Adapting conservation efforts to face climate change: Modifying nest-site provisioning for lesser kestrels

Inês Catry, Aldina M.A. Franco, William J. Sutherland

1. Introduction

The two main policy responses to global warming are mitigation and adaptation (IPCC, 2007). While most of the debate has been about mitigation to reduce the rate of climate change, there is growing evidence that adaptation – “adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects” (IPCC, 2007) – will be essential to address its impacts. The ecological impacts and costs of predicted weather-related extreme events, such as extreme temperatures, are not fully understood and may present unexpected challenges to conservationists that require solutions. In Portugal, provisioning of artificial nests has been the main driver of the spectacular increase in the endangered lesser kestrel population. Nevertheless, atypically high temperatures recorded during the 2009 breeding season coincided with a mortality of 22% of surveyed chicks in provided nests. Hot days did not affect prey delivery rates to the nestlings, suggesting that the die-off was due to chicks’ acute dehydration. Chick mortality was significantly higher amongst younger individuals. Within survivors, physiological costs of high temperatures significantly affected chick growth and body condition at fledging. Nest-site microclimate was influenced by nest-type and compass orientation: wooden nest-boxes attained the highest temperatures, exceeding 55 °C when facing south, so explaining the recorded higher mortality, lower growth rates and lower fledging body condition among broods in these nests. Simulated scenarios of global warming with increasing occupation rate of artificial nests due to reductions in alternatives predicted a reduction in population growth rate. In the worst scenario, with a 100% occupancy of nest-boxes, the population growth would decline on average 7% per year. The impact of high temperatures on lesser kestrel breeding success highlights a need for actions to modify and research to adapt conservation efforts and future planning to account for climate change.

Adaptation to climate change has recently become a crucial element on the climate change policy agenda as it is now recognized that even the most stringent mitigation efforts may not arrest the effects of climate warming. The ecological impacts and costs of predicted weather-related extreme events, such as extreme temperatures, are not fully understood and may present unexpected challenges to conservationists that require solutions. In Portugal, provisioning of artificial nests has been the main driver of the spectacular increase in the endangered lesser kestrel population. Nevertheless, atypically high temperatures recorded during the 2009 breeding season coincided with a mortality of 22% of surveyed chicks in provided nests. Hot days did not affect prey delivery rates to the nestlings, suggesting that the die-off was due to chicks’ acute dehydration. Chick mortality was significantly higher amongst younger individuals. Within survivors, physiological costs of high temperatures significantly affected chick growth and body condition at fledging. Nest-site microclimate was influenced by nest-type and compass orientation: wooden nest-boxes attained the highest temperatures, exceeding 55 °C when facing south, so explaining the recorded higher mortality, lower growth rates and lower fledging body condition among broods in these nests. Simulated scenarios of global warming with increasing occupation rate of artificial nests due to reductions in alternatives predicted a reduction in population growth rate. In the worst scenario, with a 100% occupancy of nest-boxes, the population growth would decline on average 7% per year. The impact of high temperatures on lesser kestrel breeding success highlights a need for actions to modify and research to adapt conservation efforts and future planning to account for climate change.

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Among birds, extreme air temperatures that exceed species' physiological limits can lead to direct mortality due to dehydration (McKechnie and Wolf, 2010), especially among embryos and nestlings, which are more sensitive to thermal and hydric conditions at the nest (Lloyd and Martin, 2004).

The lesser kestrel is a small colonial falcon classified as globally threatened due to the recent sharp declines in its Western European populations (BirdLife International, 2004). It is closely associated with open agricultural habitat with nesting colonies usually either in isolated abandoned farmhouses or in buildings such as castles and churches, within villages or towns. Nests are usually located in cavities in the walls or under tiled roofs. In Portugal, the restoration of historic buildings and poaching within urban areas has led to the extinction of most known urban colonies (Araújo, 1990). As a consequence, most of the population is now in rural areas, but the disintegration and collapse of farm buildings has led to a shortage of nest-sites (Franco et al., 2005).

