagnostics were evaluated with the "performance" package (Lüdecke et al., 2021). For all mixed models, predictors were mean-centered, and any nonsignificant interactions ($p > .05$) were removed to facilitate interpretation in one step. Final models retained all main effects and statistically significant interaction terms. Significance of fixed predictors in LMMs and GLMMs was assessed using likelihood ratio tests (Singmann et al., 2015). Unless

Journal Pre-proof

otherwise specified, means and parameter estimates (including text notes) are reported with their standard error.

3. Results

3.1 Effects of shading on nest temperature

A heatwave (mean maximum air temperature = 38.3 ± 0.5°C; Table 1; Catry et al. (2015)), hit the study area six days after the mean end of the supplementation experiment (Fig. 1), when nestling were around 21 days old. Nest box shading effectively reduced nest temperature by ~4.0°C during both the development and the heatwave periods (Table 1) compared to control and food-supplemented nest boxes, which did not differ in nest temperature (Table 1).

3.2 Effects of extra food and shading on nestling size

At around 15 days post-hatching, nestlings from control nest boxes attained significantly lower body mass and smaller tarsi than those in both supplemented and shaded nest boxes (Table 2; Fig. 2). Differences in body mass and tarsus length between nestlings from food-supplemented and shaded nest boxes were not statistically significant (Table 2; Fig. 2). Furthermore, high-ranking nestlings were significantly heavier and had longer tarsi compared to lower-ranking ones (Table 2).

3.3 Effects of extra food and shading on nestling mortality

During the developmental period, with ambient temperatures averaging 31°C, the mortality rate (proportion of dead nestlings) was consistently low across all experimental groups (< 0.04), predominantly affecting lower-ranking nestlings (Table 3a; Fig. 3). The mortality rate increased considerably during the heatwave period: extra food did not buffer nestling mortality, as both non-shaded (control and food-supplemented) broods displayed similar mortality rates (control

broods: 0.40, 35/87 nestlings; food-supplemented: 0.45, 19/42 nestlings; Table 3b, Fig. 3). In contrast, mortality rate in shaded nest boxes was 0.04 (4/96 nestlings). No significant effect of nestling rank on mortality rate during the heatwave event was detected, suggesting mortality events were uniformly distributed among nestlings in the brood (Table 3b). In addition, nestlings from larger broods showed a higher mortality rate (Table 3b).

3.4 Effects of extra food on parental provisioning rate

Parental provisioning rate did not differ among experimental groups ($\chi^2 = 2.94$, df = 2, p = 0.23). Males were found to bring food at a higher rate (0.85 ± 0.06 prey/h) than females (0.71 ± 0.06 prey/h; $\chi^2 = 2.94$, df = 1, p = 0.005) (see also Hernández-Pliego et al. (2017)).

4. Discussion

Using an experimental setup comprising three groups of nest boxes with different characteristics (control, food-supplemented, and shaded), our study demonstrates, under natural conditions, that extra food can partially mitigate the developmental costs associated with exposure to high nest temperatures in altricial nestlings. Nestlings in control and supplemented nest boxes, despite experiencing similar nest temperatures, differed in body size, food-supplemented nestlings being ~7-8% larger comparable to those in shaded nest boxes (where no extra food was provided). However, food supplementation was insufficient to offset the mortality impacts of extreme nest temperatures, such as those occurring during heatwaves. Mortality, likely due to hyperthermia (Conradie et al., 2024), was higher, and not significantly different, between control and food-supplemented nestlings (exceeding 40%), despite the better body condition of food-supplemented nestlings and the availability of extra food (and hence water).

When air temperatures exceed an individual's thermoneutral zone, nestlings of many bird species, including raptors (Mosher, 1976), rely primarily on panting to dissipate heat through respiratory evaporative water loss (Andreasson et al., 2018; Ricklefs & Hainsworth, 1968). This heat dissipation mechanism incurs significant metabolic costs, diverting energy away from critical growth processes (Cunningham et al., 2021; Nawaz et al., 2021; Salaberria et al., 2014), and can result in substantial evaporative water loss, with birds potentially losing up to 5% of their body mass (van de Ven et al., 2019; Wolf & Walsberg, 1996). Our findings revealed that control nestlings, exposed to high (but not critical) nest temperatures, experienced reduced body mass and skeletal size at the end of the early development (~7-8%). These results align with previous studies (Andreasson et al., 2018; Corregidor-Castro & Jones, 2021; Corregidor-Castro et al., 2023; Rodríguez & Barba, 2016; van de Ven et al., 2020). However, food-supplemented nestlings, which experienced similar nest temperatures compared to control ones, reached the same size as shaded ones. Hence, doubling the natural parental provisioning rate nearly completely offset developmental costs of growing in hot nests, enabling supplemented nestlings to achieve a size similar to those raised in shaded, cooler conditions.

High nest temperatures can have sublethal effects on nestling development; however, extreme weather events, such as heatwaves, can drive nest temperatures beyond the critical thresholds for survival (Catry et al., 2015; Corregidor-Castro et al., 2023; Holt & Boersma, 2022; Quintana et al., 2022). When nest temperatures exceed this upper critical temperature (Mitchell et al., 2018), heat-related mortality may occur primarily through lethal dehydration, when cumulative evaporative water loss surpasses the tolerance limits for dehydration, or hyperthermia (Albright et al., 2017), when achievable rate of evaporative water loss is insufficient to maintain body temperature below the lethal threshold.

In our study, during the developmental period, nest temperatures in all the experimental groups remained on average well below the critical threshold for 50% mortality in nestlings,

Journal Pre-proof

estimated at approximately 44°C (Catry et al., 2015; Corregidor-Castro et al., 2023). Indeed, mortality rates under these conditions were relatively low and comparable across groups, with an estimated ~4% mortality in control nestlings and ~2% mortality in supplemented and shaded nestlings. Under non-critical temperature conditions, mortality primarily affected low-ranking, late-hatched nestlings, likely due to their smaller size and competitive disadvantage with their siblings for parentally provided resources (Aparicio, 1997; Corregidor-Castro et al., 2023; Podofillini et al., 2019).

