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RESEARCH ARTICLE

Experimental nest cooling reveals dramatic effects of heatwaves on reproduction in a Mediterranean bird of prey

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Abstract

Future climatic scenarios forecast increases in average temperatures as well as in the frequency, duration, and intensity of extreme events, such as heatwaves. Whereas behavioral adjustments can buffer direct physiological and fitness costs of exposure to excessive temperature in wild animals, these may prove more difficult during specific life stages when vagility is reduced (e.g., early developmental stages). By means of a nest cooling experiment, we tested the effects of extreme temperatures on different stages of reproduction in a cavity-nesting Mediterranean bird of prey, the lesser kestrel (*Falco naumanni*), facing a recent increase in the frequency of heatwaves during its breeding season. Nest temperature in a group of nest boxes placed on roof terraces was reduced by shading them from direct sunlight in 2 consecutive years (2021 and 2022). We then compared hatching failure, mortality, and nestling morphology between shaded and non-shaded (control) nest boxes. Nest temperature in control nest boxes was on average 3.9°C higher than in shaded ones during heatwaves, that is, spells of extreme air temperature (>37°C for ≥2 consecutive days) which hit the study area during the nestling-rearing phase in both years. Hatching failure markedly increased with increasing nest temperature, rising above 50% when maximum nest temperatures exceeded 44°C. Nestlings from control nest boxes showed higher mortality during heatwaves (55% vs. 10% in shaded nest boxes) and those that survived further showed impaired morphological growth (body mass and skeletal size). Hence, heatwaves occurring during the breeding period can have both strong lethal and sublethal impacts on different components of avian reproduction, from egg hatching to nestling growth. More broadly, these findings suggest that the projected future increases of summer temperatures and heatwave frequency in the Mediterranean basin and elsewhere in temperate areas may threaten the local persistence of even relatively warm-adapted species.

KEYWORDS
early development, extreme temperature, heat stress, heatwaves, nest microclimate, temperature manipulation

1 | INTRODUCTION

Anthropogenic climate change is expected to produce an increase in average global temperatures of at least 1.5°C in the next 20 years (IPCC, 2021), with further increases by the end of this century under a business-as-usual emissions scenario (Raftery et al., 2017). Besides, climate change may promote an increase in the frequency and extent of extreme meteorological events such as droughts and heatwaves (Danner et al., 2021; Robinson et al., 2021; Rogers et al., 2022; Stillman, 2019). For instance, before the 1980s, extreme heat events were limited to less than 1% of the Earth's surface and occurred mostly in hot and dry desert areas (Hansen et al., 2012). However, by the beginning of the 21st century, these anomalies have affected more than 10% of the global land surface (Hansen et al., 2012). Predicting how such extreme heat events will ultimately impact population dynamics of wild species requires knowledge of their effects on reproduction and survival (Conradie et al., 2019). Investigating the impact of extreme heat events on wild species is, however, challenging due to their unpredictability, with most of our knowledge on this topic deriving from long-term studies (Altwegg et al., 2006; Thibault & Brown, 2008).

Among wild vertebrates, the effects of extreme air temperatures (T_{air}) on fitness have been mostly addressed in taxa that live in warm and arid (i.e., desert or semi-desert) ecosystems, where heat levels are often close to upper thermal limits and where further warming can result in unsuitable conditions for reproduction and survival. These studies revealed that fitness is influenced by extreme T_{air} in several ways, for instance by impairing foraging behavior and breeding success via reduced parental care (van de Ven et al., 2020; Wiley & Ridley, 2016) or by inducing negative physiological effects in both parents and offspring (Oswald & Arnold, 2012; Ton et al., 2021).

However, even at extreme T_{air}, animals can experience highly variable ambient temperatures due to large differences in local temperatures within their home range (so-called "microsites," such as shaded areas). When T_{air} is very high, mobile vertebrates manage indeed to remain within their thermoneutral zone (i.e., the range of ambient temperature within which body temperature is regulated with minimal energy and water expenditure) by relocating to cooler microsites, becoming active in cooler hours, or reducing activity levels to avoid overheating (Cunningham et al., 2015; van de Ven et al., 2019). Fitness costs of such behavioral adjustments to extreme T_{air} may be considerable, especially if extreme heat events occur during the reproductive phase, and mostly relate to missed opportunities (van de Ven et al., 2019). For instance, to avoid hyperthermia, parents attending offspring may be forced to alter their parental care or provisioning rates, eventually increasing offspring predation risk, or decreasing the amount and/or quality of food provided to their progeny (Sharpe et al., 2021; Tapper et al., 2020; van de Ven et al., 2019; Wiley & Ridley, 2016).

Although behavioral adjustment may to some extent buffer the direct physiological and fitness costs of excessive temperature, this may prove difficult or impossible in some circumstances or in specific phases of the life cycle. For instance, during early development, offspring of altricial avian species are tied to their natal location (nest site) where they may experience nest ambient temperature (T_{nest}) that may be higher than T_{air}, with limited or no opportunities to relocate to avoid dehydration and/or hyperthermia. In these conditions, whenever T_{nest} exceeds the threshold at which excessive heat can be passively dissipated (upper critical temperature, UCT; Mitchell et al., 2018), heat dissipation can only occur through evaporative water loss, which also implies an increase of metabolic rates in species that rely on panting to cool down (e.g., raptors and passerines; McKechnie et al., 2021; Mosher, 1976). Prolonged exposure to temperatures above the UCT (but still within the survival zone) may lead to heat-related mortality via two main physiological pathways (Albright et al., 2017). On the one hand, lethal dehydration occurs when cumulative evaporative water loss exceeds lethal dehydration tolerance limits; this may be especially frequent in smaller bodied individuals/species that are subjected to relatively higher mass-specific evaporative water loss (Albright et al., 2017; McKechnie & Wolf, 2010). On the other hand, especially at T_{nest} approaching the upper limit of the survival zone, lethal hyperthermia may occur whenever the highest possible rate of evaporative water loss is lower than the evaporation rate required to keep the body temperature below the lethal level (Albright et al., 2017; Mertens, 1977; Mitchell et al., 2018). Hence, extreme T_{nest} conditions, which typically occur during heatwaves, are frequently associated with extensive die-offs in offspring of wild bird species (Catry et al., 2011, 2015; Conradie et al., 2020). Yet, energetic costs of cooling when the heat load is high (but below lethal levels) may hamper offspring development and survival (e.g., McKechnie et al., 2016). Such sublethal effects can also affect population dynamics by impairing local recruitment, eventually leading to population declines and local extinctions (Iknayan & Beissinger, 2018).

The mechanisms underlying the negative impacts of extreme T_{air} exposure on avian reproduction may be diverse. Offspring survival and growth may be negatively affected both directly (by exposure to elevated T_{nest}) and indirectly (by decreased prey availability and/or reduced foraging opportunities of parents experiencing elevated T_{air}; Marcelino et al., 2020; van de Ven et al., 2019). We separated these effects by experimentally manipulating T_{nest} during different stages of reproduction, from incubation to nestling-rearing, in a cavity-nesting bird of prey from the Mediterranean region, the lesser kestrel (*Falco naumanni*), thereby decoupling the effects of exposure to elevated T_{air} from those of

elevated T_{nest} on fitness. Previous correlative studies of this species have documented an increase of nestling mortality under extreme T_{air}, nestlings showing reduced chances of survival when T_{air} exceeded 37°C during a heatwave (Catry et al., 2015). Although extreme T_{air} most likely resulted in nestling heat stress and severe dehydration, whether such a sensitivity of nestlings to extreme T_{air} is explained by a concomitant variation in parental prey provisioning rate and/or in prey quality brought to nestlings is unclear. Moreover, previous studies correlated nestling mortality events with high T_{air} rather than with high T_{nest}, which could be much higher. Furthermore, elevated mean daily T_{air} during the incubation period may jeopardize egg hatching success, especially for clutches laid by females in poor condition (Serrano et al., 2005). However, whether elevated T_{nest} has a causal role in affecting hatching failure remains unclear, because seasonal and condition-mediated effects could interact in complex ways that can hardly be discerned in correlational studies (Serrano et al., 2005).

