# Impact of temperature on the breeding performance and selection patterns in lesser kestrels *Falco naumanni*

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Adjusting breeding phenology to climate fluctuations can be problematic for migratory birds as they have to account for local environmental conditions on the breeding grounds while migrating from remote wintering areas. Predicting general responses to climate change is not straightforward, because these responses vary between migrant species due to the species-specific ecological drivers of breeding behaviour. Therefore more information is needed on species with different ecological requirements, including data on heritability of migration, factors driving phenological changes and how climate affects selection pressures.

Here, we measure heritability in settlement dates and the effect of local climate at the breeding grounds on settlement dates, reproductive success and selection patterns in a French population of a trans-Saharan migratory insectivorous raptor, the lesser kestrel *Falco naumanni*, monitored and ringed since 1996.

Heritability of settlement dates was low ($0.07 \pm 0.03$), indicating a weak evolutionary potential. Nevertheless, plasticity in settlement dates in response to temperatures allowed earlier settlement when early spring was warmer than average. Reproductive success and selection patterns were strongly affected by temperature during settlement and chick rearing respectively. Warmer spring decreased selection for earlier settling and warmer early summer increased reproductive success. Interestingly, selection for earlier settling was more intense in cooler springs, contrasting with patterns from passerines lagging behind food peaks.

Altogether, these results suggest a positive effect of warmer temperatures on breeding performances of lesser kestrels most likely because the French population is at the coolest boundary of the species European breeding range.

The current unprecedented rate of climate change (Adger et al. 2007) is resulting in large-scale ecological responses, such as poleward distribution shifts in temperate species and changes in phenology – e.g. earlier breeding dates (McCarty 2001, Stenseth et al. 2002, Walther et al. 2002, Root et al. 2003) or earlier arrival dates for migrant bird species (Jonzén et al. 2006). Despite these responses, it is becoming increasingly apparent that many species are not fully adapting to these climate changes. Inappropriate behavioural and physiological responses can lead to the mistiming of life history events, such as breeding failing to coincide with peak food availability (Visser et al. 2006) or a mismatch between environmental conditions on departure and arrival grounds for migrant species (Inouye et al. 2000). Although evidence for earlier arrival in response to warming temperatures has been shown for many migrant species (Ahola et al. 2004, Jonzén et al. 2006, Møller et al. 2008), they may still be especially susceptible to phenological mismatches (Dunn 2004, Sparks et al. 2005) because the timing of migration constrains the entire breeding period (Both and Visser 2001, Pulido 2007b). Indeed, migratory birds that do not show phenological responses to climate

change are the species demonstrating the strongest population declines (Both et al. 2006, Møller et al. 2008).

The mistiming of life history events due to climate change is likely to affect the intensity of the relationship between fitness and phenological traits – i.e. the strength of selection. A commonly cited example being the mismatch between earlier peak food availability as a result of climate change and the timing of breeding in avian populations (Nielsen and Møller 2006, Both et al. 2009). If bird populations are able to sufficiently adjust their behaviour to accommodate climate-induced temporal shifts in food availability, the strength of selection on the timing of breeding should remain the same. However, if the mean population response is smaller than that required to account for an earlier food peak, the relative benefit of breeding early to individuals in that population will increase; hence an increase in the strength of selection over time is evidence that species are unable to track progressive environmental changes. This has been shown in migrant Dutch pied flycatchers *Ficedula hypoleuca* (Both and Visser 2001) and resident Dutch great tits *Parus major* (Visser et al. 1998), where selection for earlier laying has intensified

with time. In contrast, Charmantier et al. (2008) found no temporal trend for selection in resident British great tits. Thus responses to climate change can occur at the local population level and may differ between organisms with otherwise similar life histories, or the same species.

