Animal Behaviour 219 (2025) 123006

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Facing the heat: nestlings of a cavity-nesting raptor trade safety for food when exposed to high nest temperatures

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ARTICLE INFO

Article history:
Received 3 January 2024
Initial acceptance 17 March 2024
Final acceptance 30 July 2024
Available online 8 November 2024
MS. number: 24-00010R

Keywords:
behavioural thermoregulation
climate change
Falco naumanni
lesser kestrel
nest temperature
predation risk
temperature manipulation
trade-off

Increasing temperatures due to climate warming may expose many species to thermally dangerous conditions, especially during less mobile phases of their life cycle when the chances of relocating to cooler sites are limited. We investigated how altricial nestlings of cavity-nesting lesser kestrels, *Falco naumanni*, respond to elevated nest temperatures. In the study system, nestlings develop in nestboxes placed on roof terraces. Before fledging, they often rest outside the nestbox, near the entrance hole, where they can be fed by parents and rapidly re-enter if threatened. This behaviour is similar to premature fledging observed in some species during heatwaves, which causes extensive nestling mortality. We experimentally tested whether high nest temperatures increased the likelihood of nestlings temporarily leaving their nest, thereby exposing themselves to higher predation risk. This may occur either because nestlings attempt to escape unbearable temperatures inside the nest or because resting outside provides them with priority access to parentally delivered food. After the eggs hatched, we reduced the maximum nest temperatures by ca. 4 °C by shading the nestboxes. We found that nestlings from control (unshaded) nestboxes were twice as likely to be detected outside than those from shaded ones. Regardless of shading, nestlings left the nestboxes more frequently in the early morning when nest temperatures were lowest. Notably, hourly nest temperature did not significantly affect the probability of nestlings being detected outside. Nestlings resting outside monopolized parentally delivered food; however, parental provisioning did not differ between shaded and control nests, implying a costly, zero-sum competition game among nestmates. Our results suggest that exposure to high nest temperatures associated with climate warming can increase mortality due to dehydration and impaired growth and may also induce nestlings to trade their safety for enhanced access to food, thereby exacerbating the negative effects of climate warming on birds' reproduction.

Global temperatures are expected to rise by 1.5 °C in the next few decades because of climate change, with maximum temperatures forecasted to increase by as much as 5 °C in some regions (Intergovernmental Panel on Climate Change, 2021). Such an increase, coupled with a projected increment in both frequency and intensity of extreme temperature bursts (i.e. heatwaves; Robinson et al., 2021; Rogers et al., 2022; Stillman, 2019), will push many organisms outside of their optimal temperature range. Because the occurrence of these heatwaves is predicted to increase globally, including areas historically buffered from such events (Perkins-Kirkpatrick & Lewis, 2020), and because such extreme events are expected to increasingly affect wild organisms (Murali

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https://doi.org/10.1016/j.anbehav.2024.10.020

et al., 2023), understanding animals' responses to elevated temperatures will improve our forecasts of climate change effects on biodiversity and ecosystems functioning.

In homeotherms, heat can no longer be passively dissipated when ambient temperatures exceed the upper limit of the thermoneutral zone, that is, the range of temperature within which individuals can maintain optimal body temperature with minimal energy and water expenditure (Diehl et al., 2023; Norris & Kunz, 2012). To avoid overheating, individuals are forced to switch to more energetically demanding strategies, such as evaporative cooling, which involves actively increasing water evaporation by, for example, panting, sweating or gular fluttering (Mitchell et al., 2018). Although effective in the short term, evaporative cooling has two side effects: an increased risk of dehydration (Czenze et al., 2020) and an increased metabolic rate, especially in species that rely on panting (Loughran & Wolf, 2023; McKechnie et al., 2021; Mitchell et al., 2018). Panting is energetically costly and increases body heat production, so the effectiveness of evaporative cooling in maintaining body temperature within the physiological limits is restricted by energy and water availability as well as the ratio between heat production and dissipation. Therefore, in the medium term, evaporative cooling may impair body condition by exhausting water and energy reserves and is generally not sustainable for a prolonged period, leading to death because of overheating or lethal dehydration (Albright et al., 2017).

In some circumstances, overheating may be avoided by behavioural adjustments to elevated temperatures (Huey et al., 2003; Muñoz, 2022). Rapid temperature peaks may trigger short-term emergency thermoregulatory responses (Sears et al., 2011), ranging from selection of cooler microsites (referred to as thermal refugia; Hall et al., 2016; Ruth et al., 2020) to alterations of foraging behaviour (Cunningham et al., 2015). However, these responses may entail fitness costs including impaired foraging activity (Cunningham et al., 2015), loss of reproductive opportunities (Ruth et al., 2020) or reduced parental care (Wiley & Ridley, 2016).