Relying on a nest box-breeding population, we experimentally reduced T_{nest} by shading some nest boxes from direct sunlight (shaded nest boxes), while others (matched with experimental ones for laying/hatching date and sun exposure) were left unmanipulated (control nest boxes). By means of this novel experimental setup, we examined the effects of cooler nest temperatures on egg hatching failure, nestling mortality, and early growth trajectories, irrespective of variation in T_{air}. The experiment was conducted in 2 consecutive years, during which the study area was hit by severe heatwaves (ISAC, 2022), which are becoming increasingly frequent in the Mediterranean region (Díaz-Poso et al., 2023; Serrano-Notivoli et al., 2022). Given that T_{air} affecting the surrounding environment was similar for all parents, we could disentangle the effect of elevated T_{air}, which may negatively affect foraging efficiency of parents and/or prey availability, from the direct effect of elevated T_{nest} exposure on reproduction. We expected higher egg hatching failure, higher mortality, and impaired nestling growth in control nest boxes compared to shaded ones. On the contrary, lack of differences in hatching rate or nestling fitness between control and shaded nest boxes, associated with higher T_{nest} in control versus shaded nest boxes, would indicate that extreme T_{air} negatively affected reproduction mainly indirectly, by impairing parental brooding or provisioning behavior.

2 | MATERIALS AND METHODS

2.1 | Study species, study area, and general field procedures

The lesser kestrel is a small (ca. 120 g) colonial breeding bird of prey. European populations are migratory, spending the non-breeding season in the Sahel region and reaching their breeding grounds between February and April (Sarà et al., 2019). Egg laying takes place between late April and mid-May. Females lay clutches of three to five eggs, which are incubated by both parents for ca. 30 days. After hatching, nestlings are fed at the nest by both parents until they fledge when ca. 40 days old.

The study was carried out during April–July 2021 and 2022 in the city of Matera, southern Italy (40°66′ N, 16°61′ E). This small city hosts a large breeding population of about 1000 breeding pairs (La Gioia et al., 2017), some of which breed in nest boxes (Morinay et al., 2021). During June 21–24, 2021 and June 27–28, 2022, the study area was hit by strong heatwaves, with a maximum June monthly temperature anomaly of up to +2.5°C (2021) and +3.5°C (2022) relative to the 1991–2020 reference mean (ISAC, 2022). According to Catry et al. (2015), we defined a heatwave as a period when maximum T_{air} reached values >37°C for at least 2 consecutive days.

We performed our T_{nest} manipulation experiment on nest boxes located on the roof terraces of two buildings (Provincia, approx. 600 m^2, and Genio, approx. 300 m^2). A nest box consisted of a hollow refractory brick (300 × 300 × 370 mm) closed by two wooden panels (300 × 300 × 20 mm) with an entrance hole (65 mm diameter) in the frontal one and four smaller (10 mm diameter) holes in both panels to increase airflow within the nest box (Figure 1). Nest boxes were placed along the perimeter of terraces, at a minimum distance of ~2 m from each other. From the beginning of May, we monitored nest boxes twice a week to record breeding parameters (i.e., laying date, hatching date, hatching failure, and brood size). Upon hatching, nestlings of the same brood were individually marked with a different combination of small black dots on the crown and nape using a black permanent marker (Podofillini et al., 2018). We collected morphometric data from each nestling during two to five different monitoring sessions, until nestlings were ca. 15 days old. We recorded body mass with an electronic balance (accuracy 0.1 g) and tarsus length with a digital caliper (accuracy 0.01 mm). In addition, we assessed nestling infestation by *Carnus hemapterus* ectoparasitic flies on three body regions (interclavicular depression, and right and left underwings). We scored ectoparasites as the maximum number of flies detected in each region according to a 0–3 scale (0: no visible flies, 1: 1–3 flies, 2: 4–6 flies, and 3: >6 flies) and expressed ectoparasite load as the mean value of ectoparasite score across the three body regions (Podofillini et al., 2018, 2019; Romano et al., 2021). Nestlings were ringed with metal rings when ca. 10 days old. Because eggs hatch asynchronously (Aparicio, 1997; Podofillini et al., 2018), we ranked each nestling in a given nest box according to hatching order (the nestling that hatched first was assigned the highest rank, i.e., rank 1; high-ranking nestlings were thus the earlier hatched in a clutch) (see Podofillini et al., 2019 for details on rank assignment). We did not systematically collect data from nestlings that were older than 15 days to reduce the risk of inducing premature fledging (Podofillini et al., 2018). When a nestling was found for the first time, a small blood sample (~50 μL) was collected in capillary tubes by puncturing the brachial vein using sterile needles. Nestlings were sexed by means of a PCR amplification of the sex-specific CHD-1 gene, following standard protocols (Griffiths et al., 1998; Podofillini et al., 2018). In both years, some nestlings were not

FIGURE 1 Left panel: control nest box with shading cover on the side; right panel: shaded nest box, with the shading cover preventing direct sunlight exposure while allowing air to flow on both sides and top of the nest box. The quarry tile that was used to shade the rear wooden panel (on the internal side of which the temperature logger was attached) is also visible behind the nest box in the left panel. The wall fencing the experimental roof terraces, which prevents nestlings from falling down the terraces when abandoning their nest box, is visible on the background.

sexed for different reasons, including missing or degraded blood samples (15 of 172 nestlings in 2021 and 54 of 175 nestlings in 2022).

Nestling mortality was assessed directly by retrieving corpses of marked nestlings within nest boxes or in their immediate surroundings (parents may take corpses of nestlings outside the nest box). In some instances, however, nestlings were not present in the nest box and corpses could not be found. This could happen because corpses were scavenged by jackdaws (*Corvus monedula*), very abundant in the study area, which regularly inspect roof terraces to feed on dead nestlings or lesser kestrel prey remains. In addition, our nest boxes are located on flat roof terraces enclosed by short walls, with limited possibility of falling (Figure 1). Hence, a missing nestling (even when the corpse was not recovered) could be confidently regarded as dead.

2.2 | Nest temperature manipulation

2.2.1 | Nest box shading and nest temperature recording

To reduce T_{nest}, nest boxes were provided with a cover that prevented direct sunlight exposure (shaded nest boxes). The cover consisted of three 5 mm thick plywood planks (410 × 360 × 450 mm), forming an open box around the nest box, leaving 50 mm on each side and top to allow airflow (Figure 1). Control nest boxes were left exposed to natural sunlight. To assess the effects of shading on T_{nest} and the direct effects of variation in T_{nest} on reproduction, we recorded temperature inside both shaded and control nest boxes using miniaturized temperature loggers (Elitech RC-5+, Elitech, UK; accuracy 0.5°C) tightly attached with a rope to the inner side of the back wooden panel. We leant a quarry tile (400 × 400 × 30 mm) against the outer side of the rear panel (sloping by ~45° compared to the panel) (Figure 1, left panel) to shade it from direct sunlight (which could bias T_{nest} recordings upward), while still allowing air to flow within the nest box through the small back panel holes. We set the loggers to record temperature every 15 min during the experimental period. Temperature loggers were certified as being individually calibrated by the supplier. Before deployment, loggers were placed in a thermostatic chamber at constant temperature for 12 h; all loggers correctly recorded the reference temperature, with negligible differences between loggers. Hourly T_{air} data were obtained from a nearby weather station (http://www.centrofunzionalebasilicata.it/, Matera weather station).