Studies on the impact of climate change to avian phenology are largely restricted to species with a clearly defined and narrow food peak of leaf-mining insect larvae (see above); however, these may not be representative of phenological trends in the majority of species (Dunn and Winkler 2010). Species in non-seasonal habitats or with generalist diets are likely to show different responses to climate change from those dependent on a narrow food peak (Dunn 2004, Both et al. 2010). Similarly, differences in migration strategy (short vs long-distance migrants, Gienapp et al. 2007, Moussus et al. 2011), food resources (insectivorous vs omnivorous diets; Dunn 2004), or changes in local temperatures (Dunn 2004, Pulido 2007b) will result in heterogeneous patterns of climate change responses. Knowledge of the different factors driving these patterns is needed to predict and ultimately manage species responses.

Here, we investigated the response of breeding parameters to climate for a long-distance migrant raptor not reliant on the larval food peak of leaf-mining insects, the lesser kestrel *Falco naumanni*. In this species, prey are likely to be affected by climatic conditions both in terms of phenology and abundance (Rodriguez et al. 2010), and migration is expected to constrain the flexibility of settlement time. As a consequence, lesser kestrels may adjust their migration to conditions that drive food availability at the breeding grounds in order to accurately track climate change. Because long-term phenotypic adjustments in breeding parameters could reflect phenotypic plasticity and/or microevolution (Gienapp et al. 2008, Sheldon 2010) we were interested in the evolutionary potential of phenology as it relates to the timing of arrival and settlement. Our aim was hence threefold: 1) assessing the evolutionary potential of the timing of breeding settlement (onset of breeding period), 2) testing for the existence of plasticity in the phenological response to climate on the breeding grounds – with temperature and rainfall being considered as proxies of local climatic conditions, and 3) evaluating the impact of climatic conditions on reproductive success and on the selection pressures acting on settlement dates in order to identify the main driver of the response to climate in this species.

If breeding success in lesser kestrels is constrained by an inability to adequately adjust breeding time to changing conditions at the breeding ground, we expect that: 1) average reproductive success will decline with increasing temperatures, and 2) the strength of selection on breeding time should increase in warmer years.

## Material and methods

### Lesser kestrels in southern France

The lesser kestrel is a small migratory falcon that feeds mostly on invertebrates in open landscapes of agropastoral systems (Donázar and Hiraldo 1993). The species breeds in the Mediterranean region and western European populations winter in western Sahel (Rodriguez et al. 2009). In 1994, lesser kestrels were classified as 'vulnerable to extinction' by the IUCN red list. Thanks to conservation measures, such as European Life Nature projects, lesser kestrel were classified as 'least concern' in 2011 (IUCN 2011). In France, the three known breeding populations – two natural and one reintroduced – are carefully protected and monitored.

The present study used monitoring data from the population breeding in the Crau Plain in southern France (43°30′N, 4°50′E) where the species is present from early March to late September (Mihoub et al. 2010). This is the oldest of the three French populations and is located in the nature reserve of Coussouls de Crau. This environment is an open pseudo-steppic plain surrounded by cultivated rice fields and orchards. In addition to the resources offered by the steppe, rice fields provide common foraging places for lesser kestrels at least at the beginning of the breeding season. In the study area, lesser kestrels prey mainly on arthropods (Choisy et al. 1999, Lepley et al. 2000). During the breeding settlement period, their preferred prey are Orthoptera (mole cricket *Gryllotalpa gryllotalpa*: 34%) and *Coleoptera* sp. (38%). During egg laying and incubation, main prey items are *Scolopendridae* sp. (38 and 50% respectively) and mole crickets (40 and 25% respectively). Orthoptera largely dominate the diet during the chick rearing period (75%), with locusts (*Acrididae*, 26%) and bush crickets (*Tettigoniidae* sp., 43%, information available at <http://crecerellette.lpo.fr/biologie_ecologie/biologie_ecologie.html >). The population dynamics of arthropods such as Orthoptera are very sensitive to both temperature and rainfall local conditions (Frampton et al. 2000, Rodriguez et al. 2010); thus, we expect the timing of breeding and breeding success to be correlated to the weather variables that largely influence the bird's food supply.