Behavioural thermoregulatory responses and their associated costs and benefits are usually studied in adult individuals (Cunningham et al., 2021). However, it is increasingly evident that early developmental stages may be highly sensitive to exposure to elevated temperatures (Bourne et al., 2020; Catry et al., 2015; Corregidor-Castro et al., 2023; Corregidor-Castro & Jones, 2021). Offspring are often less mobile than adults and in many taxa are constrained to their natal environment during development. This is particularly true for offspring of altricial bird species that, until fledging, are largely confined to their nest site (Nuhlickova et al., 2021). For example, the capability of nestlings to seek thermal refugia depends on nest structure and location. In species that breed in relatively large cavities nestlings may differentially use nest space at an early age, for example, for food acquisition, resting or defecating (Nuhlickova et al., 2021), but also for thermoregulation, as they can huddle within a nest cavity in response to low ambient temperatures to reduce hypothermia (Dreiss et al., 2016). Yet, very little is known about nestling behaviour in response to high nest temperatures. For example, frequent reports of premature fledging events in nestlings from cavity-nesting species during heatwaves have been interpreted as an attempt to avoid lethal hyperthermia or dehydration by escaping extreme temperatures occurring within the nest (Brambilla et al., 2023; Catry et al., 2015), but direct evidence for such an extreme behavioural response to nest thermal conditions is lacking. Leaving the nest prematurely can be very costly, as it may cause injuries when falling from a nest located high above the ground, it may increase the risk of predation once out in the open, and it may increase the risk of starvation; for instance, if parents avoid feeding offspring when outside the nest (Catry et al., 2011, 2015). Hence, such a response is expected to occur only when the physiological costs of cooling within the nest become prohibitive.

We focused on a Mediterranean cavity-nesting bird species, the lesser kestrel, *Falco naumanni*. The Mediterranean region has experienced a pronounced increment in the frequency and intensity of heatwaves in recent decades (Díaz-Poso et al., 2023), with temperature extremes expected to increase well above predicted global averages (Seneviratne et al., 2016). Heatwaves may create unsuitable conditions for the persistence of this species, as those occurring during the breeding season can have dramatic effects on nestling growth and survival (Catry et al., 2015; Corregidor-Castro et al., 2023). In particular, both in this and in other cavity-nesting species, extensive mortality is often associated with premature fledging events (i.e. nestlings that leave the nest before they are able to fly), which more frequently occur during and after heatwaves (Bourne et al., 2020; Catry et al., 2015; Quintana et al., 2022). In the study system, nestboxes are placed on roofs of buildings, and starting from 10 days of age (i.e. well before fledging, which takes place at 35–40 days) nestlings are frequently observed to temporarily leave their nestbox, resting near its entrance and rapidly going back into the nest when an observer (or a potential predator) approaches. Parents regularly feed their offspring even when outside the nestbox, but once outside, nestlings may easily fall prey to avian scavenging species that regularly patrol the roofs (mostly Eurasian jackdaw, *Corvus monedula*, and kites, *Milvus* spp.; A. Corregidor-Castro & D. Rubolini, personal observations), whereas they are safe when inside the nestbox because the entrance hole size (see Methods) prevents scavengers from entering.

We hypothesized that temporarily leaving the nest, which is similar to premature fledging, is causally associated with exposure to elevated nest temperatures. To test this hypothesis, we experimentally reduced nest temperature in some nestboxes from hatching to fledging by means of a shading protocol (shaded nestboxes), while other nestboxes, matched with shaded ones for hatching date and orientation, were exposed to natural temperature conditions (control nestboxes). If persistently high average temperature within the nest cavity is causally associated with nestlings leaving their nest prematurely, we predicted that nestlings from shaded nestboxes should be less likely to be detected outside them. This could be the case for two main reasons.

First, nestlings may leave the nest as an emergency response when the temperature within the nestbox becomes too high to sustain (e.g. when surpassing the upper limit of their thermoneutral zone; Mitchel et al., 2018). Under such circumstances, leaving the nest may provide immediate physiological relief, reducing dehydration and the energetic costs of active thermoregulation, thus avoiding death by overheating (Mitchell et al., 2018). If this is the case, we expected a higher likelihood of detecting nestlings outside nestboxes when the temperature inside the nestbox is highest, for instance during the hottest hours of the day (i.e. at midday), or when the internal temperature is considerably higher than the external one, irrespective of whether being outside the nestbox affects the likelihood of obtaining food from parents.

Second, control nestlings are in poorer health and needier, as they show reduced growth and ca. 20% lower body mass compared to shaded ones (Corregidor-Castro et al., 2023) and may be more prone to leave the nest to gain privileged access to the food provided by the parents. Resting just outside the nest entrance should indeed increase the chances of being fed by attending parents, in line with previous studies demonstrating that lesser kestrel nestlings monopolizing the nest entrance are more likely to obtain parentally delivered food (Soravia et al., 2021). Hence, we tested whether resting outside the nest increased the chances of a nestling being fed compared to nestmates remaining inside. Further, parents may be expected to respond to increasing signalling of need

by their offspring by increasing their foraging effort and provisioning rate (Kilner & Johnstone, 1997; Royle et al., 2012; Wright & Leonard, 2007). We thus compared parental provisioning rates of nestlings from control and shaded nestboxes.