2.2.2 | Manipulation of nest temperature during incubation

To test the effects of a reduction of T_{nest} during incubation on hatching failure and to evaluate the additional effects of shading during incubation on nestling mortality and growth, in 2022 we deployed shading covers to a sample of nest boxes from one of the two roof terraces (Genio) from the onset of incubation (defined as the first monitoring session when clutch size did not change from the previous monitoring session, implying that egg laying was completed) until nestlings were ca. 25 days old. We established temporally matched groups of nest boxes ("synchronous groups") consisting of at least two nest boxes that started incubation within

1–3 days. One of the nest boxes within each synchronous group was randomly assigned to receive shading, whereas the other nest boxes in the group were not shaded and considered as temporally matched controls. Overall, we established nine synchronous groups, each of which included one shaded and 1–6 control nest boxes (for a total of $n = 24$ nest boxes, nine of which shaded and 15 controls).

2.2.3 | Manipulation of nest temperature during nestling-rearing

To investigate the effects of T_{nest} after hatching on nestling fitness (mortality and growth), hence disentangling pre- from post-hatching effects of elevated T_{nest} exposure, we applied shading covers to a sample of nest boxes from one roof terrace (Provincia) both in 2021 and 2022. Upon hatching of the first nestling in a nest box (hatching date hereafter), we matched it with at least another nest box whose first nestlings were also hatching on the same day, establishing a synchronous group. One nest box of this group was then randomly assigned to receive shading, whereas the other nest boxes were considered as temporally matched controls. Overall, across the 2 years, we established 43 synchronous groups, each of which including one shaded and 1–2 control nest boxes (2021: 24 shaded and 24 control nest boxes; 2022: 19 shaded and 22 control nest boxes).

2.3 | Statistical analyses

2.3.1 | Effects of shading on nest temperature

To assess the extent of T_{nest} reduction induced by shading during the different breeding phases, we assessed whether daily diurnal (6 a.m. to 10 p.m., UTC + 2) maximum T_{nest} differed between control and shaded nest boxes using linear mixed models (LMMs) with nest box and synchronous group identity as random intercept effects (the latter reflecting the pairwise nature of the experimental design and included also in all subsequent mixed models). We fitted separate LMMs for (a) the egg incubation stage (from onset of incubation to the day of hatching of the first egg); (b) the nestling-rearing stage (from hatching of the first egg to the subsequent 20 days, excluding the days assigned to heatwave events); (c) heatwave events. We further tested whether the difference in T_{nest} between control and shaded nest boxes varied among these stages by fitting an LMM of the difference in maximum daily T_{nest} between control and shaded nest boxes (within a given synchronous group; for control nest boxes, the mean value of daily maximum T_{nest} was computed if more than one control nest box was present), including stage (three-level factor: incubation, nestling-rearing, heatwave) as a fixed effect and synchronous group identity as a random intercept effect.

2.3.2 | Effects of shading and nest temperature on hatching failure

To investigate the effects of T_{nest} on egg hatching failure, we fitted binomial generalized linear mixed models (GLMMs), with the probability of hatching failure of each egg (0 = hatched, 1 = not hatched) as the binomial dependent variable, and clutch (=nestbox) identity as a random intercept effect. To account for seasonal variation in parental quality and breeding success, as well as for seasonal variation in ecological conditions, we included synchronous group identity as a further random intercept effect. We fitted two separate models: (1) in a first model, aimed at testing the cumulative effects of shading during incubation on embryo development and egg hatching, we included shading as a two-level fixed factor; (2) in a second model, aimed at analyzing the immediate effects of T_{nest} experienced by embryos around hatching (when near-term embryos may be particularly vulnerable; McCowan & Griffith, 2021) on hatching failure, we included the maximum T_{nest} during the 3 days before and after hatching of the first egg as a covariate. To further investigate the immediate effects of T_{nest} on hatching failure, we fitted two additional binomial GLMMs including only data from those nest boxes that were shaded from hatching of the first egg (Provincia roof terrace). Shading was included as a two-level fixed factor in the first model, while in the second one we included maximum T_{nest} in the 3 days after shading as a covariate. In these models, we only considered eggs hatched between the deployment of nest box cover and the subsequent nest box monitoring sessions (i.e., excluding eggs that hatched before shading was applied [before hatching of the first nestling], and thus before a synchronous group was established). Before deploying nest box covers, control and nest boxes that were eventually shaded did not differ in hatching failure rates (control nest boxes: 0.51 [100/195 eggs]; shaded nest boxes: 0.47 [86/185 eggs]; binomial GLMM with clutch and synchronous group identity as a random intercept effect and shading as a two-level fixed factor, effect of shading: $Z = 0.88$, $p = .38$).

2.3.3 | Effects of shading on nestling mortality and growth

Nestling mortality was concentrated during heatwaves that occurred a few days after hatching in both years (see Section 3). We thus investigated the effect of shading on nestling mortality through the heatwave events by means of a binomial GLMM with nestling mortality (0 = alive after the heatwave; 1 = dead) as the response variable, including shading as a three-level fixed factor (control, shaded from onset of incubation, shaded from hatching), brood (=nestbox) identity and synchronous group identity as random intercept effects. As additional predictors, we included brood size, nestling rank, and sex (0 = females, 1 = males), all variables that could potentially affect lesser kestrel nestling survival

and fitness (Podofillini et al., 2019), and their two-way interactions with shading. Because only few nestlings from shaded nest boxes died during the heatwave event (two in 2021 and 13 in 2022; see Section 3), we fitted a further binomial GLMM on the sample of individuals from control nest boxes including maximum T_{nest} between the two monitoring sessions encompassing the heatwave event (i.e., before and after the event), brood size, nestling rank, and sex as predictors (together with their two-way interactions with shading), and brood identity as a random intercept effect. Finally, as pre- and post-heatwave mortality occurred also in shaded nest boxes, we fitted a binomial GLMM of nestling mortality until the last monitoring session, investigating whether shading had persistent effects on nestling survival when considering mortality occurring during non-heatwave periods only. Besides shading, we included brood size, rank, sex, and their two-way interactions with shading as predictors. Brood and synchronous group identity were included as random intercept effects.

The effect of shading on nestling growth (body mass and tarsus length) of individuals surviving up to 15 days after hatching (corresponding to the linear growth phase, see Romano et al., 2021) were investigated using LMMs, including shading (three-level factor), brood size, laying date, age, ectoparasite load, rank, and sex as fixed effects. Nestling, brood, and synchronous group identity were included as random intercept effects. In initial models, we included (1) all two-way interactions between age, rank, and shading, to test for differential nestling growth according to rank and shading (Podofillini et al., 2018, 2019; Romano et al., 2021); (2) two-way interactions between shading and the other covariates (sex, brood size, and ectoparasite load); (3) a three-way interaction between age, rank, and shading to test if nestlings of different ranks grew at different rates in either experimental groups (Romano et al., 2021).

2.3.4 | Cumulative effects of shading on reproduction

To assess the cumulative effects of shading on reproduction (from the onset of incubation to the last nestling monitoring session, i.e., 15 days after hatching), we plotted survival curves of propagules (both eggs and/or nestlings) for all clutches assigned to the three experimental groups (control, shaded from onset of incubation, shaded from hatching). We included only clutches where egg laying was completed and where incubation had started (as judged by the presence of brooding parents in the nest box during monitoring). As we aimed at providing a general overview of breeding success in the study population according to experimental groups, we considered among control clutches also all those clutches (both from 2021 and 2022) that were not included in any synchronous group (e.g., clutches that were abandoned before hatching, as assessed by the presence of cold, non-incubated eggs and/or when brooding adults disappeared during incubation). Clutches that were shaded at hatching were considered as controls before nest box covers were deployed. As a consequence, the survival curve for control clutches bifurcates at the time of hatching into two distinct curves, one for clutches that remained in the control group (were shading was never applied) and the other for clutches that were shaded after hatching. We set the bifurcation time point at day 31 from the onset of incubation, corresponding to the mean time elapsed from onset of incubation to hatching of the first egg in a clutch (1.99 SD, minimum–maximum values 21–37 days).