Conservation efforts, including a massive provisioning of artificial nest-sites, has been shown to be an effective measure by mitigating the lack of traditional breeding sites, allowing the establishment of new sites, by reducing predation rate and reducing interspecific competition; as a result both breeding success and establishment of new sites, by reducing predation rate and reducing mortality. Chicks were individually marked with cable ties at hatching (and ringed later); body mass was weighed to the nearest 0.1 g using a portable electronic balance. Monitored nests (all artificial) included six stone cavities, six adobe cavities and four wooden nest-boxes. Because, as described below, some chicks died on the 12th of June, we chose six more wooden nest-boxes and three concrete cavities (in a breeding wall) to increase the sample, these contained chicks aged between 5 and 15 days. Mean brood size was 3.72 ± 1.1 for a total of 25 nests and 93 chicks.

2. Methods

2.1. Study area

The study was conducted in the Castro Verde plains, Alentejo, Southern Portugal. This is the main area of cereal steppe in Portugal with a national and international importance regarding the conservation of many endangered bird steppe species (Costa et al., 2003). The area is classified as a meso-mediterranean bioclimatic stage (Rivas-Martínez, 1981), with hot dry summers (30–35 °C on average in July), fairly cold winters (averaging 5–8 °C in January) and over 75% of annual rainfall (500–600 mm) concentrated in October–March (Moreira et al., 2005). Presently, the Castro Verde Special Protection Area (SPA), comprising 85,000 ha, contains 430 pairs (around 40 colonies), almost 80% of the total Portuguese lesser kestrel population (Catry et al., 2009).

Most colonies are located either in old adobe-built abandoned farmhouses (nests are located in cavities in walls or in the roof, under the tiles) or artificial nesting structures. Since 1996, but mostly from 2003, about 800 artificial nest-sites were provided in the area including new cavities opened in abandoned existing buildings, wooden nest-boxes, clay pots and breeding walls and towers (adobe and concrete-built structures with many available cavities). In 2007, about 50% (n = 212 pairs) of the Portuguese population used artificial nests (Catry et al., 2009).

Lesser kestrels return to Castro Verde from their African wintering grounds mainly in early February (Catry et al., 2011) and lay typically 4–5 eggs in April and May (mean laying date = 28 April for 2003–2006, n = 1532; Henriques et al., 2006).

2.2. Data collection

Between 25 May and 5 July 2009, on a 2 day rotation, we visited four lesser kestrel colonies (range size: 19–66 pairs) to estimate nesting growth rates from hatching to fledging and assess chick mortality. Chicks were individually marked with cable ties at hatching (and ringed later); body mass was weighed to the nearest 0.1 g using a portable electronic balance. Monitored nests (all artificial) included six stone cavities, six adobe cavities and four wooden nest-boxes. Because, as described below, some chicks died on the 12th of June, we chose six more wooden nest-boxes and three concrete cavities (in a breeding wall) to increase the sample, these contained chicks aged between 5 and 15 days. Mean brood size was 3.72 ± 1.1 for a total of 25 nests and 93 chicks.

2.2.1. Estimation of direct and indirect mortality

Amongst our sampled nests, 15 chicks were found dead across the breeding period. Within a brood of six, two nestlings died from starvation and in other three broods, three chicks died from fatal injuries. Amongst these five chicks, dead was preceded by a clear pattern of decrease in body weight. The remaining 10 chicks were found dead inside the nests, with no sign of injuries, parasite infection or predation. Nine died in the 12 of June (the first very hot day) and one in the hottest day. None of the deaths were preceded by lost of weight in previous days being therefore attributed to the high temperatures (direct mortality).