We used a 13-yr dataset (1996–2008) of intense individual monitoring of the Crau breeding population. All nestlings were individually marked with alphanumeric rings to allow future identification if they recruited. From the first arrival until the end of the breeding season, all possible nesting cavities were monitored daily through binocular observations and individual breeding activities (settlement, copulation, incubation, chick rearing) recorded. Thus, the age, breeding status and the reproductive success were known for all individuals returning to the colony. The number of breeding pairs regularly increased during the study period from 42 in 1996 to 125 in 2008. The number of available nesting cavities in the study area was estimated to be 300; thus nesting cavities did not represent a factor limiting the breeding population. We defined a bird to be settled if it was observed during 5 consecutive days at the same breeding cavity, with settlement date being the first of those 5 d. Reproductive success for each individual was measured as the number of fledged offspring. Laying date was not systematically monitored to minimize disturbance at the nest during the early stages of the breeding cycle. Due to the restricted geographic area of the breeding population and to the colonial breeding behaviour in this species, we are confident that virtually

all of the breeding pairs in the Crau population were identified and recorded throughout the study period. Of 1633 ringed nestlings, 736 were later resighted at least once as breeder during the study; birds only resighted as non-breeders are not included in these analyses. Birds can be recruited into the breeding population as one-year-olds (63%, n = 390), two-year-olds (34%, n = 215) and three-year-olds (3%, n = 18). Here we only included birds older than 2 yr.

The pedigree describing the genealogical relationships between individuals was constructed using ringing records and observed social relationships. However, in some cases, although offspring were ringed for identification, one or both parents were unmarked and remain unknown. In such cases, we created dummy identities for parents to group those offspring as siblings. Extra-pair paternity is low in lesser kestrels (Negro et al. 1992) and in its close relative, the European kestrel *Falco tinnunculus* (ca 7%, Korpimäki et al. 1996), so we assume the related bias of incorrectly assigning paternal links is minimal (Charmantier and Réale 2005). Out of 1660 individuals, 258 had dummy parents for both mother and father. For 871 individuals, both parents were known. The resulting pedigree contained eight generations and 2009 individuals (including dummy parents).

## Heritability estimation

An individual based 'animal model' was fitted in order to break down phenotypic variances (settlement dates) into components of additive genetic variance and other random effects while controlling for fixed effects (Lynch and Walsh 1998, Kruuk 2004). Individual age was fitted as a quadratic fixed effect to control for age dependent variation and potential senescence. Settlement date had repeated measurements for individuals breeding in different years. To control for permanent environment effects associated with the individual we included individual identity as an additional random effect unlinked to the pedigree. Because year of breeding also likely described common environment effects, it was also added as a random variable.

The model can thus be described as:

$$V_P \sim Va + Vpe + Vy + Vr \tag{1}$$

where $V_P$ is the total phenotypic variance, Va the additive genetic variance, Vpe the permanent environment variance i.e. the between individual variance due to other effects than additive genetic components, Vy the between-year variance and Vr is the residual variance. We assessed the significance of variance components by using likelihood ratio tests to compare models with and without particular random effects (Wilson et al. 2006).

The narrow-sense heritability ($h^2$) was estimated as the ratio of the additive genetic variance ($V_A$) to the total phenotypic variance ($V_P$): $h^2 = V_A/V_P$. Variance components and heritabilities were estimated using a mixed model restricted maximum likelihood procedure (REML; Shaw 1991) using the software ASReml (Gilmour et al. 2006).

## Estimation of selection

Since we were interested in studying how selection varied between years, we estimated annual directional selection gradients on settlement date using annual fledging success as the measure of fitness. Selection gradients were estimated for each year by regressing relative fitness (fitness divided by annual mean) on standardised settlement dates (annual zero mean, unit variance, Lande and Arnold 1983). We also estimated non-linear selection by including a quadratic term in the regression. The significance of selection gradients was assessed using fledging success, i.e. absolute and not relative fitness, with a generalized linear model with Poisson errors. Selection gradients are reported as estimates with their associated standard error throughout the text. In addition, we also report the selection gradient over all years, estimated from a linear mixed model with both individual identity and year fitted as random effects to account for non-independence of data.