METHODS

Study Species, Study Area and General Field Procedures

The lesser kestrel is a small (ca. 140 g), long-distance, Afro-Palearctic migratory raptor. Populations breeding in Europe reach their breeding grounds between February and April (Sarà et al., 2019) and lay eggs during late April or early May. This species is a secondary cavity-nester, that is it does not build its own nest, but breeds in holes and cavities such as rocks, ruins or roof tiles in buildings (Negro & Hiraldo, 1993), and readily uses nestboxes (Catry et al., 2011). Females lay three to five eggs in a single clutch. Incubation is performed by both parents (Ramellini et al., 2022) and lasts approximately 30 days from laying of the last egg (Corregidor-Castro et al., 2023). Lesser kestrel nestlings hatch asynchronously (Podofillini et al., 2018; Soravia et al., 2021), leading to a strong size hierarchy among siblings, where last-hatched often die when food is scarce (Aparicio, 1997). Nestlings are fed at the nest by both parents until they fledge when ca. 40 days old. Lesser kestrels mainly feed on invertebrates, lizards and small mammals (Rodríguez et al., 2010) captured in farmland areas surrounding the colony (Morganti et al., 2021; Morinay et al., 2023).

The study was conducted during the breeding season of 2021 (end of April to mid-July) in the city of Matera, southern Italy (40°66′N, 16°61′E). This city hosts one of the largest colonies of lesser kestrel in Europe, with around 1000 breeding pairs (La Gioia et al., 2017), some of which breed in nestboxes (Morinay et al., 2021). Nestboxes consisted of a hollow refractory brick (30 × 30 cm and 37 cm high) sealed with a frontal and a rear wooden panel (30 × 30 cm and 2 cm high). The frontal panel had a 6.5 cm diameter entrance hole (see Podofillini et al., 2018 for more details), which effectively prevented any other bird species in the study area (including feral pigeons, *Columba livia* var. *domestica,* and scavengers or predators, such as the Eurasian jackdaw) from entering the nestbox. Nestboxes were placed at a minimum distance of 2 m from each other along the perimeter of the roof terrace and were monitored twice a week from the beginning of the breeding season until the fledging of most nestlings. At each monitoring visit to nestboxes, we determined clutch size, hatching date of the first egg (hereafter hatching date and brood size and recorded nestling body mass (to the nearest 0.1 g using an electronic scale). Shortly after the eggs hatched, we collected a small blood sample (ca. 50 µl) from each nestling by brachial venipuncture using sterile needles, to be used for molecular sex determination. Sex was assigned by polymerase chain reaction amplification of the sex-specific *CHD-1* gene, following established protocols (Griffiths et al., 1998; Podofillini et al., 2018).

During 21–24 June 2021, the study area was exposed to a strong heatwave, with maximum air temperatures reaching values >37 °C (mean daily maximum air temperature during the heatwave = 38.3 °C; estimate based on hourly maximum air temperature obtained from a nearby weather station, http://www.centrofunzionalebasilicata.it/, Matera weather station). Besides this extreme event, which occurred before our behavioural observations (see Nestling Behaviour and Parental Food Provisioning Rate), June and July 2021 were very hot months, with a temperature anomaly exceeding 2.5 °C above the long-term (1991–2020) average maximum temperatures for both months (ISAC, 2023).

Experimental Cooling of Nestboxes

Dyads of synchronous nests (i.e. with the same hatching date, similar orientation and roof sector) were randomly assigned to each of the two experimental groups: one nestbox was shaded with a specially designed plywood cover (shaded nestbox) to reduce its internal temperature, whereas the other nestbox remained unshaded (control nestbox). The shading cover comprised thin (5 mm) plywood panels that completely covered the roof and the right and left sides of the nestbox (while allowing airflow between the panels and nestbox), thereby preventing direct exposure of these parts of the nestbox to sunlight. The frontal panel of nestboxes was similarly exposed to direct sunlight in both shaded and control nestboxes. No other shading structures were placed on the roof of the nestboxes. Shading covers were placed at hatching and removed after fledging (see Corregidor-Castro et al., 2023 for more details about experimental nest cooling). Internal nest temperature during the observation period (days when nestboxes were monitored by cameras) was measured using temperature loggers (Elitech RC-5+, Elitech, U.K.; accuracy 0.5 °C) attached to the inner side of the rear panel of each nestbox near the nestbox roof (to avoid nestlings being in contact with the loggers). In both the control and shaded nestboxes, this rear panel's outer side was protected from direct sunlight by a vertically bent quarry tile that leaned on it (40 × 40 cm; sloping by ca. 45° to allow air circulation; Corregidor-Castro et al., 2023). Data loggers were set to record temperature every 15 min (Corregidor-Castro et al., 2023).