Within wooden nest-boxes, only four chicks disappeared during the entire chick rearing period, all coincident with the two hottest days. Three chicks were found alive outside the nests, in a poor condition (having lost 11, 20 and 26 g in 2 days); 2 days after being returned to their nests, chicks’ body condition improved 18, 27 and 34 g, respectively. All missing chicks disappeared from wooden nest-boxes with brood size lower than three (making less likely competition among siblings) and three of them belonged to nest-boxes where direct mortality occurred. Amongst adobe cavities, eight chicks disappeared during the study period, all in 2 days, after the first very hot day and during the hottest day. Missing chicks belonged to broods where all chicks lost significant weight during the hottest days (see Section 3). Although some missing nestlings were slightly below the average brood weight, two of them had the best condition within their broods. Two missing chicks, older than 25 days, were excluded from mortality calculations to preclude misclassifying early fledging as mortality. Within all monitored nests, we found no evidence of predation (predation among monitored wooden nest-boxes was never detected in 6 years) or ectoparasites. Thus, indirect mortality associated with nesting mortality.
high temperatures was attributed to four and six missing chicks in wooden nest-boxes and adobe cavities, respectively.

2.2.2. Effect of temperature on feeding rates
To evaluate the effect of hot days on parental behaviour, which could indirectly affect nestling growth (by reducing foraging capacity and prey availability; Siikamäki, 1996), we recorded prey delivery rates (number of food items brought to the nest per hour and per chick) in twelve nests from 5 to 28 June 2009, with a total of 24 h of observation per nest. Four observation periods were spread through the day (8:00–10:00, 10:00–12:00, 16:00–18:00 and 18:00–20:00) avoiding the period of lower activity (delivery rates within these periods were not significantly different, Kruskal–Wallis \( \chi^2 = 5.9, p = 0.11 \)). We then compared delivery rates in days with maximum temperatures above and below 37 °C. Data on daily maximum temperatures were obtained from the closest (about 40 km) meteorological station, in Beja.

2.2.3. Nest-site microclimate
To assess nest-site microclimate, forty-six micro-T DS1922L temperature loggers (NexSens Technology, Fondriest Environment, USA) were deployed in five different artificial nest-types facing the north (cavities in adobe, concrete and stone walls, clay pots and wooden nest-boxes), recording daily temperatures at 60 min intervals between 5 June and 9 July 2010. Four devices were kept outside (in shadow) to determine external air temperatures. The devices had an accuracy of ±0.5 °C, a resolution of 0.0625 °C and an operating range of −40 to 85 °C. From 12 to 24 of July, we tested the effect of orientation on 31 wooden nest-boxes facing north, east, south or west and the difference between six clay pots that were painted white from six that were unpainted.

2.3. Statistical analyses
We used a generalized additive mixed model (GAMM) to describe the relationship between chick growth and daily maximum temperatures. For this paper, chick growth refers to the modelled difference in chick mass between two consecutive visits (every 2 days, at the same hour); thus being positive for mass gain or negative for mass loss. Dead chicks were not weighed and were, therefore, attributed with a mass loss of 25 g (mean loss of weight among the lighter chicks during the hottest days). All chicks older than 25 days were excluded from the model, as slight variations in chicks’ weight close to fledgling date is often observed. The daily maximum temperature was taken as the maximum temperature registered within each 2 days interval. We assumed a Gaussian error distribution and an identity link function. The nesting age, brood size and nest-type were also included as predictors as they may influence chick body mass; brood size was removed from the final model given its non-significant effect. The model was fitted using the “mgcv” package in R (R Development Core Team, 2008) and the degree of smoothing for the non-linear terms (age and maximum temperature) was estimated using cross-validation (Zuur et al., 2009). The use of mixed-effects models allowed us to include both chick and nest identity as random factors. Model selection was based on identifying which explanatory variables had significant effects. We checked that there were no trends in residuals.