2.3.5 | Statistical software

All statistical analyses were performed using R (version 4.0.1; R Core Team, 2020). LMMs and binomial GLMMs were fitted using the "lme4" and "glmmTMB" libraries, respectively (Bates et al., 2014; Brooks et al., 2017). We checked for collinearity and inspected residual diagnostics using the "performance" package (Lüdecke et al., 2021). In all mixed models, we mean centered the predictors and removed three-way interactions (if tested) when nonsignificant ($p > .05$). We then refitted models including two-way interactions and removed nonsignificant interactions in a single step. Final models included all main effects and statistically significant interaction terms. In addition, when the variable sex did not have any significant effect, we removed it and refitted the model including also non-sexed nestlings, to increase sample size and power of the analyses. Significance of fixed effects was assessed by likelihood ratio tests (Singmann et al., 2015). Means and parameter estimates are reported together with their associated standard error, unless stated otherwise.

2.4 | Ethical note

Capture and handling was performed by ISPRA under the authorization of Law 157/1992 [Art. 4 (1) and Art. 7 (5)]. Control nest boxes (where most nestling mortality occurred) were part of a long-term population monitoring project (started in 2016) and were exposed to natural sunlight and temperature. Hence, mortality of nestlings within those nest boxes should resemble naturally occurring mortality. Nest boxes were specifically made of refractory brick, which is expected to result in lower T_{nest} compared to, for example, other nest box materials (such as wood, Catry et al., 2015). Although mortality rates within nest boxes might be higher than within natural cavities, no additional mortality within shaded nest boxes could be attributed to the experimental manipulation. On the contrary, the total mortality of nestlings within shaded nest boxes by the age of 15 days was similar (shaded from incubation: 34.4%, 11/32 nestlings; shaded from hatching: 25.8%, 39/151 nestlings) to the mortality of nestlings recorded by the same age in a previous year (when

no heatwaves occurred and no shading was deployed; 31%, 44/143 nestlings; Podofillini et al., 2019).

3 | RESULTS

3.1 | Variation in air and nest temperature and lesser kestrel breeding phenology

In both study years, a heatwave, with maximum T_{air} surpassing 37°C for at least two consecutive days (mean maximum T_{air} = 38.0 ± 0.6°C), hit the study area within the first 10–15 days after median egg hatching date (Figure 2). The heatwave pattern was similar in the 2 years (Figure 2). Although the heatwave was more severe and persistent in 2021 compared with 2022, during 2022 T_{air} values > 30°C were already recorded during the egg hatching phase (Figure 2). Nest box shading effectively reduced maximum T_{nest} by ~3°C during both incubation and nestling-rearing phases. The cooling effect was even more pronounced during heatwaves (~4°C; Table 1), with maximum T_{nest} showing markedly higher values in control (45.7 ± 0.3°C, min–max: 40.5–50.0°C) compared to shaded nest boxes (41.8 ± 0.2°C, min–max: 38.2–45.5°C). These maximum daily T_{nest} differences between control and shaded nest boxes were significantly larger during heatwaves (3.68 ± 0.34°C) than in egg incubation (2.15 ± 0.32°C) and nestling-rearing stages (3.15 ± 0.29°C) (LMM, $\chi^2 = 49.5$, df = 2, $p < .001$).

3.2 | Extreme nest temperatures increase hatching failure

Shading from incubation produced a large decrease in egg hatching failures (0.20, 8/40 eggs failing to hatch) compared to matched control nest boxes (0.50, 31/62 eggs), but the difference was marginally nonsignificant (Table 2). However, maximum T_{nest} around egg hatching had an immediate effect, higher T_{nest} resulting in significantly higher egg hatching failures (Table 2; Figure 3). Maximum T_{nest} of 44°C around egg hatching was associated with a 50% hatching failure (Figure 3; note that shaded nest boxes did not reach these high ambient temperatures). A similar effect of maximum T_{nest} on hatching failure was also observed for the group of nest boxes that were shaded at hatching. Although shading per se did not significantly decrease egg hatching failure in this sample of nest boxes (hatching failure of eggs hatched after the first egg had hatched: control, 0.59 [59/100 eggs]; shaded, 0.47 [40/86 eggs]), inter-nest differences in T_{nest} affected hatching failure, as there was a significant increase in egg hatching failure with increasing maximum T_{nest} during hatching (Table 2). Hence, elevated nest temperatures around hatching, rather than constantly elevated nest temperatures during the egg incubation stage, had a relatively stronger effect on hatching failure, suggesting that elevated T_{air} during the critical hatching stage may have a disproportionately negative effect on breeding success compared to elevated T_{air} occurring during the rest of the incubation stage.

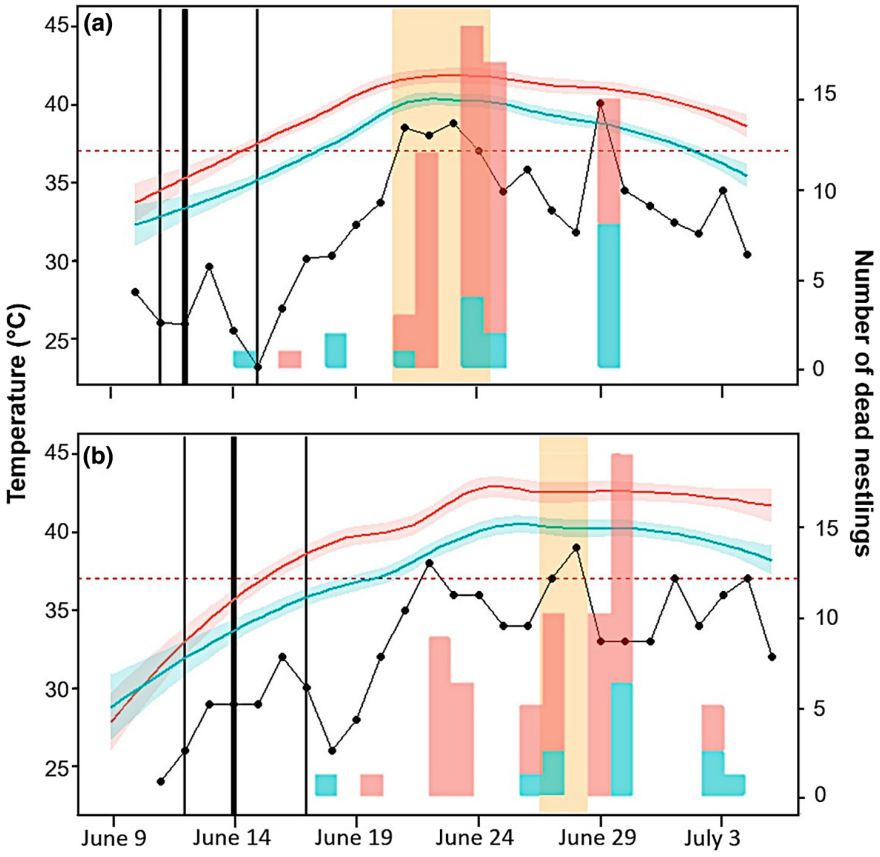

FIGURE 2 Daily maximum T_{air} (black dots and line) and mean maximum T_{nest} per day in control (red line) and shaded (blue line) nest boxes during 2021 (a) and 2022 (b). Vertical bars represent the number of dead nestlings per day (red: control nest boxes; blue: shaded nest boxes; to facilitate comparisons, T_{nest} and mortality data for 2022 refer to nest boxes shaded from hatching only. The orange rectangles represent the heatwave periods, when air temperatures surpassed the 37°C threshold (dashed horizontal red line) for ≥2 consecutive days. The vertical thick black line represents the median hatching date (thin lines: 25th and 75th percentiles).