Nestling Behaviour and Parental Food Provisioning Rate

The occurrence of nestlings outside the nestbox was assessed by camera traps (Boly Scout Guard BG310-M, Shenzhen, China) equipped with a motion detector 18 MP camera powered by two lithium batteries and solar panels. Cameras were placed approximately 1.5 m away from the entrance of the nestbox, at a height of around 10 cm from the ground, and set to record 30 s videos, with the trigger set as 'High' to detect and record as many events as possible. We placed the camera traps in front of nestboxes when the oldest nestling was ca. 10 days old, the age at which nestlings begin to temporarily leave the nest (Podofillini et al., 2019). Camera traps were deployed synchronously at dyads of control and shaded nestboxes. Nestboxes were continuously monitored by camera traps between one or two subsequent nest monitoring visits. Data from days when the camera trap was deployed (i.e. monitoring visit days) were excluded from the analyses to avoid any effect of observer presence on the roofs. In total, the observation period lasted 5.0 ± 0.8 days (mean ± SE) per nestbox (minimum age of nestlings at camera trap deployment 13.1 ± 1.2 days) from seven synchronous dyads (seven control and seven shaded nestboxes). We recorded nestlings out of the nestbox only between 0500 and 2000 h (approximately from dawn to dusk). Hence, for each hour during the recording period (a total of 16 h per day), we assessed whether at least one nestling was detected outside the nestbox in any given video. At the same time, for each hour, we recorded all food provisioning visits by parents (i.e. the number of food items brought to the nestlings), and whether parents fed nestlings that were outside or inside the nestbox for every food provisioning event. In the sample of broods included in the analyses, brood sex ratio (proportion of males) was not significantly different between control and shaded nestboxes (control broods: 0.54, $N = 13$ nestlings; shaded broods: 0.44, $N = 23$; binomial generalized linear mixed model (GLMM) with sex (0 = female, 1 = male) as the dependent variable, shading as predictor and brood identity as a random intercept effect: $Z = 0.60$, $P = 0.55$).

Recordings were performed between 24 June and 7 July, after the heatwave event (see Study Species, Study Area and General Field Procedures). During these days, the mean daily maximum air temperature was nevertheless relatively hot (34.3 ± 0.7 °C), and the temperature inside the nestboxes reached up to 45 °C (see Results).

Statistical Analyses

To assess the extent of nest temperature reduction induced by shading, and the differences in the daily thermal profile of the two nestbox types, we fitted a linear mixed model (LMM) including hourly maximum temperature within the nestbox (T_{max}) during the observation period as a response variable, shading (0 = control, 1 = shaded), time of day and their interaction as predictors. Time of day was included as a three-level factor (morning [0500–0900 h], midday [1000–1500 h], afternoon [1600–2000 h]; see also below for justification for selection of these timeframes). Nest identity and synchronous dyad were included as random intercept effects (the former to account for repeated measures of the same nest and the latter to reflect the pairwise nature of the experimental design; see Corregidor-Castro et al., 2023).

To test whether the likelihood of detecting a nestling outside the nestbox varied according to shading, we relied on a binomial GLMM with the hourly probability of detecting a nestling out of the nest (0 = no nestling detected outside the nestbox in a given hour; 1 = at least one nestling detected outside the nestbox) as the binomial dependent variable and shading as a fixed effect predictor. As additional predictors, we included time of day, brood size and the age of the oldest nestling (both recorded at the monitoring visits before and after the recording). Time of day (three-level factor) was included in the models instead of hour of the day because in exploratory analyses we detected a nonlinear variation in the probability of detecting a nestling outside the nest with the hour of the day (higher values being observed in the early hours of the day, lowest values at midday and in the evening). The other two covariates, brood size and nestling age, were included to take into account that in larger broods the likelihood of detecting at least one nestling outside the nestbox may be higher, and because nestlings are expected to increase their mobility (and hence the likelihood of temporarily leaving the nestbox) when growing older. To investigate whether shading differentially affected the likelihood of detecting a nestling outside the nestbox in relation to time of day, we included in the model the interaction between shading and time of day. Nest identity and synchronous dyad were included as random intercept effects. The response variable was expressed on an hourly scale (rather than at more frequent time intervals) to limit the number of occasions with no nestlings outside the nestbox and hence an excess of zeros in the models. Individual nestlings could not be identified and could be recorded on more than one video recording in each hour. This is because it was not possible to determine whether, for example, a nestling left its nest on several (short) occasions, or the camera was triggered several times during the same (prolonged) event of a nestling being outside. We relied on a binomial variable (rather than using the maximum number of nestlings detected outside the nestbox per hour) because there were few hourly intervals when more than a single nestling was outside the nestbox (only 53 out of 1120 hourly intervals, i.e. 4.7%; see also Results).

To test whether the likelihood of detecting a nestling outside the nestbox reflected an emergency response to potentially dangerous perceived nest temperatures, we fitted a second GLMM with the same fixed and random effect structure as the above models (with time of day as a three-level factor) but including hourly T_{max} as a predictor instead of shading, and including the interaction between time of day and T_{max}. We did not include shading as a factor in this model because it was collinear (by design) with T_{max} (because shading was applied to reduce T_{max}).

Because the probability of leaving the nest may be affected by the difference in temperature between T_{max} and external ambient temperature, with nestlings expected to leave the nest more frequently when outside temperatures were cooler than internal ones, we fitted an additional GLMM with the same fixed and random effect structure as the previous one but including temperature difference (T_{diff}; difference between T_{max} and external maximum hourly air temperature) instead of T_{max}. The effect of shading on nestling body mass (the last available measurement during the observation period) was tested in an LMM with shading, brood size, nestling sex (0 = female; 1 = male) and age (days from hatching) as predictors and nest (= brood) identity and dyad as random intercept effects. We investigated whether resting outside the nestbox increased the chance of a nestling obtaining food brought by parents compared to nestmates remaining inside. To this end, we tested whether the probability that a nestling resting outside obtained food was higher than expected by chance (i.e. 0.5), considering only those food provisioning events when at least one nestling was resting outside and there was at least one nestmate inside the nestbox. This was achieved by fitting an intercept-only binomial GLMM (with nest identity as a random effect) and testing whether the intercept was larger than 0.5 (or 0 on the logit scale).