Nestling growth curves were estimated using a non-linear regression to fit a logistic growth curve for the entire data set of nestlings weighed \( n = 93 \). Three other growth curves were fitted, accounting for nestlings of each nest-type (nestlings from concrete cavities were not included due to the small sample size and lack of mass measurements in young chicks). Chick body condition at fledging was calculated using a body condition index \( BCI = 1 - \) (residual OM)/TM (Le Corre et al., 2003) where OM is the observed mass (g), TM is the theoretical mass (g) calculated with the non-linear regression between mass and age, and residual OM is the difference between TM and OM. With this equation, a BCI of 1 means that the individual has its normal mass for its age; BCI below 1 means that the bird is lighter than expected (low body condition) and a BCI exceeding 1 means that the bird is heavier than expected (high body condition). Comparisons of chick body condition among different nest-types were assessed using a one-way ANOVA followed by post hoc Tukey tests.

We used a linear regression analysis to assess the relationship between the amount of weight lost or gained in the first very hot day (12 June) and chick body condition at fledging. Differences between delivery rates in days with maximum temperatures above and below 37 °C were compared by Mann–Whitney U tests. Nest-site microclimate amongst nest-types was compared using one-way ANOVA and t-tests.

All analyses were performed with R (R Development Core Team, 2008).

2.4. Demographic model and population trends
We used matrix population models to investigate potential long-term impacts of extreme temperatures on lesser kestrel population dynamics through its effect on breeding success. Firstly, we developed a female-based model to estimate the growth rate of the Portuguese lesser kestrel breeding population and then use this model to predict future trends under different simulated scenarios of nest-site occupancy and related chick mortality. Using program ULM (Legendre and Colbert, 1995), we constructed a matrix population structured by population stages. The general formulation for the matrix projection invariant in time takes the form \( N_{t+1} = MN_t \), where \( M \) is the population projection matrix, incorporating data on fertility and survival probabilities for each population stage and \( N_t \) is a vector with the abundance of individuals in each of the life-cycle stages (see Hiraldo et al. (1996) for details). The population of females was divided in two age classes: yearlings and adults (individuals two or more years old). The demographic parameters used in the model were obtained from both our own work and literature. The number of adult and yearling females was calculated based on the number of breeding pairs estimated in 2007 \(( n = 540, \text{Catry et al., 2009}) \) and on the proportion of birds that attempt to breed (following the values of Hiraldo et al., 1996). Breeding success \((2.006 \pm 0.318)\) was assessed for the 2003–2007 period, when most Portuguese colonies were monitored (LPN and I. Catry unpublished data). Adult survival probability was estimated from capture-recapture data of ringed lesser kestrels between 1998 and 2005 in the two largest Portuguese colonies. We used the Robson–Pollock model (Pollock, 1975), which is obtained when fitting the Cormack–Jolly–Seber model separately for each age class (Lebretón et al., 1992). Using program MARK (White and Burnham, 1999) and starting from the full-time dependent model, we considered several sub-models, in which parameter dependence in relation to time was not included. We performed goodness-of-fit tests using program U-CARE (Choquet et al., 2009) to test global homogeneity assumptions. The most parsimonious model was selected, using likelihood ratio tests and the Akaike Information Criterion (AIC). Estimation of survival (\( p \)) and recaptures (\( p \)) probabilities was derived from maximum likelihood methods. According to the best fitting model, \( p_S(p_0(1), \text{adult survival was estimated at 0.71} \pm 0.04 \) (for detailed methods and results see Catry, 2005). For juvenile survival we used data from the French population \((0.499 \pm 0.021, \text{Mihoub et al., 2010}) \). Estimates of population growth rate and probability of extinction were obtained by running 1000 Monte Carlo simulations during 100 years. Stochastic models were used in order to incorporate environmental effects on demographic parameters (adult and
juvenile survival, Legendre and Colbert, 1995). Based on the main model, we estimated the population growth rate for three possible scenarios by replacing the value of the breeding success in the population projection matrix (Table 4). Breeding success was estimated by considering the breeding success used in the main model corrected for chick mortality associated with the high temperatures assessed in 2009 for each artificial nest-type. Therefore, all the scenarios account for the same annual chick mortality (equal to 2009) being the number of breeding pairs in each nest-type that determines the final breeding success. In the first scenario, we considered that the proportion of breeding pairs amongst different nests followed the distribution observed in 2007 for the whole population (as the main model). The second and third scenarios simulate the absence of lesser kestrel pairs breeding in natural nest-sites. As in other countries, the Portuguese lesser kestrel population is likely to become highly dependent on artificial nest-sites due to the high risk of collapse and restoration of abandoned farmhouses (Catry et al., 2009). Thus, in the second scenario all pairs were distributed amongst provided artificial nest-types, in the proportions observed in 2007. Since wooden nest-boxes are one of the most common nest-types provided worldwide for this species (e.g. García and Guzmán, 1991; Bux et al., 2008; Schulman et al., 2002; Ivanov, 2007), the third scenario considers only nest-boxes to be used by the entire population. For nest-types where chick mortality due to high temperatures was not assessed (e.g. clay pots, nests under tiles) we took a conservative approach, considering such chick mortality to be null.