3.3 | Extreme nest temperatures impair nestling survival and growth

Nestling mortality was concentrated during heatwaves, but mortality spikes occurred whenever maximum T_{air} exceeded 37°C even for a single day, and mostly involved nestlings from non-shaded nest boxes (Figure 2). Mortality occurring during heatwaves involved nestlings that were, on average, 9.21 days old (range: 4–18 days old, $n = 61$) in control nest boxes, and 10.57 days old (range: 5–15, $n = 15$) in shaded ones. Mortality during heatwaves was significantly reduced by shading, as nestlings from control nest boxes were more likely to die (0.55, 61/110 nestlings) than those from shaded ones (both from incubation and at hatching pooled: 0.10, 15/157 nestlings; Table 3, Figure 3). Similarly, low-ranking nestlings (i.e., smaller and late-hatched) showed higher mortality rates (as denoted by a positive association between probability of dying and rank; Table 3). Analyses focusing only on control nest boxes showed that maximum T_{nest} had a strong positive effect on nestling mortality, irrespective of brood size and nestling rank (Table 3). The predicted probability of dying surpassed 50% when maximum T_{nest} exceeded 44°C (Figure 3). Even excluding heatwave conditions, nestling mortality occurred more frequently in control (mortality rate: 0.46, 43/94 nestlings) than in shaded nest boxes (0.21, 35/168 nestlings; Table 3), suggesting that the protective cooling effect of shading occurred also outside heatwave events. Similar to previous models, we detected a strong effect of rank, low-ranking nestlings showing a higher probability of dying (Table 3).

By 15 days post-hatching, nestlings from control nest boxes attained significantly lower body mass and smaller skeletal size than those from shaded ones (shading × age interaction, Table 4, Figure 4; estimated means at day 15, body mass: control = 78.1 ± 2.3 g; shaded from incubation = 110 ± 6.9 g; shaded from hatching = 94.5 ± 1.8 g; tarsus length: control = 35.5 ± 4.3 mm; shaded from incubation = 37.5 ± 2.3 mm; shaded from hatching = 37.0 ± 1.7 mm). Although nestlings from nest boxes shaded from incubation grew heavier than those shaded from hatching (by ~17%, Figure 4), the difference between the two shaded groups was not significant (Table 4). Nestlings from clutches laid later in the breeding season and low-ranking nestlings attained lower body mass and smaller skeletal size (Table 4). The analysis of morphometric traits also showed that high-ranking nestlings were significantly heavier and grew faster than low-ranking ones (significant rank × age interactions, Table 4), and that nestlings from late clutches were significantly lighter and attained smaller skeletal size than those from early clutches (Table 4), in accordance with previous analyses of lesser kestrel early growth patterns (see Section 2). Nestling sex did not significantly contribute to any model of mortality or growth and was thus removed from all final models (see Section 2).

TABLE 1 Daily maximum T_{air} (mean ± SE) to which all nest boxes were exposed, as well as nest temperatures (T_{nest}) (°C) in control and shaded nest boxes during egg incubation, nestling-rearing stages, and during 2021 and 2022 heatwave events. Differences in temperature between control and shaded nest boxes during each breeding stage and heatwave periods were tested using LMMs of maximum daily T_{nest} with nest box and synchronous group identity as random intercept effects (see Section 2 and table footnotes).

T recording	Egg incubation[a]	Nestling-rearing[b]	Heatwave[c]
T_{air}	26.9 ± 0.8	33.0 ± 0.5	38.0 ± 0.6
T_{nest}—control nest boxes	38.1 ± 0.5	40.4 ± 0.3	45.7 ± 0.3
T_{nest}—shaded nest boxes	35.3 ± 0.6	37.4 ± 0.3	41.8 ± 0.2

Note: Estimated differences between control and shaded nest boxes:
[a]Egg incubation ($n = 24$ nests): estimate −2.67 ± 0.56, $t = -3.48$, $p = .003$.
[b]Nestling-rearing ($n = 102$ nests): −2.89 ± 0.32, $t = -9.01$, $p < .001$.
[c]Heatwave ($n = 102$ nests): −3.72 ± 0.30, $t = -12.40$, $p < .001$.

3.4 | Cumulative effects of nest cooling on reproduction

Overall, shading markedly improved survival of propagules (eggs and/or nestlings) from the onset of incubation to 15 days post-hatching (Figure 5). At day 31 (average time to hatching from the onset of incubation), the overall proportion of potentially surviving propagules was 0.73 in control clutches (525/723 eggs) and 0.93 in those shaded from incubation (37/40 eggs) (see also Section 3.2). Upon hatching, survival sharply decreased in all experimental groups due to naturally occurring mortality in the critical early days of life (especially of low-ranking nestlings/embryos from last-laid eggs).

TABLE 2 Binomial GLMMs of the effect of shading or maximum T_{nest} around egg hatching on egg hatching failure in: (a) nest boxes shaded from incubation; (b) nest boxes shaded from hatching of the first egg (excluding eggs that were already hatched before the synchronous group was established, i.e., before experimental shading; see Section 2). Marginal R^2 was computed according to Nakagawa et al. (2017).

Predictors	Estimate ± SE	df	χ^2	*p*
(a) Nest boxes shaded from incubation				
Shading ($n = 102$ eggs, $n = 24$ nests; $R^2 = .32$)	−2.51 ± 1.53	1	3.03	.08
Maximum T_{nest} ($n = 102$ eggs, $n = 24$ nests; $R^2 = .33$)	0.62 ± 0.24	1	9.66	.002
(b) Nest boxes shaded from hatching of the first egg				
Shading ($n = 186$ eggs, $n = 81$ nests; $R^2 = .03$)	−0.59 ± 0.44	1	1.75	.19
Maximum T_{nest} ($n = 157$ eggs, $n = 71$ nests; $R^2 = .13$)	0.24 ± 0.10	1	6.97	.010