Finally, differences in parental food provisioning rate (parental visits/h) between shaded and control nestboxes were tested by fitting a Poisson GLMM with shading, time of day, brood size and age as predictors. Time of day was included as a three-level fixed factor as in previous GLMMs because the food provisioning rate was highest at midday compared to morning and afternoon (Cecere et al., 2020). In addition, we tested the interaction between shading and time of day. Nest identity and dyad were included as random intercept effects.

All LMMs/GLMMs were fitted using the R 'glmmTMB' library (Brooks et al., 2017). No models showed evidence for collinearity (variance inflation factor always <2.9; check_collinearity function of the R 'performance' package; Lüdecke et al., 2021) and residual diagnostics were largely acceptable. All predictors were mean-centred, and interactions were removed when nonsignificant. The 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. Probabilities were reported with their associated 95% confidence intervals (CI) or standard errors, either model-based or computed according to the method recommended by Newcombe (1998) for proportion data.

Ethical Note

We did not detect any obvious disturbance to nestlings or to adults originating from deploying shading covers at hatching (Corregidor-Castro et al., 2023) or positioning camera traps in front of the nests. In fact, during previous field and video observations, adults were often seen using camera traps as perching spots, suggesting that these were not perceived as a threat. Capture, blood sampling and handling of the nestlings were performed by Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA) staff under the authorization of Law 157/1992 [Art. 4 (1) and Art. 7 (5)].

RESULTS

Hourly T_{max} was significantly higher during midday than during the morning and afternoon (ca. 4 °C; Fig. 1), and was markedly higher in control than in shaded nestboxes during midday, whereas

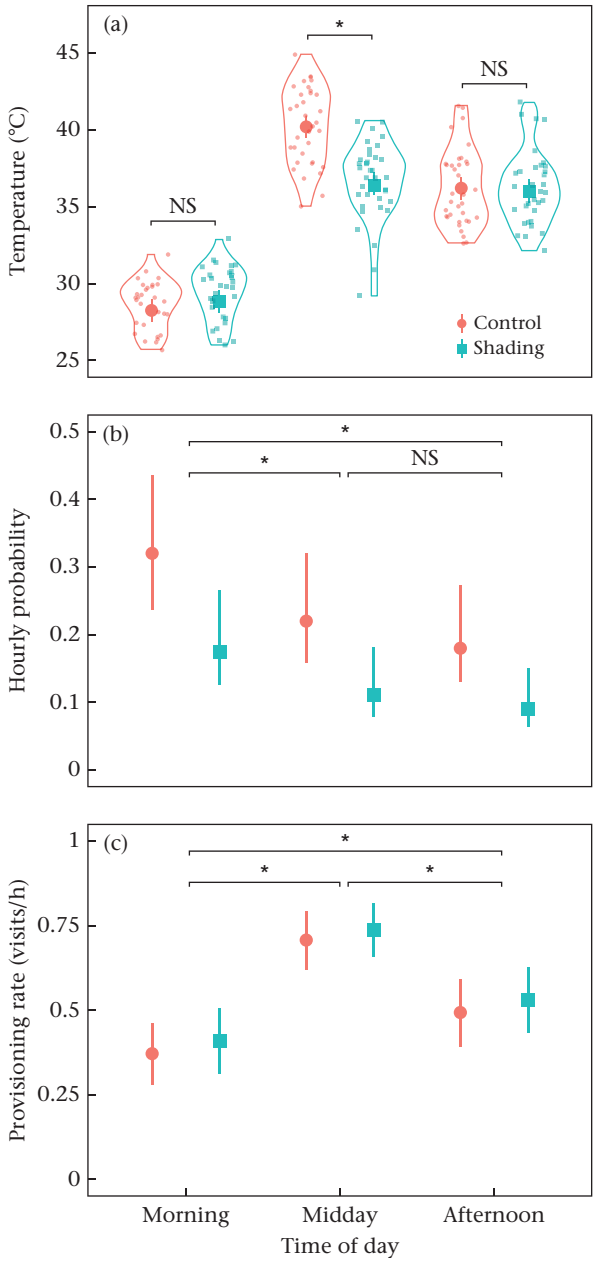

Figure 1. (a) Variation in maximum hourly nest temperature (T_{max}) during the observation period (see 'Methods'), with variation represented using violin plots (Hintze & Nelson, 1998), (b) hourly probability of detecting a nestling out of the nestbox and (c) parental food provisioning rate according to time of day (morning, midday, afternoon) and shading of the nestbox. Error bars represent standard errors; in (b) these were computed according to Newcombe (1998). *$P < 0.05$; post hoc tests between nestbox types within time of day groups (in (a) from a statistically significant shading * time of day interaction) and between the three time of day groups, irrespective of shading (in (b) and (c) post hoc tests from the fixed effect of time of day; see footnotes to models reported in Tables 1 and 2, respectively).

it did not vary significantly according to shading during the morning and afternoon (Fig. 1; LMM: shading * time of day interaction: $\chi^2_2 = 19.58$, $P < 0.001$; other model details not shown for brevity).