3. Results

3.1. Daily maximum temperature, chick growth and mortality

Maximum temperatures exceeding 39 °C were registered for 3 days during the study period (12, 20 and 21 of June), with an average maximum daily temperature of 36.9 °C (SE = 2.7) between the first and last hottest day (Fig. 1). Twenty out of the 93 (22%) chicks died from starvation, predation or heat (some chicks perished inside the nests). chick mortality coincident with high temperatures was observed: surveyed chicks died within this period. Both direct and indirect mortality took place in both wooden nest-boxes and adobe cavities (Table 1).

Results from the GAMM model show a significant effect of daily maximum temperature, chick age and nest-type on chick growth (Table 2). The fitted curves in Fig. 2 show that an increase in daily maximum temperatures is associated with a higher probability of losing weight. As expected, age was an important predictor of chick growth (Fig. 2d) and nest-type was also retained in the model, showing that chick growth in wooden nest-boxes is significantly lower than in other nest-types (Table 2, Fig. 2c). Overall, the three predictors included in the model explained 61% of the variance in chick growth (Table 2).

Comparison of fitted growth curves for nestlings in different nest-types is shown in Fig. 3a–c. Observed growth rates in both adobe and stone cavities were coincident or higher than the average growth rate (including all nestlings), whereas in wooden nest-boxes the opposite was observed. In adobe cavities, because chicks were of similar ages in all nests, the decline in chick growth associated with the hottest days is clearly visible (Fig. 3a). Nestlings from wooden nest-boxes showed the highest residuals (|predicted

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<td><strong>Direct and indirect chick mortality expressed as absolute values and proportions inflicted by high temperatures in each artificial nest-type. Sample sizes are given as both chicks and nests.</strong></td>
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a Two complete broods of three and four chicks and single chicks in two broods of three and one brood of two.

b Three of these chicks were prevented from certain death, after being rescued from the ground in a weak condition.

Fig. 1. Daily maximum temperature (solid diamonds) in the study area from 25 May to 5 July 2009. Within this period, maximum temperatures above 39 °C (dashed line) were registered for 3 days. Average daily maximum temperatures (open circles) and standard deviations from 2003 to 2008 are shown for comparison.
We found a significant positive relationship between the amount of mass gained (or lost) in the first of the hottest days and chick body condition at fledging ($R^2 = 0.26$, $F_{1,38} = 14.86$, $p = 0.0004$), showing that chicks do not recover totally from previous losses of weight. Chicks' body condition index was significantly different among nest-types ($F_{2,49} = 3.79$, $p = 0.029$, followed by post hoc Tukey tests) showing significant differences between wooden nest-boxes and stone cavities (means ± SE adobe cavities: 1.01 ± 0.09, $n = 15$; wooden nest-boxes: 0.94 ± 0.13, $n = 18$; and stone cavities: 1.05 ± 0.09, $n = 21$; Fig. 3d).