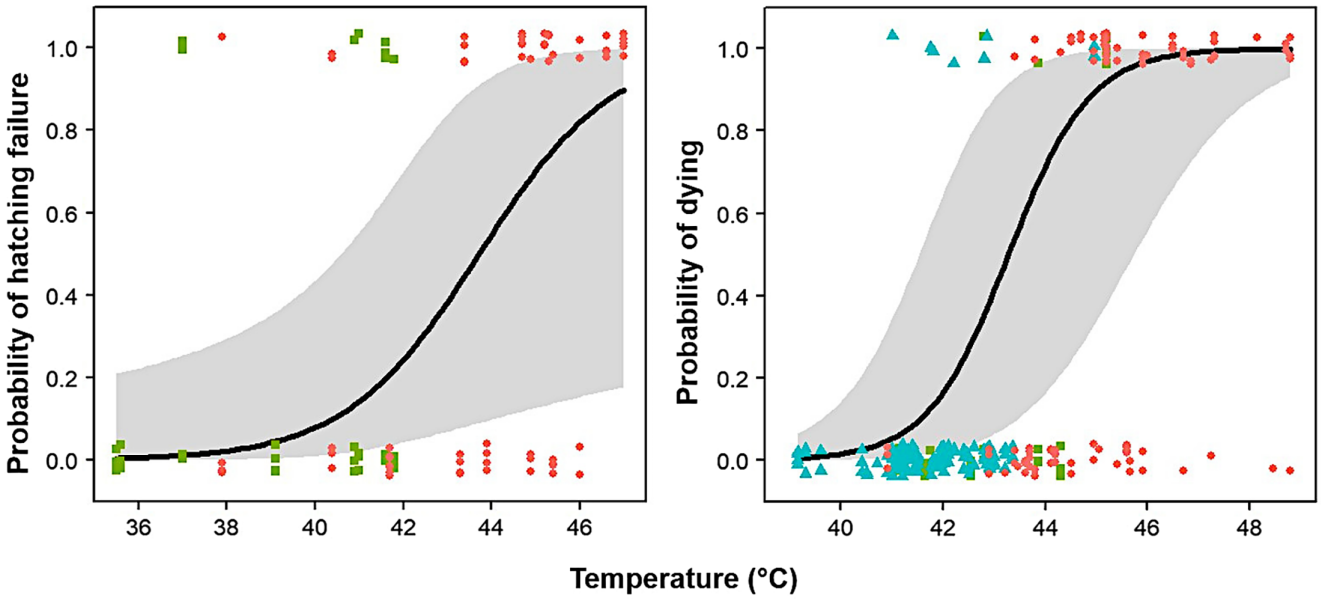

FIGURE 3 Probability of egg hatching failure and nestlings' probability of dying according to maximum T_{nest}. The fitted lines (with 95% confidence bands) were derived from GLMMs reported in Table 2 (egg hatching failure in control nest boxes and in nest boxes shaded from incubation, effect of maximum T_{nest}) and Table 3 (nestling mortality during heatwaves—control nest boxes; in the latter case, although the model was fitted to data from control nest boxes, where most of the mortality occurred, data for shaded nest boxes are also plotted). Red dots: eggs/nestlings from control nest boxes; green squares: eggs/nestlings in nest boxes shaded from incubation; blue triangles: nestlings in nest boxes shaded from hatching. A limited vertical jittering was added to better distinguish overlapping data points.

TABLE 3 Binomial GLMMs of the effect of shading or maximum T_{nest} on nestling probability of dying during a heatwave event for (a) all nest boxes and (b) control nest boxes. Model (c) shows instead the effect of shading on nestling mortality probability during non-heatwave periods. Marginal R^2 was computed according to Nakagawa et al. (2017).

Predictors	Estimate ± SE	df	χ^2	p
(a) Heatwave mortality—all nest boxes (n = 267 nestlings, n = 86 broods; R^2 = .33)				
Shading[a]	—	2	27.80	<.001
Brood size	−0.10 ± 0.47	1	0.04	.84
Rank	0.51 ± 0.23	1	5.26	.022
(b) Heatwave mortality—control nest boxes (n = 98 nestlings, n = 33 broods; R^2 = .32)				
Maximum T_{nest}	1.82 ± 0.62	1	12.57	<.001
Brood size	−0.14 ± 0.45	1	0.09	.76
Rank	0.04 ± 0.31	1	0.02	.90
(c) Non-heatwave mortality (n = 262 nestlings, n = 89 broods; R^2 = .25)				
Shading[d]	—	2	12.25	.002
Brood size	−0.01 ± 0.32	1	0.01	.99
Rank	1.00 ± 0.25	1	21.38	<.001

Note: Different superscript letters for estimated mean values indicate statistically significant differences (p < .05) in mortality between groups at post hoc tests. [a]Estimated mean values, control = 0.63 ± 0.17[b], shaded from incubation = 0.03 ± 0.04[c], shaded from hatching = 0.01 ± 0.01[c]. [d]Estimated mean values, control = 0.48 ± 0.12[e], shaded from incubation = 0.08 ± 0.08[f], shaded from hatching = 0.08 ± 0.04[f].

However, offspring survival in nest boxes shaded from incubation and those shaded from hatching showed similar temporal patterns up to 15 days post-hatching (mortality rate × 100 nestlings: 0.013 vs. 0.019 nestlings per day, respectively), whereas survival decreased more markedly in control nest boxes (mortality rate × 100 nestlings: 0.040 nestlings per day). Survival by 15 days post-hatching was remarkably low in control clutches (0.29), intermediate in clutches shaded from hatching (0.52), and relatively high in those shaded from incubation (0.75; Figure 5).

4 | DISCUSSION

By means of a novel field experiment performed during naturally occurring heatwaves, we showed that cooling of nest cavities resulted in clear positive effects on reproduction in the lesser kestrel, a Mediterranean bird of prey of European conservation interest (Annex I of the Birds Directive, Council Directive 79/409/EEC). Even before heatwaves occurred, elevated nest temperatures during the critical perinatal stage (a few days before hatching) increased hatching failures, which reached values above 50% when nest temperatures surpassed 44°C. During heatwaves, dramatic nestling mortality was detected in control nest boxes (~55% of nestlings), whereas in shaded nest boxes it was considerably lower (~10%). In control nest boxes, the probability of dying of nestlings during a heatwave was above 50% when maximum nest temperature surpassed 44°C. Even among nestlings surviving heatwaves, exposure to elevated nest temperature had persistent effects throughout the

TABLE 4 LMMs of the effect of shading on nestling growth (body mass and tarsus length) up to day 15 post-hatching. Marginal R^2 was computed according to Nakagawa et al. (2017).

Predictors	Estimate ± SE	df	χ^2/Z	p
Body mass (n = 184 nestlings, n = 70 broods; R^2 = .85)				
Shading	–	2	14.63	<.001
Brood size	0.01 ± 0.03	1	0.07	.79
Rank	−0.07 ± 0.02	1	17.41	<.001
Laying date	−0.13 ± 0.03	1	13.23	<.001
Age	0.73 ± 0.02	1	73.75	<.001
Ectoparasite load	0.02 ± 0.02	1	1.09	.30
Shading × age[a]	–	2	100.56	<.001
Rank × age	−0.06 ± 0.01	1	25.68	<.001
Tarsus length (n = 184 nestlings, n = 70 broods; R^2 = .92)				
Shading	–	2	2.93	.23
Brood size	0.03 ± 0.02	1	2.26	.13
Rank	−0.02 ± 0.01	1	2.91	.09
Laying date	−0.06 ± 0.02	1	7.18	.010
Age	0.89 ± 0.02	1	142.42	<.001
Ectoparasite load	0.01 ± 0.02	1	0.14	.71
Shading × age[d]	–	2	54.85	<.001
Rank × age	−0.04 ± 0.01	1	18.92	<.001

Note: Different superscript letters for estimated mean values indicate statistically significant differences (p < .05) in trait values between groups at post hoc tests. [a]Slopes: control = 0.73 ± 0.02, shaded from incubation = 1.22 ± 0.05, shaded from hatching = 0.92 ± 0.01; estimated mean values (day 15): control = 78.1[b] ± 2.3 g, shaded from incubation = 110.0[c] ± 6.9 g, shaded from hatching = 94.5[c] ± 1.8 g. [d]Slopes: control = 0.89 ± 0.02, shaded from incubation = 1.16 ± 0.03, shaded from hatching = 0.98 ± 0.01; estimated mean values (day 15): control = 35.5[e] ± 4.3 mm, shaded from incubation = 37.5[f] ± 2.3 mm, shaded from hatching = 37.0[f] ± 1.7 mm.