During 1120 observation hours, we detected 205 hourly intervals during which nestlings were outside the nestbox, corresponding to an hourly probability of being outside the nest equal to 0.18 (95% CI: 0.16–0.21). In most cases, a single nestling was observed resting outside the nestbox (152 of 205 hourly intervals; 74.1%); two nestlings were simultaneously outside the nest in 45 hourly intervals (22.0%), and three nestlings in eight hourly intervals (3.9%). We documented one predation event during our observations, when a Eurasian jackdaw killed and consumed one 11-day-old nestling detected outside the nestbox (Fig. 2a).

Nestlings from control nestboxes were twice as likely to be observed outside the nest (model-based probability estimates, 0.24 [95% CI: 0.20–0.27]) compared with those from shaded ones (0.13 [95% CI: 0.10–0.16]) (Table 1, Fig. 1). In particular, the probability of detecting a nestling outside a control nestbox was highest in the morning (0.30 [95% CI: 0.23–0.37]) than during midday and afternoon (Table 1, Fig. 1). The probability of detecting a nestling outside the nestbox was not significantly predicted by T_{max} or T_{diff} (Table 1).

The mean body mass of nestlings in the control nestboxes (65.7 ± 6.2 g) was significantly lower than that of nestlings in the shaded ones (77.3 ± 5.7 g; Table 2; Corregidor-Castro et al., 2023). Parents commonly fed nestlings when they were outside the nestbox (Fig. 2b). In the 106 feeding events that occurred when nestlings were both inside and outside the nestbox, nestlings outside the nest were significantly more likely to receive food from their parents than their nestmates inside the nestbox (87% of cases, 92 of 106 food provisioning events; intercept-only binomial GLMM: estimated probability 0.91 [95% CI: 0.65–0.98], $Z = 2.70$, $P = 0.007$; $N = 7$ nestboxes).

Parental food provisioning rate peaked at midday (0.67 ± 0.09 visits/h), was lowest in the morning and afternoon (Fig. 1) and did not differ significantly between control and shaded broods (Table 2). The food provisioning rate declined significantly with increasing nestling age (Table 2).

DISCUSSION

Our experiment provided evidence that control nestlings, which were exposed to higher average temperatures during their early posthatching development than their shaded counterparts, were more likely to temporarily leave their nest cavity. This behaviour occurred mainly in the early morning, when the temperature inside the nestbox was relatively low compared to the temperature recorded in the nest during midday and afternoon, and did not differ between control and shaded nestboxes. Accordingly, the probability of detecting a nestling outside the nestbox during each hour of observation was not associated with the corresponding temperature in the nestbox nor with the difference between internal and external temperature. Confirming the results from a previous study (Corregidor-Castro et al., 2023), nestlings growing in control nestboxes had a lower body mass and were thus in a poorer nutritional state. Although parents did not increase the foraging rate for needier control nestlings, resting outside the nestbox greatly improved their chances of obtaining parentally delivered food.

The observation that nestlings from control nestboxes were almost twice as likely to be detected outside the nestbox than those from shaded ones is in line with the hypothesis that resting outside the nestbox reflects carry-over effects of persistent exposure to relatively hotter temperatures during early posthatching development. Under prolonged thermal stress, nestlings' growth rate probably decreased because of different combined mechanisms, including water loss and an increase in metabolic rates to actively dissipate heat. Indeed, when temperature surpasses the critical value above which passive heat dissipation is sufficient to thermoregulate, nestlings of many bird species (including raptors; Mosher, 1976) increase their evaporative heat loss by panting or gular fluttering, which may lead to severe dehydration, starvation,

Figure 2. Illustrative frames obtained from 30 s videos recorded with camera traps; (a) a Eurasian jackdaw, *Corvus monedula*, kills and consumes an 11-day-old nestling outside the nestbox (red circle), while its nestmates remain within the nestbox; (b) the nestling on the left is consuming a prey provided by the female parent while resting outside the nestbox.

Table 1
Binomial GLMMs of the effect of shading, T_{max} and T_{diff} on the hourly probability of detecting a nestling resting outside the nestbox

Predictors	Estimate ± SE	*df*	χ^2	*P*
Effect of shading ($N = 1120$ observation hours, $N = 14$ nests; $R^2 = 0.49$)				
Shading	−2.94 ± 1.06	1	5.96	0.015
Time of day[a]	–	2	18.28	<0.001
Brood size	1.62 ± 0.35	1	30.10	<0.001
Age of the oldest nestling	0.26 ± 0.11	1	5.33	0.02
Shading * time of day[b]	–	2	1.98	0.37
Effect of T_{MAX} ($N = 1120$ observation hours, $N = 14$ nests; $R^2 = 0.37$)				
T_{MAX}	−0.11 ± 0.15	1	0.53	0.47
Time of day[c]	–	2	8.22	0.016
Brood size	1.64 ± 0.40	1	26.90	<0.001
Age of the oldest nestling	0.24 ± 0.11	1	4.57	0.03
T_{MAX} * time of day[b]	–	2	2.63	0.27
Effect of T_{DIFF} ($N = 1120$ observation hours, $N = 14$ nests; $R^2 = 0.46$)				
T_{DIFF}	−0.03 ± 0.11	1	0.01	0.97
Time of day[d]	–	2	13.90	<0.001
Brood size	1.63 ± 0.39	1	26.72	<0.001
Age of the oldest nestling	0.25 ± 0.11	1	4.98	0.03
T_{diff} * time of day[b]	–	2	0.44	0.80