### 3.2. Effect of temperature on feeding rates

Results from colony observations revealed no significant differences on prey delivery rates during days with maximum temperature below compared with those above 37°C (1.62 ± 0.94 and 1.59 ± 0.31 prey h⁻¹ chick⁻¹; mean temp = 28.0 ± 4.0 and 37.6 ± 0.6°C, respectively; Mann–Whitney U test $W = 831$, $p = 0.65$). The age of chicks was similar in both sample periods (15.9 ± 7.9 and 15.2 ± 4.8 days Mann–Whitney U test $W = 907$, $p = 0.89$).

### 3.3. Nest-site microclimate

Fig. 4a shows the maximum temperatures registered in each nest-type for 8 days in 2010, when the exterior temperature exceeded 35°C. Mean daily temperature inside wooden nest-boxes was significantly higher than in any other nest-type and clay pots.
were significantly hotter than adobe and stone cavities (Table 3). During the hottest day (air temp = 40.0 ± 1.5°C) the temperature reached 47.2 ± 7.4°C inside wooden nest-boxes (n = 6), 44.6 ± 4.0°C in clay pots (n = 7) and 41.1 ± 0.7°C in cavities in concrete walls (n = 6). Among cavities located in adobe or stone walls the daily maximum temperatures were always lower than the outside temperature, reaching 37.9 ± 1.2°C (n = 6) and 38.2 ± 0.7°C (n = 7) during the hottest day, respectively (Fig. 4a). Temperature

Fig. 3. Comparison of nestling growth curves (a–c) and chick body condition index at fledging (d) in adobe cavities, wooden nest-boxes and stone cavities. Logistic curves were fitted separately for chicks in each nest-type (solid line) and all nestlings (dashed line). Solid diamonds correspond to observation values used to fit the curves; values of “zero” for chick mass represent dead or missing chicks and were not included for growth curve estimation. The arrow in panel a shows the effect of the first very hot day (12 June). In panel d, an index of 1 means that the individual has its normal mass according to its age; below 1 means that the bird is lighter than expected (low body condition) and a over 1 means that the bird is heavier than expected.

Fig. 4. Maximum daily temperatures recorded in: (a) different nest-types and (b) wooden nest-boxes facing different orientations during the chick rearing period in 2010. Air temperature in the exterior (grey box) is shown for comparison. Median, upper and lower quartiles (box) and the range (whiskers) are represented.
variability between wooden nest-boxes attached to walls with different orientations is showed in Fig. 4b. The north-oriented nest-boxes had significantly lower daily maximum temperatures (33.5 ± 4.1) than the west (38.3 ± 4.0), east (42.1 ± 3.6) and south-oriented ones (42.9 ± 5.3; Table 3); the last ones reached the highest temperatures, achieving 54.8 ± 2.4°C (38.5 ± 1.6°C) and 40.0 ± 3.4°C (37.4 ± 0.6°C) compared to white painted ones (40.0 ± 3.4°C, n = 4, Table 3).

### 3.4. Effect of chick mortality on population dynamics

The main model, not accounting for chick mortality due to high temperatures, predicted a long-term growth rate of 1.08 (SE = 0.0003), with an average population increase of 8% per year (Table 4). However, when considering an annual constant mortality (equal to the one reported in 2009, scenario 1), the population growth rate decreases to 1.05 (SE = 0.0002). The two scenarios that assume all lesser kestrel pairs breeding in artificial nests would reduce even more the population growth rate (Table 4). While under scenario 2 (most pairs using artificial adobe cavities) the population would remain stable (λ = 1.01 ± 0.0002); under scenario 3 (all pairs using wooden nest-boxes) the population would decline on average 7% per year (λ = 0.93 ± 0.0001, Table 4). Under scenario 3, the probability of extinction would be 99% in 110 years, although with such a decline density dependence is likely to slightly reduce the extinction rate. We should stress that our approaches are conservative, considering no mortality in concrete cavities or clay pots (where maximum temperatures exceed the ones in adobe cavities).