In contrast, during the heatwave, nest temperatures in most non-shaded boxes (control and supplemented) exceeded the critical threshold, with average temperatures reaching 46°C. Mortality among both control and food-supplemented nestlings rose dramatically (40% and 45%, respectively) compared to shaded ones, which experienced a similar mortality as in the previous period (4%). Despite their larger body size and higher mass when exposed to the heatwave, and even after receiving additional food (the only source of water while in the nest), food-supplemented nestlings exhibited mortality rates similar to controls. Observations of uneaten fresh locusts nearby dead nestlings suggested that dehydration was not the primary cause of mortality. Instead, it is likely that mortality resulted from hyperthermia, as nestlings were unable to dissipate sufficient heat to survive these extreme conditions (Albright et al., 2017; Conradie et al., 2024; Mitchell et al., 2018). Thus, when temperatures are higher than the critical threshold (such in the case of heatwaves), even compensatory feeding activity by parents is unable to offset the effects of temperature on mortality.

Importantly, all findings were unaffected by parental provisioning rates, which indeed did not vary among parents attending control, shaded or food-supplemented broods. However, we cannot exclude the possibility that adult provisioning behaviour was somehow disrupted during the heatwave, thus leading to reduced food delivery to the nestlings and potentially increasing mortality risk. Still, in a previous study (Corregidor-Castro et al., 2025) we showed

that provisioning rates were more frequent at midday, when daily temperatures are highest. It is therefore unlikely that extreme ambient temperatures may be particularly harmful for foraging parents. Even if this was the case, the potential effects of heatwaves on parental provisioning would have influenced all the experimental groups similarly, and therefore, if food scarcity (and thus associated lack of water) had been the primary cause of mortality, similar increases in nestling deaths would have been observed also among shaded nestlings.

Another minor limitation of this study is the absence of a fourth treatment group (shading and extra food), which could not be established due to logistical and resource constraints. The inclusion of such a treatment group would have allowed us to disentangle potential additive and/or interactive effects between shading and extra food provisioning. However, the absence of this group did not affect our conclusions regarding the mechanisms underpinning nestlings' mortality under extreme heat.

In conclusion, our findings suggest that impaired nestling size following exposure to elevated nest temperatures mainly arises through resource limitation, because extra food provisioning nearly offset such handicap. Yet, nest microclimate was the key factor in affecting offspring mortality under extreme heat, likely through hyperthermia, irrespective of available resources and physiological state. Whereas parents may potentially buffer negative offspring development under high temperature by doubling their provisioning efforts, this is unlikely to be adaptive because trade-offs between current and future reproduction exist and because offspring mortality during extreme climate is unavoidable. Hence, extreme heat events can disrupt reproduction and threaten species' persistence, even for those taxa adapted to relatively warm climates such lesser kestrels from the Mediterranean (western) lineage (Ferrer-Obiol et al. 2025). Selecting relatively cooler microhabitats for nesting may become an increasingly important determinant of lifetime fitness for avian species breeding in hot/arid climates under contemporary and future global warming scenarios where an increased frequency of heatwaves

is expected. Finally, these results emphasize the importance of carefully considering nest microclimate when planning conservation interventions. For instance, a frequently adopted conservation measure favouring cavity-nesting species is the provisioning of nest boxes aimed at increasing nest site availability. To maximise the conservation impact of such interventions, we recommend that nest box design, materials and positioning should be carefully evaluated in order to buffer the escalating threats posed by climate warming and extreme climatic conditions (Catry et al., 2009; 2011; Welman & Pichegru, 2023), especially in warmer regions of the world.

Journal Pre-proof

6. References

Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E., & Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences*, *114*(9), 2283-2288. doi:10.1073/pnas.1613625114

Andreasson, F., Nord, A., & Nilsson, J.-Å. (2018). Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings. *Journal of Avian Biology*, *49*(2), jav-01620. doi.org/10.1111/jav.01620

Andrew, S. C., Hurley, L. L., Mariette, M. M., & Griffith, S. C. (2017). Higher temperatures during development reduce body size in the zebra finch in the laboratory and in the wild. *Journal of Evolutionary Biology*, *30*(12), 2156-2164. doi.org/10.1111/jeb.13181

Aparicio, J. M. (1997). Costs and benefits of surplus offspring in the lesser kestrel (Falco naumanni). *Behavioral Ecology and Sociobiology*, *41*(2), 129-137. doi.org/10.1007/s002650050372

Armstrong McKay, D. I., Staal, A., Abrams, J. F., Winkelmann, R., Sakschewski, B., Loriani, S., Fetzer, I., Cornell, S. E., Rockström, J., & Lenton, T. M. (2022). Exceeding 1.5°C global warming could trigger multiple climate tipping points. *Science*, *377*(6611). doi:10.1126/science.abn7950 Berlusconi, A., Gobbi, M., Martinoli, A., Alba, R., Assandri, G., Bona, F., & Morganti, M. (2025). Foraging niche partitioning within a recently established guild of falcons. *Ibis*. https://onlinelibrary.wiley.com/doi/full/10.1111/ibi.13399

Bonal, R., & Aparicio, J. M. (2008). Evidence of prey depletion around lesser kestrel Falco naumanni colonies and its short term negative consequences. *Journal of Avian Biology*, *39*(2), 189-197. doi.org/10.1111/j.2008.0908-8857.04125.x

Journal Pre-proof

Braziotis, S., Liordos, V., Bakaloudis, D. E., Goutner, V., Papakosta, M. A., & Vlachos, C. G. (2017). Patterns of postnatal growth in a small falcon, the lesser kestrel Falco naumanni (Fleischer, 1818) (Aves: Falconidae). *The European Zoological Journal*, *84*(1), 277-285. doi.org/10.1080/24750263.2017.1329359

Burness, G., Huard, J. R., Malcolm, E., & Tattersall, G. J. (2013). Post-hatch heat warms adult beaks: irreversible physiological plasticity in Japanese quail. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1767), 20131436. doi:10.1098/rspb.2013.1436

Catry, I., Alcazar, R., Franco, A. M. A., & Sutherland, W. J. (2009). Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. *Biological Conservation*, *142*(11), 2782-2791. doi.org/10.1016/j.biocon.2009.07.011

Catry, I., Catry, T., Patto, P., Franco, A. M. A., & Moreira, F. (2015). Differential heat tolerance in nestlings suggests sympatric species may face different climate change risks. *Climate Research*, *66*(1), 13-24. doi.org/10.3354/cr01329