T_{max} : hourly maximum temperature within the nestbox during the observation period (0500–2000 hours); T_{diff} : difference between T_{max} and external maximum hourly air temperature. Nest and synchronous dyad identity were included in all models as random intercept effects. Marginal R^2 was computed according to Nakagawa et al. (2017). Different superscript letters (e, f) for estimated mean values below indicate statistically significant difference ($P < 0.05$) in the probability of detecting a nestling outside the nestbox (post hoc tests).

[a] Estimated mean probabilities (± SE), morning = 0.24 ± 0.09[e], midday = 0.16 ± 0.06[f], afternoon = 0.13 ± 0.05[f].

[b] Term removed from the model.

[c] Estimated mean probabilities (± SE), morning = 0.27 ± 0.10[e], midday = 0.15 ± 0.06[f], afternoon = 0.13 ± 0.05[f].

[d] Estimated mean probabilities (± SE), morning = 0.28 ± 0.10[e], midday = 0.14 ± 0.05[f], afternoon = 0.12 ± 0.05[f].

Table 2
Mixed models testing the effect of shading on nestling body mass (LMM) and parental food provisioning rate (visits/h; Poisson GLMM)

Predictors	Estimate ± SE	*df*	χ^2	*P*
Nestling body mass ($N = 36$ nestlings, $N = 13$ broods; $R^2 = 0.48$)				
Shading	10.88 ± 3.97	1	6.86	0.009
Brood size	−0.81 ± 2.73	1	0.09	0.77
Sex	−1.91 ± 3.88	1	0.24	0.62
Age	5.24 ± 1.09	1	17.4	<0.001
Shading * sex[a]	−2.36 ± 8.04	1	0.09	0.77
Food provisioning rate ($N = 1120$ observation hours, $N = 14$ nests; $R^2 = 0.54$)				
Shading	0.15 ± 0.36	1	0.17	0.68
Time of day[b]	–	2	41.68	<0.001
Brood size	−0.15 ± 0.16	1	0.21	0.65
Age of the oldest nestling	−0.66 ± 0.13	1	26.2	<0.001

Nest (= brood) and synchronous dyad identity were included in all models as random intercept effects. Marginal R^2 was computed according to Nakagawa et al. (2017). Different superscript letters (c, d, e) for estimated mean values indicate statistically significant differences ($P < 0.05$) (post hoc tests).

[a] Term removed from the model.

[b] Estimated mean values, morning = 0.36 ± 0.05[c], midday = 0.67 ± 0.09[d], afternoon = 0.45 ± 0.07[e].

and ultimately death if exposure to very high temperatures persists (Albright et al., 2017; Diehl et al., 2023).

The higher chances of obtaining food brought by parents for nestlings resting outside nestboxes suggests that leaving the nest cavity constitutes an extreme (although risky) attempt to monopolize food items brought by parents under severe need. In the first days after hatching, adults feed the nestlings by directly transferring small prey items into the nestlings' gape (Romano et al., 2022). As nestlings grow, they become able to consume the prey autonomously and parents leave the prey items at the nest entrance, letting nestlings feed on their own (Soravia et al., 2021). Although this feeding strategy minimizes the time parents spend at the nest, increasing the time available for foraging in a period when food demand by the brood is highest, it also allows larger or more aggressive or needier nestlings to get priority access to food (Epting & Delotelle, 2009; Soravia et al., 2021). Waiting for the parents outside the nest may therefore provide an advantage in competition for food over siblings. Yet, parents from control nestboxes did not provide more food to their nestlings than their shaded counterparts, indirectly suggesting that increasing levels of nestling need, possibly signalled by the presence of nestlings outside the nest, did not elicit a stronger investment by parents, as could be predicted based on theoretical models of parent - offspring communication (Kilner & Johnstone, 1997; Wright & Leonard, 2007). Such a lack of response by control parents to the poorer nutritional status of their offspring suggests that parents in the study population may be constrained in their foraging effort. The study colony consists of nearly a thousand breeding pairs, whose foraging home ranges are considerably larger than those of pairs settled in smaller colonies, likely due to prey depletion in the areas

immediately surrounding the colony (Cecere et al., 2018). Indeed, during nestling rearing, birds from the study colony fly on average 15 km to bring a single food item to the nest, in most cases a large cricket (Ramellini et al., 2022). In contrast, in smaller colonies birds generally forage in the immediate surroundings of the colony, up to a maximum of 3 km (Assandri et al., 2022; Cioccarelli et al., 2022). Unsurprisingly, the parental food provisioning rate reported in this study colony is considerably lower than in other much smaller colonies consisting of a few breeding pairs only (on average about 3.00 visits/h versus 0.53 in the present study; Morganti et al., n.d.).