Temporal trends in directional selection gradients were estimated using a weighted regression (weight = 1/se) to account for the error on the estimation of selection gradients. As selection can be different in males/females regarding differential behavioural or physiological features, such as reproductive experience or energetic investment for breeding, selection was estimated for both sexes separately.

## Impact of climate on settlement dates, reproductive success and selection

Daily rainfall (mm) and temperature (°C) data were obtained from the French meteorological survey institute (Météo France, < http://france.meteofrance.com >) from the closest weather station to the population (Istres station (43°31′N, 4°56′E), about 5 km from the core of the colony) for 1996–2008. Because we had no a priori assumptions on the exact temporal window during which climate variables could affect settlement dates, reproductive success and selection, we used a sliding window analysis to assess the time period that had the highest correlation between temperatures or rainfalls and the annual mean of the trait of interest. In these analyses, a routine systematically estimated the squared correlation coefficient ($R^2$) and AIC of a regression between the annual mean trait (either settlement date, selection or reproductive success for males or females) and annual climate means, for all windows which ranged in size between 10 and 30 d from 1 February (day 32 from 1 January, a month before first sighting of kestrels) to 5 August (day 217, latest observation of chick rearing). Time periods related to sliding windows were numbered according to their starting dates and length. The first period started on day 1 for a window of 10 d (from 1 to 11 January), period 2 started on day 1 but for a window of 11 d (from 1 to 12 January) and so on. The regression was weighted by the standard error of the trait to account for the variable precision in the estimates of the population. We then plotted all resulting correlations against the time periods to visualise whether the correlations between traits and times were essentially random or if there were clear peaks suggesting the existence of critical time periods (for a total of 3465 periods). For the traits where peaks could be seen in these sliding window plots, we used a multi-model inference approach (Burnham and Anderson 2002) to account for model selection uncertainty in determining the position and length

of the time window. To do this, we first generated the AIC-weight for each regression model and used these weights to calculate the relative importance of each day within the search period (i.e. all days between 1 February and 5 August). For example, to calculate the relative importance of 15 June, the AIC weights for all regression models that contained 15 June in their time window were added together. This was repeated for each day and allowed a relative comparison for the strength of support in the data for every day within the search period (cf. 'relative variable importance' in Burnham and Anderson 2002). Although this gave a much clearer indication of where the time windows were located, this method can only roughly approximate the start and end date of the time windows of interest. As a means of determining these start and end dates, we first identified the day with the maximum relative variable importance value and then included in the time window all days which had an equivalent relative variable importance value as the maximum. To determine this 'equivalence' we considered that models within 2 AIC of the best model had an equivalent level of support from the data (Burnham and Anderson 2002). Thus, we included all days within this range of the maximum relative variable importance weight; this was calculated using the ratio of AIC weights between the maximum day and each day (a ratio of AIC weights $<2.7$ is the same as a difference in AIC of $<2$). This yielded time windows which were slightly larger, but included, the range of dates specified by the correlation coefficient analysis – suggesting that this additional AIC-weight analysis captured the model selection uncertainty.

## Results

### Age and sex effects

For settlement dates, we found no differences between males and females, which is consistent with settlement being the onset of breeding in this monogamous raptor (sex effect: $-0.02 \pm 1.08$, $z = -0.02$, $p = 0.99$). Birds settled increasingly earlier until they were 8 yr old, before this reversed for older birds that settled later (linear effect: $-7.14 \pm 1.17$, $z = -6.12$, $p < 0.0001$; quadratic effect: $0.43 \pm 0.12$, $z = 3.60$, $p < 0.0001$).

### Heritability estimate

We found a significant yet low heritability of the settlement dates ($h^2 \pm SE = 0.066 \pm 0.034$, $\chi^2_1 = 6.02$, $p = 0.014$, see Table 1 for details of the estimates). This heritability arises both from low additive genetic variance and high residual variance (Table 1).