Catry, I., Franco, A. M. A., & Sutherland, W. J. (2011). Adapting conservation efforts to face climate change: Modifying nest-site provisioning for lesser kestrels. *Biological Conservation*, *144*(3), 1111-1119. doi.org/10.1016/j.biocon.2010.12.030

Christakis, C. E., & Sfougaris, A. I. (2021). Foraging Habitat Selection by the Lesser Kestrel *Falco naumanni* During the Different Phases of Breeding and the Post Breeding Period in Central Greece. *Ornithological Science*, *20*(2), 175-183, 179. doi.org/10.2326/osj.20.175

Conradie, S. R., Wolf, B. O., Cunningham, S. J., Bourne, A., van de Ven, T., Ridley, A. R., & McKechnie, A. E. (2024). Integrating fine-scale behaviour and microclimate data into

biophysical models highlights the risk of lethal hyperthermia and dehydration. *Ecography*, *n/a*(n/a), e07432. doi.org/ 10.1111/ecog.07432

Conradie, S. R., Woodborne, S. M., Cunningham, S. J., & McKechnie, A. E. (2019). Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences*, *116*(28), 14065-14070. doi.org/10.1073/pnas.1821312116

Conradie, S. R., Woodborne, S. M., Wolf, B. O., Pessato, A., Mariette, M. M., & McKechnie, A. E. (2020). Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. *Conservation Physiology*, *8*(1). doi.org/10.1093/conphys/coaa048

Corregidor-Castro, A., & Jones, O. R. (2021). The effect of nest temperature on growth and survival in juvenile Great Tits Parus major. *Ecology and Evolution*, *11*(12), 7346-7353. doi.org/10.1002/ece3.7565

Corregidor-Castro, A., Militti, S., Morinay, J., Romano, A., Morganti, M., Cecere, J. G., Rubolini, D., & Pilastro, A. (2025). Facing the heat: nestlings of a cavity-nesting raptor trade safety for food when exposed to high nest temperatures. *Animal Behaviour*, *219*, 123006. doi.org/10.1016/j.anbehav.2024.10.020

Corregidor-Castro, A., Morinay, J., McKinlay, S. E., Ramellini, S., Assandri, G., Bazzi, G., Glavaschi, A., De Capua, E. L., Grapputo, A., Romano, A., Morganti, M., Cecere, J. G., Pilastro, A., & Rubolini, D. (2023). Experimental nest cooling reveals dramatic effects of heatwaves on reproduction in a Mediterranean bird of prey. *Global Change Biology*, *29*(19), 5552-5567. doi.org/10.1111/gcb.16888

Cramp, S. (Ed.). (1998). The complete birds of the Western Palearctic on CD-ROM. Oxford University Press.

Journal Pre-proof

Cunningham, S. J., Gardner, J. L., & Martin, R. O. (2021). Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment*, *19*(5), 300-307. doi.org/10.1002/fee.2324

Dawson, R. D., Lawrie, C. C., & O'Brien, E. L. (2005). The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia*, *144*(3), 499-507. doi.org/10.1007/s00442-005-0075-7

Di Maggio, R., Campobello, D., & Sarà, M. (2018). Lesser kestrel diet and agricultural intensification in the Mediterranean: An unexpected win-win solution? *Journal for Nature Conservation*, *45*, 122-130. doi.org/10.1016/j.jnc.2018.08.009

Díaz-Poso, A., Lorenzo, N., & Royé, D. (2023). Spatio-temporal evolution of heat waves severity and expansion across the Iberian Peninsula and Balearic islands. *Environmental Research*, *217*, 114864. doi.org/10.1016/j.envres.2022.114864

Diehl, J. N., Alton, L. A., White, C. R., & Peters, A. (2023). Thermoregulatory strategies of songbird nestlings reveal limited capacity for cooling and high risk of dehydration. *Journal of Thermal Biology*, *117*, 103707. doi.org/10.1016/j.jtherbio.2023.103707

Ding, C., Newbold, T., & Ameca, E. I. (2024). Assessing the global vulnerability of dryland birds to heatwaves. *Global Change Biology*, *30*(1), e17136. doi.org/10.1111/gcb.17136

Ferrer-Obiol, J., Bounas, A., M. Brambilla, G. Lombardo, S. Secomandi, J. R. Paris, A. Iannucci, J. R. Whiting, G. Formenti, A. Bonisoli-Alquati, G. F. Ficetola, A. Galimberti, J. Balacco, N. Batbayar, A. E. Bragin, M. Caprioli, I. Catry, J. G. Cecere, B. Davaasuren, F. De Pascalis, R. Efrat, K. Erciyas-Yavuz, J. Gameiro, G. Gradev, B. Haase, T. E. Katzner, J. Mountcastle, K. Mikulic, M. Morganti, L. G. Pârâu, A. Rodríguez, M. Sarà, E.-A. Toli, N. Tsiopelas, C. Ciofi, L. Gianfranceschi, E. D. Jarvis,

A. Olivieri, K. Sotiropoulos, M. Wink, E. Trucchi, A. Torroni, Rubolini, D. 2025. Evolutionarily distinct lineages of a migratory bird of prey show divergent responses to climate change. *Nature Communications* 16, 3503. doi.org/s41467-025-58617-5

Ferretti, S., Macali, A., Mazza, V., & Carere, C. (2025). Marine heatwaves as selective filters on the behaviour of native and non-native invertebrates. *Biological Invasions*, 27, 218. doi.org/10.1007/s10530-025-03674-6

Franco, A., & Andrada, J. (1977). Alimentación y selección de presa en *Falco naumanni*. *Ardeola*, *23*, 137-187.