Parental food provisioning rate peaked at midday. Lesser kestrels mainly prey on small insects (Christakis & Sfougaris, 2021; Di Maggio et al., 2018; Franco & Andrada, 1977), which are consumed by nestlings immediately upon delivery. During the night, nestlings fast and do not have access to food or water. Prolonged night-time fasting may thus exacerbate their hunger the next morning to a point that it may force them to exit the nest cavity to beg for food; this would explain the higher frequency of nestlings observed outside the nestbox in the early morning. Alternatively, the lower probability of observing nestlings outside the nestbox during the hottest hours of the day (at midday and in the afternoon) may be related to avoidance of being directly exposed to sunlight and to the risk of overheating.

Further, the probability of observing a nestling outside the nestbox was not associated with the nest temperature or with the difference between internal and external temperature, indicating that nestlings do not leave the nest to access a more favourable thermal environment. Thus, although we cannot exclude the possibility that nestlings avoid leaving the nest at midday to prevent direct exposure to sunlight, it is highly likely that the reason why control nestlings were more likely to temporarily leave their nest than their shaded counterparts was their poorer nutritional state due to prolonged exposure to relatively higher internal nest temperatures. However, it should be mentioned that maximum air temperatures recorded during this study were mostly at a sublethal level, that is, 4 °C lower than those recorded during the heatwave period occurring shortly before our observations, which led to widespread nestling mortality (Corregidor-Castro et al., 2023). However, most of these mortality events were recorded inside (rather than outside) nestboxes, possibly because of lethal hyperthermia and/or excessive dehydration occurring upon exposure to unbearable nest temperatures (Corregidor-Castro et al., 2023).

Our findings thus indicate that nestlings facing relatively higher nest temperatures during early development are in poorer nutritional state, and are likely to be experiencing prolonged water loss and higher energetic demands due to the increased physiological costs associated with thermoregulation. We suggest that these conditions make nestlings more likely to trade their safety for higher chances of acquiring food, as leaving the nest undoubtedly increases exposure to predators. In our study system, additional costs associated with the risk of being unable to re-enter the nest cavity are very low, as nestboxes are placed on the floor of a plain roof and nestlings can easily re-enter their nest if needed. However, in other study systems, such as when nests are located in holes in walls or when nestboxes are attached to building walls (which is often the case for the lesser kestrel and other bird species), temporarily leaving the nest is not possible and nestlings cannot re-enter their nest site once they leave it (Catry et al., 2015). This may be fatal, because predation risk, including by mammalian scavengers, increases exponentially in those conditions and parents often avoid feeding nestlings that fall on the ground (Catry et al., 2009).

We conclude that temporarily leaving the nest cavity is a consequence of prolonged exposure to relatively high nest temperatures and associated poor nutritional state during early growth rather than being an emergency response to escape unbearable temperatures within the nest. Whether premature fledging events are generally driven by poor nutritional condition associated with prolonged heat exposure within the nest, or by an attempt to escape unbearable peak nest temperatures, will require more extensive investigation in a range of temperature conditions and species in which such events have been reported to occur. Yet, our findings highlight that globally warming temperatures may induce sublethal effects, including behavioural responses, that increase predation risk and add to the negative effects directly deriving from dehydration, increased energy expenditure associated with active thermoregulation and overall poorer nutritional state.

Author Contributions

Alejandro Corregidor-Castro: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Andrea Romano:** Writing – review & editing, Data curation. **Andrea Pilastro:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Conceptualization. **Diego Rubolini:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis, Conceptualization. **Jacopo G. Cecere:** Writing – review & editing, Conceptualization. **Jennifer Morinay:** Writing – review & editing, Data curation. **Michelangelo Morganti:** Writing – review & editing, Funding acquisition, Conceptualization. **Simone Militti:** Writing – review & editing, Formal analysis, Data curation.

Data Availability

The data that support the findings of this study are openly available in Research Data Unipd at https://doi.org/10.25430/researchdata.cab.unipd.it.00001261.

Declaration of Interest

The authors declare no conflicts of interest.

Acknowledgments

We thank Ç. Akçay, J. Martínez-Padilla and two anonymous referees for constructive criticism that helped improve the manuscript. We are grateful to E. De Capua and E. Eletti for supporting fieldwork in Matera. Nestboxes were built and purchased under the framework of the LIFE Project 'Rapaci Lucani' (LIFE05NAT/IT/00009) and were designed by G. Ceccolini. The study received partial financial support from the European Union LIFE Program (project LIFE FALKON, LIFE17 NAT/IT/000586), the PRIN 2017 funding scheme (grant number 20178T2PSW to D.R. and A.P.) and 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 National Biodiversity Future Centre-NBFC [funded by the European Union, NextGenerationEU under the National Recovery and Resilience Plan (NRRP) M4C2 Investment Line 1.4: 'Strengthening of research facilities and creation of 'national R&D champions' on some Key Enabling Technologies', project CN_00000033]. D.R. was also partly supported by Ecosistema MUSA – Multilayered Urban Sustainability Action (funded by the European Union – 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).

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