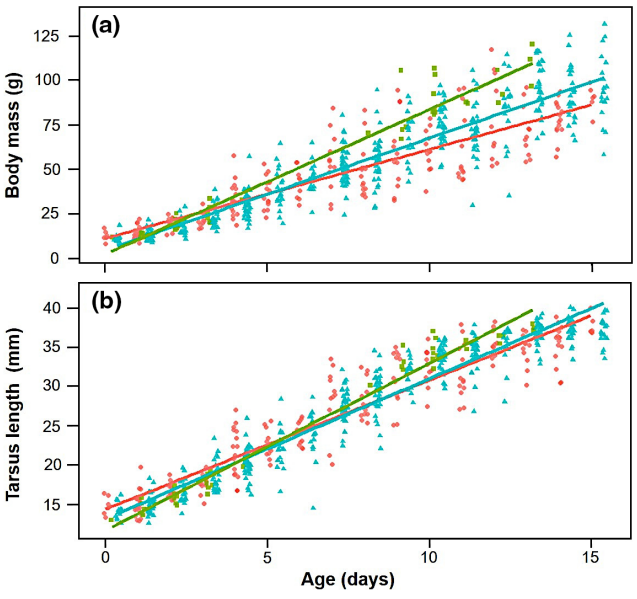

FIGURE 4 Nestling growth ([a] body mass; [b] tarsus length) in control (red circles) and shaded nest boxes (from incubation: green squares; from hatching: blue triangles) during the linear growth period (up to ca. 15 days post-hatching). Fitted lines were derived from the corresponding LMMs reported in Table 4. For each age, data belonging to different experimental groups were represented with slightly modified x-axis values and a slight horizontal jittering to reduce overlap and improve clarity.

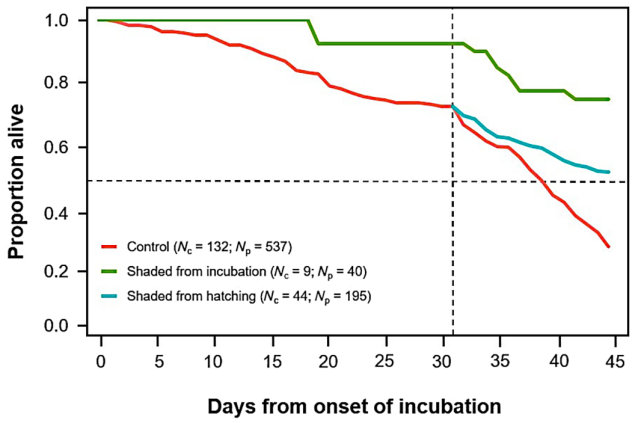

FIGURE 5 Survival curves of propagules (eggs/nestlings) from the onset of incubation to day 15 post-hatching in control nest boxes and in those shaded from incubation or from hatching. N_c = number of clutches, N_p = number of propagules (initial number of eggs). Reported sample size for control nest boxes refers to post-hatching values; the overall sample size for control clutches between onset of incubation and hatching was N_c = 176 and N_p = 732. The horizontal dashed line indicates a survival probability of .5, while the vertical dashed line denotes the mean time to hatching in the population (31 days).

rest of the rearing period: nestlings from control nest boxes grew lighter (by ~20%–30%) and attained a smaller skeletal size by the end of the linear growth period than those from shaded nest boxes.

Overall, only 29% of eggs resulted in a nestling being alive at day 15 in control nest boxes, compared to >50% in shaded nest boxes (similar to non-heatwave years; Podofillini et al., 2019).

4.1 | Lethal effects of heatwaves on embryos

It has long been known that hyperthermia in avian embryos can induce harmful or lethal effects (Romanoff et al., 1938; Webb, 1987; White & Kinney, 1974). In laboratory experiments, exposing developing embryos to temperatures ≥39.5°C for long periods reduces egg viability, although upper critical temperature values may be species-specific (Romanoff et al., 1938; Webb, 1987) and eggs of some desert-adapted species may cope well even with higher temperatures (up to 42°C) for prolonged periods (Arieli et al., 1988). Avian embryos are unable to thermoregulate autonomously and providing an optimal developing temperature by parents, through behavioral regulation of brooding patterns, is a key element of egg viability (Arieli et al., 1988; Deeming & Reynolds, 2015; Malacarne et al., 1992). However, while open-nesting species may buffer temperature variation by altering brooding behavior (e.g., by shadowing instead of brooding their eggs when exposed to high T_{air}; Clauser & McRae, 2017), such an option may be more limited in cavity nesters. Indeed, the nest cavity may overheat without any possibility for parents to buffer exposure of their eggs to elevated T_{nest}, and may even expose attending parents themselves to overheating and dehydration (van de Ven et al., 2020). For instance, nest box-breeding zebra finches exposed to prolonged naturally occurring heatwaves with T_{air} exceeding 40°C for several consecutive days (with T_{nest}>45°C), suffered a nearly complete hatching failure (McCowan & Griffith, 2021). Moreover, elevated mean T_{air} during incubation increased hatching failures in lesser kestrels, but only among poor condition females (Serrano et al., 2005). However, the latter finding may be confounded by a concomitant seasonal decline in parental quality (Catry et al., 2016) and a seasonal increase of mean T_{air} (rather than an increase in T_{nest}) during the breeding season, which may negatively affect resource availability (Serrano et al., 2005). Our results confirmed that elevated T_{nest} do indeed directly affect hatching failures, pointing out that T_{nest} conditions experienced in the few days around hatching have a stronger impact than persistent cooling during the entire egg incubation stage. Hence, the exposure to even short bursts of high temperature at the perinatal stage, a critical period of embryo development when lung ventilation begins and embryos spend a considerable amount of energy in breaking the eggshell (Vleck & Bucher, 1998), could lead to a reduction of embryo viability, likely due to lethal hyperthermia. Such high T_{nest} bursts may thus have a disproportionately larger negative impact on reproduction compared to elevated T_{nest} occurring during the rest of the incubation stage.

4.2 | Lethal effects of heatwaves on nestlings

When experienced temperature exceeds an individual's thermoneutral zone (i.e., it surpasses the UCT; Mitchell et al., 2018), one of the main routes by which nestlings of many bird species dissipate heat is via respiratory evaporative water loss through panting (Andreasson et al., 2018; Ricklefs & Hainsworth, 1968). Panting is commonly observed in raptors under heat stress (Mosher, 1976) and was indeed documented in video recordings of lesser kestrel nestlings inside the nest boxes (Authors' pers. obs.). While panting may effectively allow keeping own body temperature below lethal levels in the short term, it results in increased metabolic heat production (Angilletta et al., 2010; Smit et al., 2016; Whitfield et al., 2015; Wolf & Walsberg, 1996) and hence a faster exhaustion of water reserves if excessive heat exposure persists (Albright et al., 2017), which may ultimately cause death because of dehydration (Conradie et al., 2020; Skwarska et al., 2021). At T_{nest} approaching the upper limit of the survival zone, death may occur also because of lethal hyperthermia (Mertens, 1977; Mitchell et al., 2018). Although mortality events in control nest boxes were concentrated during heatwaves, isolated T_{air} peaks coincided with excess mortality, suggesting that exposure to even relatively short spells of elevated temperatures may be lethal for growing nestlings.

These results are in line with previous correlative evidence in several avian taxa, whereby elevated T_{air} was associated with dramatic effects on nestlings' fitness. For instance, Catry et al. (2015) documented a mortality of 32% of lesser kestrel nestlings due to lethal hyperthermia and/or dehydration when T_{air} exceeded 37°C for ≥2 consecutive days. Similarly, van de Ven et al. (2020) showed that the likelihood of successful fledging of nestling hornbills (*Tockus leucomelas*) fell below 50% when T_{air} surpassed 35°C, due both to indirect effects (a reduction of parental provisioning rate) and an increase of nestling thermoregulation costs.