Gutiérrez, J. S., Catry, T., Espinosa-Colín, M., Masero, J. A., & Granadeiro, J. P. (2023). Heat stress increases risk taking in foraging shorebirds. *Functional Ecology*, *37*(4), 1005-1019. doi.org/10.1111/1365-2435.14288

Hernández-Pliego, J., Rodríguez, C., & Bustamante, J. (2017). A few long versus many short foraging trips: different foraging strategies of lesser kestrel sexes during breeding. *Movement Ecology*, *5*(1), 8. doi.org/10.1186/s40462-017-0100-6

Holt, K. A., & Boersma, P. D. (2022). Unprecedented heat mortality of Magellanic Penguins. *Ornithological Applications*, *124*(1). doi.org/10.1093/ornithapp/duab052

ISAC. (2024). Retrieved 27 September 2024, from https://www.isac.cnr.it/climstor/DPC/ARCHIVIO/TMX/2024/TMX_ANOM_ITA_2024_06.png

La Gioia, G., Melega, L., & Fornasari, L. (2017). Piano d'Azione Nazionale per il grillaio (Falco naumanni). *Quad. Cons. Natura*, *41*.

Lv, L., van de Pol, M., Osmond, H. L., Liu, Y., Cockburn, A., & Kruuk, L. E. B. (2023). Winter mortality of a passerine bird increases following hotter summers and during winters with higher maximum temperatures. *Science Advances*, *9*(1), eabm0197. doi:10.1126/sciadv.abm0197

Journal Pre-proof

McKechnie, A. E., Gerson, A. R., & Wolf, B. O. (2021). Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling. *Journal of Experimental Biology*, *224*(Suppl_1). doi.org/10.1242/jeb.229211

McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, *6*(2), 253-256. doi:10.1098/rsbl.2009.0702

Mitchell, D., Snelling, E. P., Hetem, R. S., Maloney, S. K., Strauss, W. M., & Fuller, A. (2018). Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. *Journal of Animal Ecology*, *87*(4), 956-973. doi.org/10.1111/1365-2656.12818

Morganti, M., Cecere, J. G., Quilici, S., Tarantino, C., Blonda, P. N., Griggio, M., Ambrosini, R., & Rubolini, D. (2021). Assessing the relative importance of managed crops and semi-natural grasslands as foraging habitats for breeding lesser kestrels Falco naumanni in southeastern Italy. *Wildlife Biology*, *2021*(1). doi.org/10.2981/wlb.00800

Morinay, J., De Pascalis, F., Dominoni, D. M., Morganti, M., Pezzo, F., Pirrello, S., Visceglia, M., De Capua, E. L., Cecere, J. G., & Rubolini, D. (2021). Combining social information use and comfort seeking for nest site selection in a cavity-nesting raptor. *Animal Behaviour*, *180*, 167-178. doi.org/10.1016/j.anbehav.2021.07.014

Morinay, J., Riotte-Lambert, L., Aarts, G., De Pascalis, F., Imperio, S., Morganti, M., Catoni, C., Assandri, G., Ramellini, S., Rubolini, D., & Cecere, J. G. (2023). Within-colony segregation of foraging areas: from patterns to processes. *Oikos*, *2023*(8), e09926. doi.org/10.1111/oik.09926

Mosher, J. A. (1976). Raptor energetics: a review. *Journal of Raptor Research*, *10*(4).

546 Murali, G., Iwamura, T., Meiri, S., & Roll, U. (2023). Future temperature extremes threaten
547 land vertebrates. *Nature*, *615*(7952), 461-467. doi.org/10.1038/s41586-022-05606-z
548 Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination
549 R^2 and intra-class correlation coefficient from generalized linear mixed-effects models
550 revisited and expanded. Journal of The Royal Society Interface, 14(134), 20170213.
551 doi:10.1098/rsif.2017.0213
552 Nawaz, A. H., Amoah, K., Leng, Q. Y., Zheng, J. H., Zhang, W. L., & Zhang, L. (2021).
553 Poultry Response to Heat Stress: Its Physiological, Metabolic, and Genetic
554 Implications on Meat Production and Quality Including Strategies to Improve Broiler
555 Production in a Warming World [Review]. *Frontiers in Veterinary Science*, *8*.
556 doi.org/10.3389/fvets.2021.699081
557 Negro, J. J., & Hiraldo, F. (1993). Nest-site selection and breeding success in the Lesser
558 Kestrel Falco naumanni. *Bird Study*, *40*(2), 115-119.
559 doi.org/10.1080/00063659309477136
560 Pérez, J. H., Chmura, H. E., & Krause, J. S. (2018). Tundra avian community composition
561 during recovery from the Anaktuvuk River Fire. *International Journal of Wildland*
562 *Fire*, *27*(1), 69-71. doi.org/https://doi.org/10.1071/WF17159
563 Perkins-Kirkpatrick, S. E., & Lewis, S. C. (2020). Increasing trends in regional heatwaves.
564 *Nature communications*, *11*(1), 3357. doi.org/10.1038/s41467-020-16970-7
565 Piatt, J. F., Parrish, J. K., Renner, H. M., Schoen, S. K., Jones, T. T., Arimitsu, M. L., Kuletz,
566 K. J., Bodenstein, B., García-Reyes, M., Duerr, R. S., Corcoran, R. M., Kaler, R. S.
567 A., McChesney, G. J., Golightly, R. T., Coletti, H. A., Suryan, R. M., Burgess, H. K.,
568 Lindsey, J., Lindquist, K., & Sydeman, W. J. (2020). Extreme mortality and
569 reproductive failure of common murres resulting from the northeast Pacific marine

heatwave of 2014-2016. *PLOS ONE*, *15*(1), e0226087. doi.org/10.1371/journal.pone.0226087

Podofillini, S., Cecere, J. G., Griggio, M., Corti, M., De Capua, E. L., Parolini, M., Saino, N., Serra, L., & Rubolini, D. (2019). Benefits of extra food to reproduction depend on maternal condition. *Oikos*, *128*(7), 943-959. doi.org/10.1111/oik.06067

Podofillini, S., Cecere, J. G., Griggio, M., Curcio, A., De Capua, E. L., Fulco, E., Pirrello, S., Saino, N., Serra, L., Visceglia, M., & Rubolini, D. (2018). Home, dirty home: effect of old nest material on nest-site selection and breeding performance in a cavity-nesting raptor. *Current Zoology*, *64*(6), 693-702. doi.org/10.1093/cz/zoy012

Quintana, F., Uhart, M. M., Gallo, L., Mattera, M. B., Rimondi, A., & Gómez-Laich, A. (2022). Heat-related massive chick mortality in an Imperial Cormorant Leucocarbo atriceps colony from Patagonia, Argentina. *Polar Biology*, *45*(2), 275-284. doi.org/10.1007/s00300-021-02982-6