### 4. Discussion

Rapid global warming will continue for several decades whatever future actions are taken, causing inevitable impacts across species and ecosystems (e.g., Sæther et al., 2000; Root et al., 2003; Crick, 2004; Thomas et al., 2004; Huntley et al., 2007; Amano et al., 2010). Nevertheless, there has been little consideration of the possible adaptation strategies for maintaining biodiversity (Heller and Zavaleta, 2009; Senapathi, 2010) and even fewer examples of testing their efficiency (but see Willis et al., 2009). Increasing connectivity to allow species to move significant distances, promote landscape level heterogeneity to enhance species to stay within their climate envelope and assisted colonisation or translocation have been referred as the most favourable options to face climate change (Hopkins et al., 2007; Heller and Zavaleta, 2009; Hodgson et al., 2009; Willis et al., 2009; Sutherland et al., 2010). In the other hand, the potential to adaptive management for individual sites and populations to increase their resilience and track climate change has received little attention (but see Pearce-Higgins, 2010). Overall, the absence of climate change predictions for specific areas, uncertainty about the species capacity to adapt and lack of evidence that the proposed actions will be effective are delaying the implementation of specific adaptation plans (Galatowitsch et al., 2009).

This study provides an example of how climate change may present unexpected challenges to conservationists and how conservation may adapt to minimize its impacts. In 2009, the occurrence of unusual high temperatures during the lesser kestrel breeding season provided us with a unique opportunity to evaluate the effects of such extreme weather events on chick growth and mortality, predict the impacts of its increasing frequency on population dynamics and recommend effective adaptation actions.

### 4.1. Effect of high temperatures on chicks’ fitness and survival

During the 2009 breeding season 22% of the surveyed chicks died, coinciding with registered high temperatures. Comparison of prey delivery rates between hot and mild days was similar, suggesting that reductions in offspring number and weight (to up 30 g or 27% of body mass) reflected the direct increasing costs of thermoregulation (Bradley et al., 1997; Lloyd and Martin, 2004), rather than a decrease in the availability and/or accessibility of prey. Inside the nests and during extremely hot days, thermoregulatory water requirements increase and at environmental temperatures exceeding the normal body temperature, chicks overheat quickly because of their relatively large surface area and low heat capacity (Elkins, 1983; Visser, 1998). Because mass-specific evaporative water loss rates increases with decreasing body mass, vulnerability to acute dehydration is most pronounced in smaller individuals (McKechnie and Wolf, 2010), explaining the higher mortality reported among younger nestlings. For the same reason, the abnormal mortality may have been caused essentially by the hottest
days being early in the season, affecting mostly young chicks. In our study area, temperatures above 39 °C are fairly common during the summer but daily maximum temperatures of 39 °C in the first half of June have been registered only in three amongst the last 37 years (http://www.ncdc.noaa.gov/oa/ncdc.htm). Mass loss during the chick rearing period significantly affected chick body condition at fledging. As chicks that fledge in poor condition may have reduced fat reserves and are less likely to survive throughout migration, chick body condition at fledging can be a good indicator of survival probability (Rodriguez and Bustamante, 2003) and thus, high temperatures during chick rearing can have a medium to long term negative impact on juvenile survival.