Although a reduction of foraging or nestling food provisioning activity by parents has been proposed as a possible explanation for decreased fledging rate of birds experiencing extreme T_{air} (Funghi et al., 2019; Tapper et al., 2020; van de Ven et al., 2019), we can safely rule out this possibility in our study, because: (1) the mortality rate in shaded nest boxes was similar to that observed in non-heatwave years (Podofillini et al., 2019) and (2) parents of both shaded and control nest boxes were exposed to the same T_{air} conditions while foraging and they were not (or only minimally) affected by T_{nest} during nestling-rearing as lesser kestrels only frequent the nest box during the very first days after hatching (particularly the female), and mainly during the night, when T_{nest} drops. Hence, any difference in mortality between control nest boxes and those shaded from hatching can be robustly considered a direct effect of nest temperature. Previous studies on lesser kestrels suggested that, besides direct mortality, heatwaves could increase indirect mortality by pushing nestlings outside their nest cavity to search for relief from overheating, thus causing premature fledging and increasing the risk of predation (Catry et al., 2011, 2015). For instance, with T_{air}>37°C, the number of nestlings close to fledging (yet unable to fly) found below nest cavities increased exponentially (Catry et al., 2015). We could rule out that indirect mortality occurred in our study because heatwaves occurred at an age when nestlings were still unable to abandon their nest autonomously (i.e., <10 days of age). Hence, lethal dehydration and/or hyperthermia was the main cause of nestling mortality in our study.

4.3 | Sublethal effects of heatwaves

Besides inducing mortality, exposure to elevated T_{nest} during early development impaired nestlings' body mass and skeletal growth. This finding is in line with previous studies on both wild bird species (Andreasson et al., 2018; Corregidor-Castro & Jones, 2021; Rodriguez & Barba, 2016; Shipley et al., 2022; van de Ven et al., 2020) and poultry (Nawaz et al., 2021). Two non-mutually exclusive mechanisms may explain the impaired growth in nestlings exposed to elevated T_{nest}. First, evaporative water loss upon sustained exposure to T_{nest} above UCT may considerably reduce body mass, as birds may lose up to 5% of their body mass hourly and suffer from dehydration (Wolf & Walsberg, 1996). Second, impaired growth may follow an increase of the metabolic costs of cooling (through panting) when T_{nest} exceeds the thermoneutral zone (Cunningham et al., 2013; Nawaz et al., 2021; Salaberria et al., 2014).

Alternatively, impaired growth may be related to altered begging behavior, through which nestlings solicit food to attending parents (Soravia et al., 2021). Whereas adult birds are known to respond to thermal challenges by reducing their activity level and foraging effort (Cunningham et al., 2015; Playà-Montmany et al., 2023; Ruth et al., 2020; Ryeland et al., 2017) or by reducing foraging efficiency (du Plessis et al., 2012), to our knowledge no study of begging intensity and effectiveness has been performed under elevated ambient temperatures. However, begging behavior has an optimal temperature response, implying that, at high temperatures, it may be less efficient (Choi & Bakken, 1990). Although we limited biometric recordings at ca. 15 days post-hatching, and thus, we could not assess if further increases of body mass occurred beyond the sampling period, this is the age when body mass and skeletal size reach a plateau in lesser kestrels (Braziotis et al., 2017; Catry et al., 2011; Romano et al., 2021). Hence, we can reasonably assume that a smaller body size at 15 days post-hatching is later mirrored into smaller body size at fledging. In many species, including lesser kestrels (Catry et al., 2015), a smaller body size at fledging impairs a range of fitness traits, such as survival, recruitment into the breeding population, fecundity, and breeding success (Haywood & Perrins, 1992; Magrath, 1991; Schwagmeyer & Mock, 2008). Such carry-over effects of early growth conditions on fitness can have far-reaching influences on population demographic traits and may constitute a key mechanism underlying climate change effects on population dynamics (Oswald et al., 2021; Schou et al., 2021; Sergio et al., 2022).

4.4 | Conservation implications

Urban-breeding lesser kestrels lay their eggs behind roof tiles, in wall crevices, and in other man-made structures that present a sufficiently broad cavity for breeding, where they may be exposed to excess heating similar to nest boxes. Unfortunately, access to such more "natural" nest sites is far from easy in urban settings, so it is difficult to compare their thermal environment with that of experimental nest boxes. It is thus unclear if currently used nest boxes should be regarded as suboptimal nesting sites because of their thermal properties. However, upon arrival from pre-breeding migration, lesser kestrels have access to a broad range of nest boxes differing in sun exposure, ventilation, and hence T_{nest}. Indeed, there was a broad overlap in T_{nest} between shaded and control nest boxes. Experimentally analyzing patterns of nest box selection (e.g., Morinay et al., 2021) in relation to nest box thermal characteristics may reveal whether lesser kestrel preferentially settle in those nests that provide the greatest fitness return in terms of hatching and fledging success. The large-scale deployment of nest boxes has been suggested as a key tool to strengthen local lesser kestrel populations (Gameiro et al., 2020). Clearly, our findings strongly support the idea that nest box design, material, and positioning can be key factors in determining the effectiveness of conservation interventions and in improving the resilience of target species in the face of rapidly changing climatic conditions (Catry et al., 2011). More broadly, incorporating energy-saving concepts from architecture in the design of wildlife-dedicated structures can considerably improve their thermal performance and hence the success of conservation efforts under global warming scenarios (Fontaine et al., 2021). In urban settings, integrating such structures with innovative and biodiversity-friendly architectural solutions (such as green roofs; Fernández Cañero & González Redondo, 2010) could further boost their ecological and conservation value.

4.5 | Concluding remarks

The Mediterranean area is an important biodiversity hotspot (Marcelino et al., 2020; Myers et al., 2000) whose species are facing intense pressures from climate change (Aurelle et al., 2022). This region has experienced a strong increment in the frequency and intensity of extreme heat events in recent decades (Díaz-Poso et al., 2023; Kuglitsch et al., 2010; Serrano-Notivoli et al., 2022) and it is expected to increase its maximum temperature extremes above the predicted global average (Seneviratne et al., 2016). Hence, reaching critical temperature thresholds will become increasingly frequent in the near future for many taxa, fostering redistributions, range shifts, and possibly triggering local extinctions (Chatzimentor et al., 2022). Our findings contribute to elucidate the mechanisms by which extreme climatic events can affect animal populations via a negative impact on reproduction. We showed that negative effects on reproductive success may be diverse, spanning from dramatic offspring mortality to more subtle, sublethal effects on offspring fitness-related traits potentially affecting population dynamics via carry-over effects. Ultimately, such extreme events may have long-lasting, pervasive impacts that limit population size more strongly than average climate change, triggering rapid population declines that may jeopardize conservation efforts and threaten local persistence of even relatively warm-adapted species.

AUTHOR CONTRIBUTIONS

Diego Rubolini, Andrea Pilastro, Jacopo G. Cecere, and Alejandro Corregidor-Castro conceived the study; Alejandro Corregidor-Castro, Jennifer Morinay, Diego Rubolini, Susan E. McKinlay,

Samuele Ramellini, Michelangelo Morganti, Andrea Romano, and Enrico L. De Capua organized field activities, conducted fieldwork, and collected the data; Alejandro Corregidor-Castro, Diego Rubolini, and Andrea Pilastro analyzed the data; Alejandro Corregidor-Castro, Alexandra Glavaschi, and Alessandro Grapputo performed genetic analyses; Alejandro Corregidor-Castro, Diego Rubolini, and Andrea Pilastro wrote the manuscript, with inputs from all other co-authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Research Data Unipd at doi: https://doi.org/10.25430/researchdata.cab.unipd.it.00000941.

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