R Core Team. (2024). *R: A language and environment for statistical computing*. Foundation for Statistical Computing. https://www.R-project.org/

Raftery, A. E., Zimmer, A., Frierson, D. M. W., Startz, R., & Liu, P. (2017). Less than 2 °C warming by 2100 unlikely. *Nature Climate Change*, *7*(9), 637-641. doi.org/10.1038/nclimate3352

Ramellini, S., Imperio, S., Morinay, J., De Pascalis, F., Catoni, C., Morganti, M., Rubolini, D., & Cecere, J. G. (2022). Individual foraging site fidelity increases from incubation to nestling rearing in a colonial bird. *Animal Behaviour*, *193*, 145-155. doi.org/10.1016/j.anbehav.2022.07.014

Ricklefs, R. E., & Hainsworth, F. R. (1968). Temperature Regulation in Nestling Cactus Wrens: The Development of Homeothermy. *The Condor*, *70*(2), 121-127. doi.org/10.2307/1365955

Journal Pre-proof

595 Robinson, A., Lehmann, J., Barriopedro, D., Rahmstorf, S., & Coumou, D. (2021). Increasing
596 heat and rainfall extremes now far outside the historical climate. *npj Climate and*
597 *Atmospheric Science*, *4*(1), 45. doi.org/10.1038/s41612-021-00202-w
598 Rodríguez, C., Tapia, L., Kieny, F., & Bustamante, J. (2010). Temporal Changes in Lesser
599 Kestrel (Falco naumanni) Diet During the
600 Breeding Season in Southern Spain. *Journal of Raptor Research*, *44*(2), 120-128, 129.
601 doi.org/10.3356/JRR-09-34.1
602 Rodríguez, S., & Barba, E. (2016). Nestling Growth is Impaired by Heat Stress: an
603 Experimental Study in a Mediterranean Great Tit Population. *Zool Stud*, *55*, e40.
604 doi.org/10.6620/zs.2016.55-40
605 Romano, A., Corti, M., Soravia, C., Cecere, J. G., & Rubolini, D. (2021). Ectoparasites
606 exposure affects early growth and mouth colour in nestlings of a cavity-nesting raptor.
607 *Behavioral Ecology and Sociobiology*, *75*(11), 158. doi.org/10.1007/s00265-021-
608 03098-x
609 Salaberria, C., Celis, P., López-Rull, I., & Gil, D. (2014). Effects of temperature and nest heat
610 exposure on nestling growth, dehydration and survival in a Mediterranean hole-
611 nesting passerine. *Ibis*, *156*(2), 265-275. doi.org/10.1111/ibi.12121
612 Sarà, M., Bondì, S., Bermejo, A., Bourgeois, M., Bouzin, M., Bustamante, J., de la Puente, J.,
613 Evangelidis, A., Frassanito, A., Fulco, E., Giglio, G., Gradev, G., Griggio, M., López-
614 Ricaurte, L., Kordopatis, P., Marin, S., Martínez, J., Mascara, R., Mellone, U., . . .
615 Rubolini, D. (2019). Broad-front migration leads to strong migratory connectivity in
616 the lesser kestrel (Falco naumanni). *Journal of Biogeography*, *46*(12), 2663-2677.
617 doi.org/10.1111/jbi.13713
618 Soravia, C., Cecere, J. G., & Rubolini, D. (2021). Brood sex ratio modulates the effects of
619 extra food on parental effort and sibling competition in a sexually dimorphic raptor.

Journal Pre-proof

Behavioral Ecology and Sociobiology, *75*(3), 62. doi.org/10.1007/s00265-021-02970-0

Stillman, J. H. (2019). Heat Waves, the New Normal: Summertime Temperature Extremes Will Impact Animals, Ecosystems, and Human Communities. *Physiology*, *34*(2), 86-100. doi.org/10.1152/physiol.00040.2018

van de Ven, T. M. F. N., McKechnie, A. E., & Cunningham, S. J. (2019). The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, *191*(1), 205-215. doi.org/10.1007/s00442-019-04486-x

van de Ven, T. M. F. N., McKechnie, A. E., Er, S., & Cunningham, S. J. (2020). High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird. *Oecologia*, *193*(1), 225-235. doi.org/10.1007/s00442-020-04644-6

Welman, S., & Pichegru, L. (2023). Nest microclimate and heat stress in African Penguins Spheniscus demersus breeding on Bird Island, South Africa. *Bird Conservation International*, *33*, e34, Article e34. doi.org/10.1017/S0959270922000351

Wahed, A. E., Samira, M. N., & Ahmad, A. F. (2019). Variations in chemical composition value of adults and nymphs desert locust, Schistocerca gregaria Forskal (Orthoptera: Acrididae). *Journal of Plant Protection and Pathology*, *10*(12), 677-681.

Wheeler, M., Ton, R., Brandl, H. B., Schuett, W., & Griffith, S. C. (2023). Reduced parental brood visit rate in wild zebra finches Taeniopygia castanotis is correlated with high maximum daily ambient temperature. *Journal of Avian Biology*, *n/a*(n/a), e03152. doi.org/10.1111/jav.03152

Journal Pre-proof

643 Wolf, B. O., & Walsberg, G. E. (1996). Respiratory and Cutaneous Evaporative Water Loss at
644 High Environmental Temperatures in a Small Bird. *Journal of Experimental Biology*,
645 *199*(2), 451-457. doi.org/10.1242/jeb.199.2.451
646 Woodruff, M. J., Tsueda, S. N., Cutrell, T. S., Guardado, E. A., Rusch, D. B., Buechlein, A.,
647 & Rosvall, K. A. (2024). Heat alters diverse thermal tolerance mechanisms: An
648 organismal framework for studying climate change effects in a wild bird. *Functional*
649 *Ecology*, *n/a*(n/a). doi.org/10.1111/1365-2435.14704
650
651
652
653
654
655
656
657
658
659
660
661
662
663

Journal Pre-proof

Journal Pre-proof

Tables and Figures

Tables

Table 1. Daily maximum air temperature (mean ± SE) to which all nest boxes were exposed, as well as maximum nest temperatures (T_{nest}) (°C) in control, supplemented and shaded nest boxes during the nestling development period and the heatwave (June 22–23, 2025). Differences in temperature between experimental nest boxes during each period were tested using LMMs of daily T_{nest} with nest box and synchronous group identity as random intercept effects (see *Methods*: *Effects of shading on nest temperature*). In parentheses, minimum and maximum values for each period are provided.