### Selection on settlement date

We found a significant selection for earlier settlement dates, but variation between years was very strong (for a complete list of directional selection gradients see Supplementary material Appendix 1a). The average directional selection gradient over the 13 yr was negative ($\beta_{females}$: $-0.15 \pm 0.04$, $t = -4.22$, $N_{obs} = 497$, $N_{ind} = 207$,

Table 1. Estimates and standard errors of variance components of modelling settlement date. Vp is total phenotypic variance, Vy variance due to year of reproduction, Va additive genetic variance, Vpe variance due to permanent environment effects and Vr residual variance.

|       | Estimate | SE     |
| ----- | -------- | ------ |
| Vp    | 292.1    | 19.77  |
| Vy    | 34.31    | 16.26  |
| Va    | 19.35    | 10.16  |
| Vpe   | 10.92    | 10.6   |
| Vr    | 227.6    | 11.95  |
| $h^2$ | 0.0662   | 0.0343 |

$p < 0.0001$; $\beta_{males}$: $-0.15 \pm 0.03$, $t = -3.51$, $N_{obs} = 542$, $N_{ind} = 243$, $p = 0.0004$). There was no evidence for non-linear selection in females ($\gamma_{females}$: $0.03 \pm 0.02$, $t = 1.31$, $p = 0.258$); the slight signature for curvature in males ($\gamma_{males}$: $0.05 \pm 0.02$, $t = 2.029$, $p = 0.042$) is actually due to two extreme data points only out of 542 (if those points are removed $\gamma_{males}$: $0.04 \pm 0.025$, $t = 1.67$, $p = 0.10$) and the response should thus be considered linear. Moreover, all but one annual quadratic gradient was non-significant (Supplementary material Appendix 1b). There was no correlation between male's and female's directional selection gradients ($r = 0.12$, $t_{11} = 0.416$, $p = 0.68$).

### Impact of climate on settlement date, reproductive success and selection gradients

We did not find any temporal trend in the settlement date (all $p > 0.08$), reproductive success (all $p > 0.2$) or selection gradients (all $p > 0.2$, results not shown), nor strong patterns between these traits and rainfall (results not shown). However, there were strong patterns related to temperature on these traits. Each of the three traits presented peaks of correlation with mean temperature (Fig. 1, 2). However, only some of these peaks were actually supported by relative AIC weights (Fig. 1, 2), and so only these were further retained. These differences emphasise that caution is needed when interpreting sliding window analyses, as the peaks in $R^2$ values need to be compared within an analysis to define strength of support for patterns of response. Peaks corresponded to similar dates and time periods for both sexes. However, we mainly focused on females since the pattern for females were more marked than for males (results for male breeding success and selection shown in Supplementary material Appendix 2).