4.2. Effect of chick mortality on population dynamics and offspring fitness

Nest-site characteristics and orientation can have a strong impact on nest-site selection and reproductive success through its effects on microclimate (e.g. Valkama and Korpimäki, 1999; Wiebe, 2001; Lloyd and Martin, 2004; Hilton et al., 2004; Butler et al., 2009). Our results show that during hot days, nest temperature in clay pots but especially in wooden nest-boxes can reach very high values, several degrees above the air temperature. Chick mortality was reported in wooden nest-boxes facing south, west and east but not in nest-boxes facing north, where the temperature was significantly cooler than in the other orientations. Despite being large (50 × 25 × 25 cm), wooden nest-boxes have no ventilation and, when exposed to the sun, interior temperatures can exceed 55 °C. The highest temperatures reported inside wooden nest-boxes can explain the observed pattern of nesting growth curves, the lowest value of chick body condition and the highest mortality rate between monitored nest-types. Despite not having been monitored for chick growth and survival, the high temperatures achieved in clay pots here (up to 48 °C) and in previous studies (49 and 55 °C, Pomarol, 1996 and Tella et al., 1994, respectively) suggests that some chick mortality must occur during the hottest days, particularly in nests facing south and unpainted ones. Adobe and stone cavities were the cooler nests, with mean daily maximum temperatures slightly below the air temperature. Both materials were traditionally used in house building in the region and most natural nests are located in these structures. The observed difference in chick mortality observed between these nests (0% and 23% indirect mortality in stone and adobe cavities, respectively) may be explained by its orientation, dimension or number of fledglings inside the nests. Contrarily to the monitored adobe cavities, all stone cavities faced the north, probably contributing to a more suitable nest microclimate, as suggested by the lower losses of weight registered within these nests. The size of the inner chamber and number of chicks may also affect nest microclimate. Among adobe cavities, unoccupied nests were significant cooler than occupied ones (around 5 °C, IC unpublished data) and in smaller cavities evaporative water loss and dehydration may force fledglings out of nests.

4.3. Effect of chick mortality on population dynamics and management implications

In southern Europe, climate change is projected to worsen conditions in a region already vulnerable to climate variability (Meehl and Tebaldi, 2004; IPCC, 2007). Future climatic scenarios for Portugal project increases in summer average maximum temperatures of 4–4.5 °C for the 2040s, and a significant increase in the occurrence and duration of heat waves (Santos et al., 2001; Casimiro et al., 2006). In a warmer world, chick mortality in provided artificial nests, along with the likely increase of their occupancy, is predicted to preclude the recent positive population growth (scenario 2) and even lead to the species extinction, as predicted if all pairs breed in wooden nest-boxes (scenario 3). Moreover, the expected decrease in the juvenile survival associated with high temperatures could significantly increase the negative impact on population growth as population dynamics in lesser kestrels are most sensitive to adult and juvenile survival than to fecundity (Hiraldo et al., 1996).

Wooden nest-boxes and clay pots are easy to install in any building (new or old) and have been provided worldwide. Nevertheless, the high temperatures inside these nests may result in ecological traps for the species and its future provisioning should be avoided. To reduce inside temperatures, re-designed wooden nest-boxes could be installed under roof tiles (Pomarol, 1996) and other materials should be considered (as woodcrete: http://oryxdistribuciones.com). For those nests already provided, new deployment should be considered in walls not exposed (or at shadow) and clay pots should regularly be white painted (see also Pomarol, 1996). Adobe, stone and concrete are the most suitable materials and should be used whenever is possible when providing new breeding structures. Partial reopening of cavities in buildings instead of nest-box installation, non-exposed locations and large inner chambers accounting for broods of five chicks would help maintain tolerable temperatures.

As in other species of conservation concern, nest-site provisioning is considered to be a key factor for the recovery of the Portuguese lesser kestrel population in the last decade and suggested to be crucial for its maintenance in the near future (Catry et al., 2009). However, rapid global warming may jeopardize the effectiveness of present and future conservation strategies. This study enhances the importance of addressing the effects of climate change at local or species-level in order to help adjusting conservation actions to increase their resilience to climate change in a more effective way. Conservation planning and climate adaptation strategies should be considered in the implementation of future conservation projects and integrated in the elaboration and review of the Species Actions Plans.

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