T recording	Nestling development	Heatwave
Maximum daily air temperature	30.7 ± 0.1 (21.6–37.7°C)	38.3 ± 0.5 (37.8–38.8°C)
T_{nest} – control nest boxes	39.0 ± 0.5^{a} (24.5–48.5°C)	46.7 ± 0.5^{c} (40.1–51 .3°C)
T_{nest} – supplemented nest boxes	38.5 ± 0.6^{a} (23.8–51.1°C)	46.2 ± 0.6^{c} (42.1–52.7°C)
T_{nest} – shaded nest boxes	34.7 ± 0.5^{b} (23.5–44.3°C)	42.3 ± 0.5^{d} (38.7–45.8°C)

Note: Different superscript letters for estimated mean values indicate statistically significant differences ($p < .05$) in T_{nest} between groups at post hoc tests. Estimated differences between control, supplemented and shaded nest boxes: Nestling development (n = 64 nests): control – supplemented (estimate 0.5 ± 0.7, t = 0.7, p = 0.5), control – shaded (4.3 ± 0.6, t = 7.3, $p < .001$), supplemented – shaded (3.9 ± 0.7, t = 5.6, $p < .001$); Heatwave (n = 54 nests): control – supplemented (estimate 0.5 ± 0.8, t = 0.6, p = 0.5), control – shaded (4.5 ± 0.7, t = 6.3, $p < .001$), supplemented – shaded (3.9 ± 0.8, t = 4.9, $p < .001$).

683 Table 2. Linear Mixed Models (LMMs) of the effect of food supplementation and shading on
684 nestling final size (body mass and tarsus length). Marginal R^2 was computed according to
685 Nakagawa et al. (2017). Models include all fixed predictors; all interactions between the
686 experimental group and the other considered fixed predictors were non-significant and were
687 excluded from the models.

688

Predictors	Estimate ± SE	χ^2	df	p
Body mass day 15 (n = 225 nestlings; n = 74 nests; R^2 = 0.30)				
Experimental group[a]	–	17.91	2	<0.001
Brood size	0.47 ± 1.40	0.11	1	0.74
Rank	-6.26 ± 0.69	65.57	1	<0.001
Age	13.22 ± 3.56	12.87	1	<0.001
Ectoparasite load	0.14 ± 0.85	0.03	1	0.87
Tarsus length day 15 (n = 224 nestlings; n = 74 nests; R^2 = 0.48)				
Experimental group[d]	–	68.31	2	<0.001
Brood size	0.20 ± 0.13	2.55	1	0.11
Rank	-0.34 ± 0.09	13.65	1	<0.001
Age	0.30 ± 0.43	0.47	1	0.50
Ectoparasite load	-0.04 ± 0.10	0.15	1	0.70

689

690 *Note:* Different superscript letters for estimated mean values indicate statistically significant differences
691 ($p < .05$) in morphological traits between experimental groups at *post hoc* tests. [a]Estimated mean values,
692 control = 106 ± 2.8 g[b], food-supplemented = 114 ± 3.6 g[c], shaded = 121 ± 2.7 g[c]. [d]Estimated mean
693 values, control = 35.5 ± 0.2 mm[b], food-supplemented = 38.7 ± 0.3 mm[c], shaded = 38.2 ± 0.2 mm[c].

694

695

Journal Pre-proof

696 **Table 3.** Binomial Generalized Linear Mixed Models (GLMMs) of the effect of food
697 suplementation and shading on nestling probability of dying during a) development (when most
698 nest boxes experience non-critical T_{nest}; Table 1); b) a heatwave event. Marginal R^2 was
699 computed according to Nakagawa et al. (2017) coefficient of determination for GLMMs.
700 Models include all fixed predictors; all interactions between the experimental group and the
701 other considered fixed predictors were non-significant and were excluded from the models.

702

Predictors	Estimate ± SE	χ^2	df	p
(a) Development period (n = 232 nestlings; n = 74 nests; R^2 = 0.20)				
Experimental group[a]	–	0.05	2	0.98
Brood size	-0.50 ± 1.00	0.21	1	0.65
Rank	1.09 ± 0.63	3.70	1	0.05
(b) Heatwave period (n = 225 nestlings; n = 74 nests; R^2 = 0.49)				
Experimental group[c]	–	27.62	2	<0.001
Brood size	1.40 ± 0.63	5.66	1	0.02
Rank	0.03 ± 0.25	0.02	1	0.89

703

704 *Note:* Different superscript letters for estimated mean values indicate statistically significant differences
705 ($p < .05$) in mortality between experimental groups at *post hoc* tests. [a]Estimated mean values,
706 control = 0.04 ± 0.02^{b}, supplemented = 0.02 ± 0.02^{b}, shaded = 0.02 ± 0.01^{b}. [c]Estimated mean values,
707 control = 0.40 ± 0.05^{d}, supplemented = 0.45 ± 0.08^{d}, shaded = 0.04 ± 0.02^{e}.