In both males and females there was a common correlation peak between temperature and settlement dates ($P_{SD}$, Fig. 1a, b). Females settled much earlier when the temperature was higher in early spring during $P_{SD}$ (i.e. 11 March–4 April: $-4.39 \pm 1.15$ d/°C, $t_{11} = -3.73$, $p = 0.003$, $R^2 = 0.55$, Fig. 1c, e), suggesting that breeding settlement was largely determined by temperatures in the week preceding settlement. The pattern was similar in males (14 March–5 April: $-3.23 \pm 1.27$ d/°C, $t_{10} = -3.23$, $p = 0.029$, $R^2 = 0.4$, Fig. 1d, f). There was a second peak in males (Fig. 1d) which is difficult to interpret as it corresponds to dates after the majority of adults birds were already settled (Fig. 3) and adult females did not exhibit such
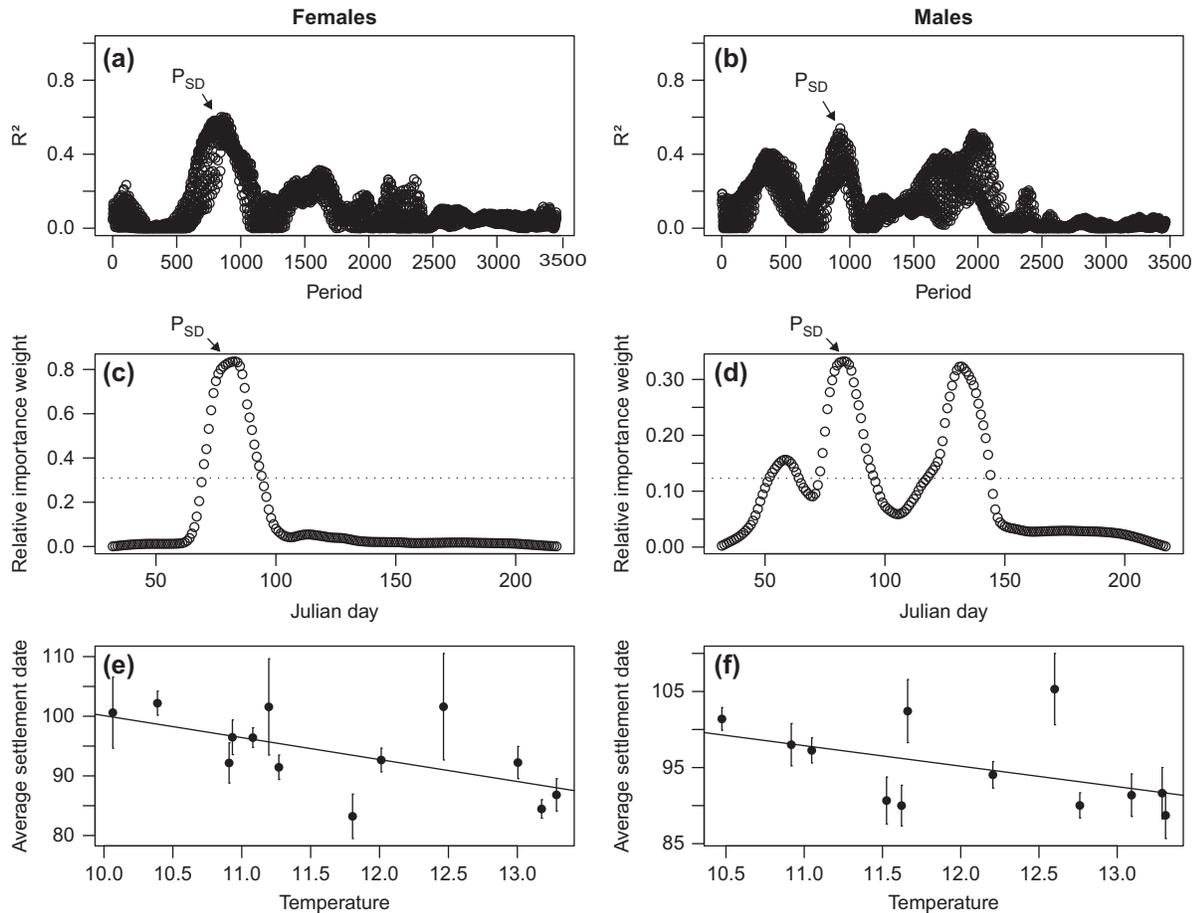
Figure 1. Impact of average temperature on settlement dates of females and males. (a, b) Peaks of correlation between yearly settlement dates and temperature throughout the season. (c, d) Relative variable importance weight of each day. The dotted horizontal line represents the weight of the day of maximum weight divided by 2.7 (see Material and methods for details). All dots above this line have equal relative weight with the maximum day and should be taken into account when defining the period during which temperature affects the trait. (e, f) Relation between mean temperature and settlement dates for the selected period.

pattern. Based on this, we only interpret the first peak for male settlement dates.

For reproductive success in females, while two correlation peaks were detected based on $R^2$ values (Fig. 2a), only one was supported by relative AIC weights ($P_{ARS2, F}$, Fig. 2c). For reproductive success in males, the correlation and AIC-supported peak was similar to the AIC-supported peak in females (Supplementary material Appendix 2); thus in both sexes, reproductive success increased with increasing temperatures in early summer ($P_{ARS2, F}$: 30 May–19 June: $0.3526 \pm 0.093$ fledging/°C, $t_{11} = 3.49$, $p = 0.005$, Fig. 2e).