708

709

710

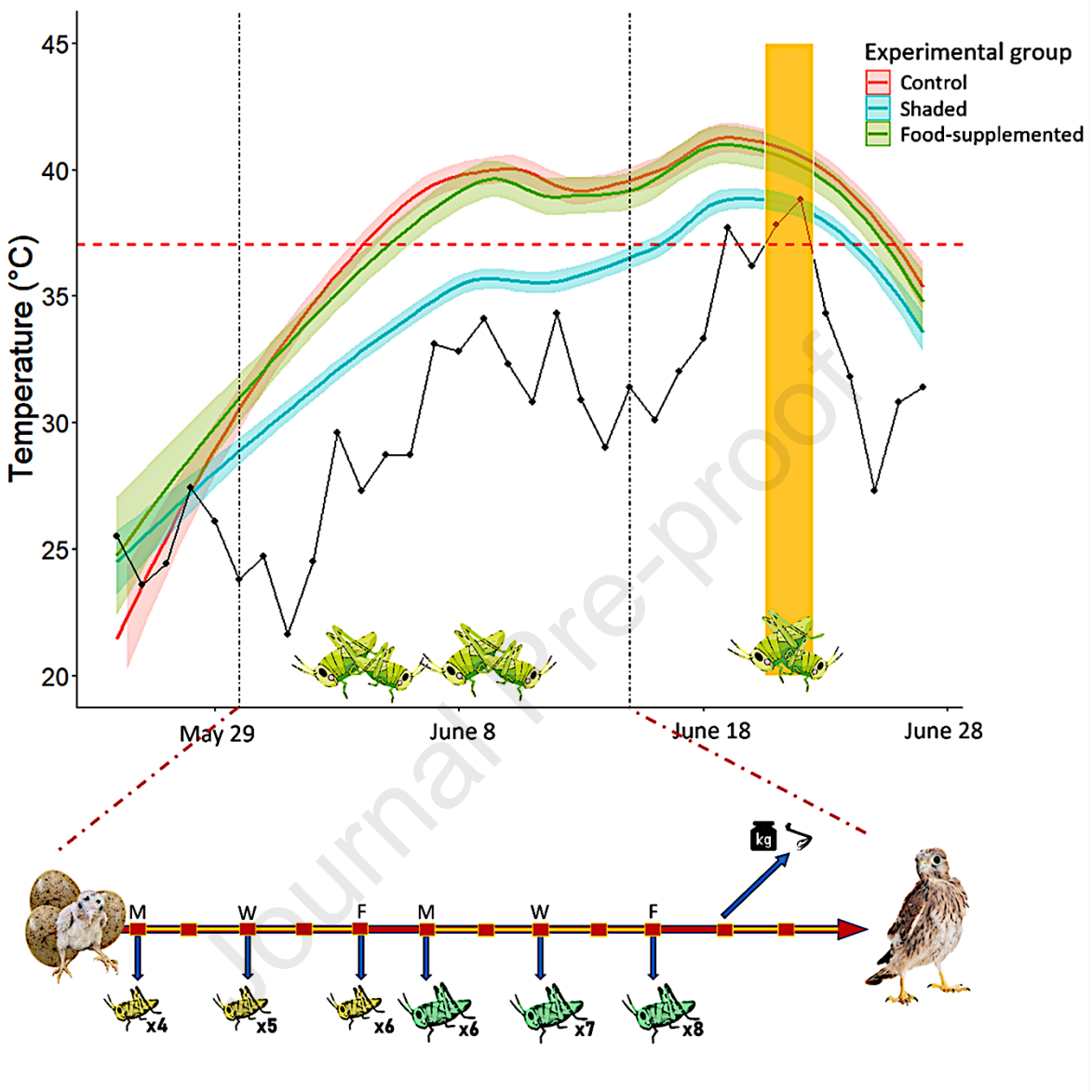
711

712

Journal Pre-proof

713 **Figures**

714



715

716 **Figure 1.** Daily maximum air temperature (black dots and line; obtained from a nearby weather
717 station: http://www.centrofunzionalebasilicata.it) and mean maximum nest temperature per day
718 in control (red line), food-supplemented (green line) and shaded (blue line) nest boxes. The
719 orange rectangle represents the heatwave period, during which air temperatures exceeded the
720 37° C threshold (dashed horizontal red line) for at least two consecutive days (June 22–23,
721 2025). The vertical dashed black lines represent the mean hatching date (left) and the last visit
722 to the nest (right; 15 days after). The 15 days development period is shown below on the

horizontal bar: during this period, supplemented nest boxes were provided with desert locust (number of locusts per nestling/day) following the procedure schematized below the graph (yellow locusts: medium size; green locusts: large size). Food-supplemented nests were provided additional locusts during the two-day period comprehending the heatwave event (for more information see *Methods: Experimental procedure*).

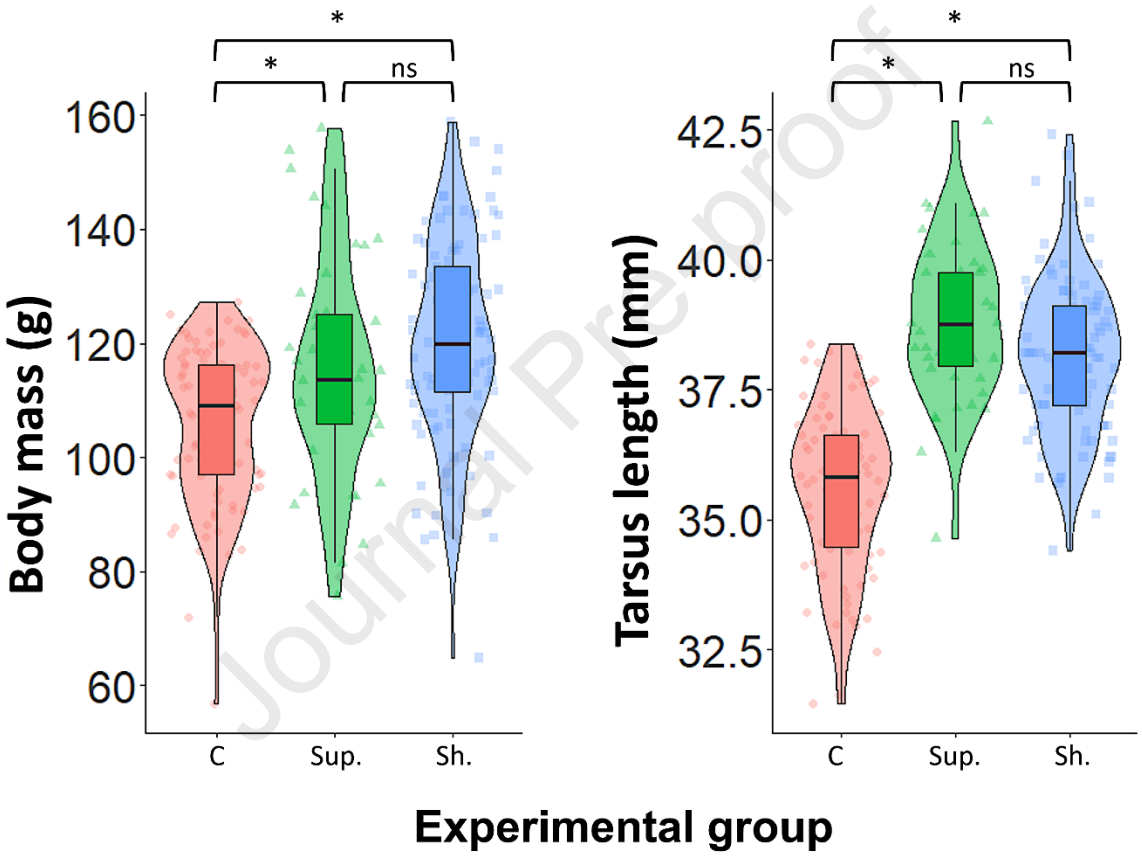
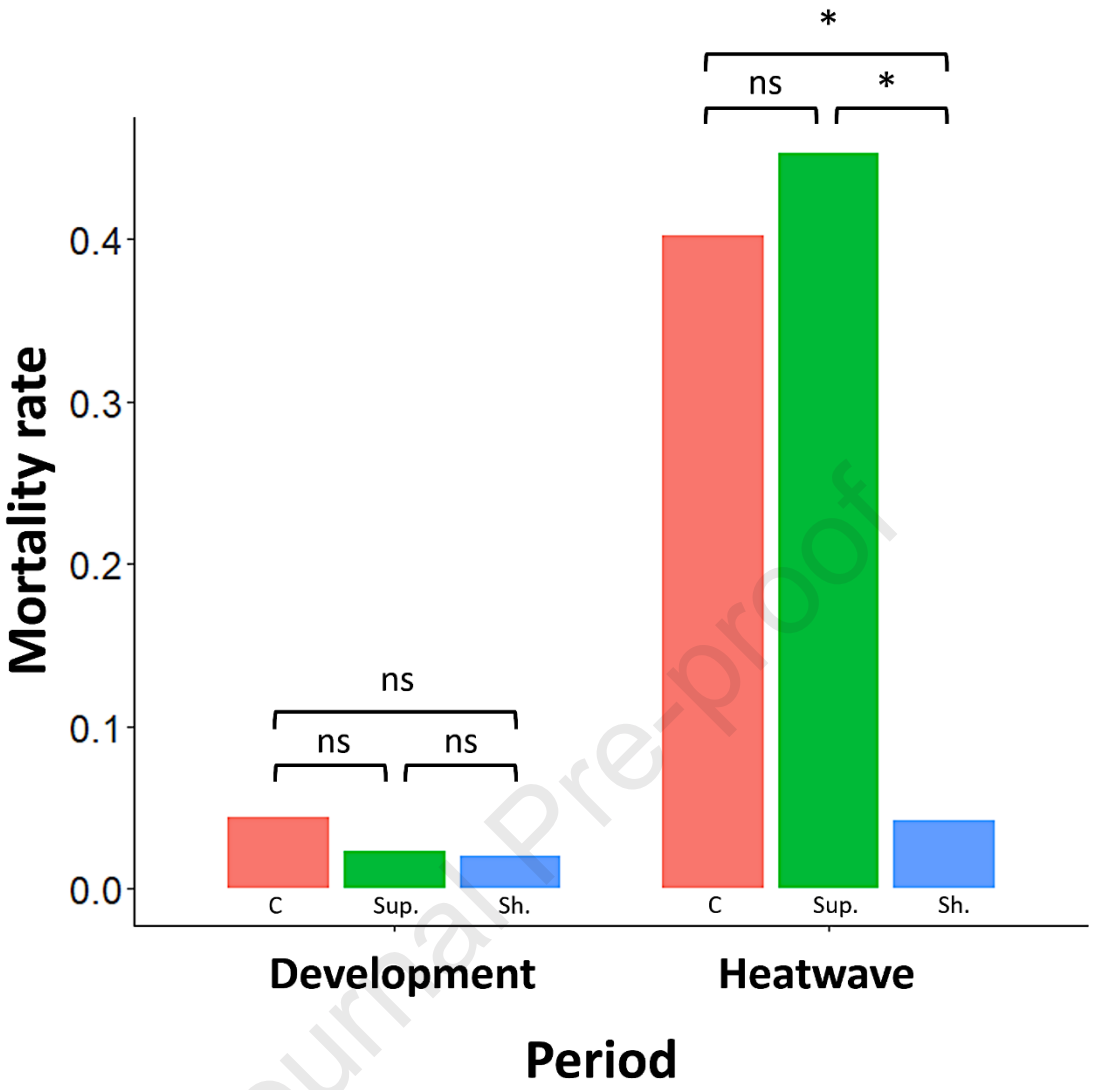


Figure 2. Body mass (left) and tarsus length (right) in control (red circles), food-supplemented (green triangles) and shaded (blue squares) nestlings during the last monitoring visit (mean age 15 ± 0.1 days old), before the occurrence of the heatwave. Data points represent raw data from models described in Table 2. * = $p < 0.05$ at *post hoc* tests (see Table 2); ns = $p > 0.05$.



736 **Figure 3.** Nestling mortality rate (proportion of dead nestlings) during both development and
737 heatwave periods according to experimental groups: control (red; C), supplemented (green;
738 Sup.) and shaded (blue; Sh.). * = $p < 0.05$ at *post hoc* tests (see Table 3); ns = $p > 0.05$.

739
740

Journal Pre-proof

Journal Pre-proof

Funding Sources

Nest boxes were built and purchased under the framework of the LIFE Project “Rapaci Lucani” (LIFE05NAT/IT/00009). Monitoring of nest boxes and acquisition of equipment was carried with partial financial support from the PRIN 2022 funding scheme (grant number 2022CWMRNH to A.R., funded by the European Union, NextGenerationEU). A.CC, M.M. and A.P. were supported by the Italian Ministry of University and Research (project funded by the European Union - Next Generation EU: “PNRR Missione 4 Componente 2, “Dalla ricerca all’impresa”, Investimento 1.4, Progetto CN00000033”). D.R. was also partly supported by Ecosistema MUSA (Multilayered Urban Sustainability Action) (funded by the European Union e NextGenerationEU under the NRRP M4C2 Investment Line 1.5: Strengthening of research structures and creation of R&D ‘innovation ecosystems’, set up of ‘territorial leaders in R&D’, project ECS_00000037).

Journal Pre-proof