Concerning selection coefficients, we identified different patterns between males and females. While we detected no correlation between temperature and selection in males (Supplementary material Appendix 2), there were three time periods where selection coefficients were strongly correlated with temperature in females (Fig. 2b). However, only two of these peaks, (peak $P_{S1, F}$ and peak $P_{S3, F}$) were supported by relative AIC weights (Fig. 2d). Interestingly, $P_{S1, F}$ (22 March–19 April) corresponds to the time of breeding settlement while $P_{S3, F}$ corresponds to the end

of the rearing period (27 July–4 August), according to census records (Fig. 3). During both time periods, selection for earlier settling was less intense as temperature increased ($P_{S1, F}$: $0.147 \pm 0.039$, $t_{11} = 3.82$, $p = 0.003$; $R^2 = 0.57$, Fig. 2f; and $P_{S3, F}$: $0.099 \pm 0.024$, $t_{11} = 4.12$, $p = 0.002$; $R^2 = 0.61$, not shown).

## Discussion

### Evolutionary potential and settlement dates

In the Crau population of the migratory lesser kestrel, we found a very low while significant heritability of the settlement dates ($0.07 \pm 0.03$), due to both low additive genetic variance and high residual variance. This is in line with many studies showing low heritability for life history traits (Kruuk et al. 2000, Merilä and Sheldon 2000, McCleery et al. 2004, Teplitsky et al. 2009). However, phenological trait heritabilities are generally larger than what we found: ~0.34 for arrival dates in long distance migrants (Pulido 2007b) and ~0.2 in laying dates

**Reproductive success**

**(a)** $P_{ARS1, F}$ $P_{ARS2, F}$

**(b)** $P_{S1, F}$ $P_{S2, F}$ $P_{S3, F}$

**Fecundity selection**

**(c)** $P_{ARS2, F}$

**(d)** $P_{S1, F}$ $P_{S3, F}$
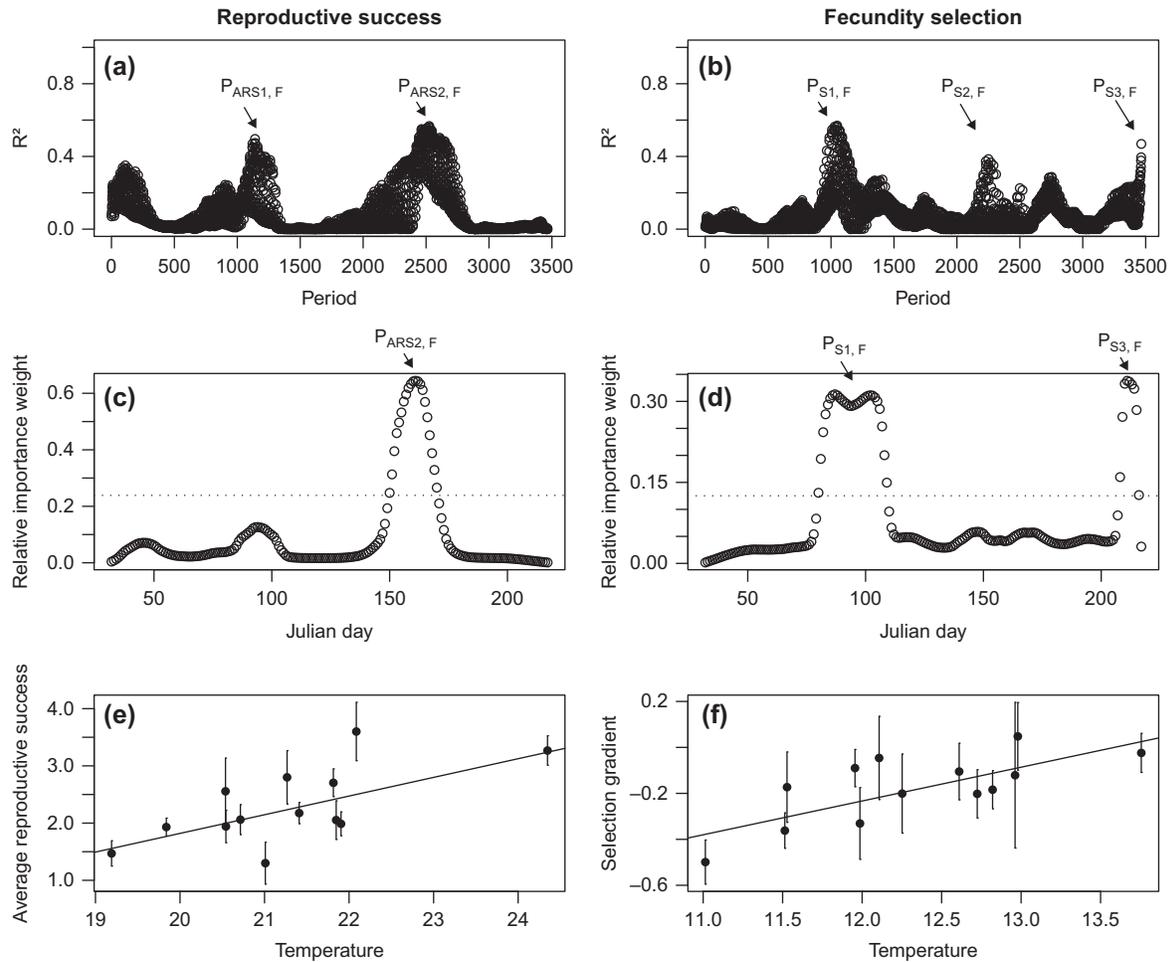
**(e)**

**(f)**

Figure 2. Impact of average temperature on reproductive success and selection pressures on fecundity in females (see Supplementary material Appendix 2 for details on males). (a, b) Peaks of correlation between yearly average reproductive success and temperature throughout the season. (c, d) Relative variable importance weight of each day. The dotted horizontal line represents the weight of the day of maximum weight divided by 2.7 (see Material and methods for details). All dots above this line have equal relative weight with the maximum day and should be taken into account when defining the period during which temperature affects the trait. (e, f) Relation between mean temperature and each trait for the selected period ($P_{ARS2, F}$ and $P_{S1, F}$, note that trends are similar for $P_{S1, F}$ and $P_{S3, F}$ except that temperature ranges from 23°C to 27°C for the latter).

(Sheldon et al. 2003, McCleery et al. 2004, Husby et al. 2010). Because of the difficulty in interpreting interspecific heritability comparisons, we will restrict our conclusion to saying that the studied population of lesser kestrel shows low evolutionary potential in settlement date.

Estimates of evolutionary potential could be further refined by adding genetic correlations between traits, e.g. migration syndrome (Dingle 2006, Pulido 2007a, Teplitsky et al. 2011) or estimates of heritabilities along the climatic gradient (Charmantier and Garant 2005). However, since previous studies suggested that genetic correlations slow down evolution (Walsh and Blows 2009) and that stressful environments decrease heritability (Charmantier and Garant 2005, Wilson et al. 2006), it is likely that refinements to our estimates would show even lower evolutionary potential than presented here. Thus, if changes in settlement dates are needed to allow birds to track climate change, microevolution will be strongly constrained because heritability is low – meaning that the population will be largely reliant on behavioural plasticity.

## Impact of climate on breeding timing and success

Male and female lesser kestrels displayed significant plasticity in the onset of breeding, with earlier settlement in response to warmer spring temperatures. This suggests that food availability, rather than life history traits or migratory behaviour, might play a dominant role in determining the settlement timing since their food source (i.e. insects) is highly dependent on local climate. This strong response to local climatic conditions in a long-distance trans-Saharan migrant species may be explained by climatic connectivity between Africa and Europe, suggesting that correlated cues might harmonise migration timing at large spatial scales (Saino et al. 2007, Saino and Ambrosini 2008). Nevertheless, the strong effect of local temperature on settlement dates could also arise because European lesser kestrels migrate relatively slowly from Africa before reaching their breeding colonies (Rodriguez et al. 2009). If lesser kestrels pursue regular stopovers along their European flyway to the Crau breeding ground, this could allow them
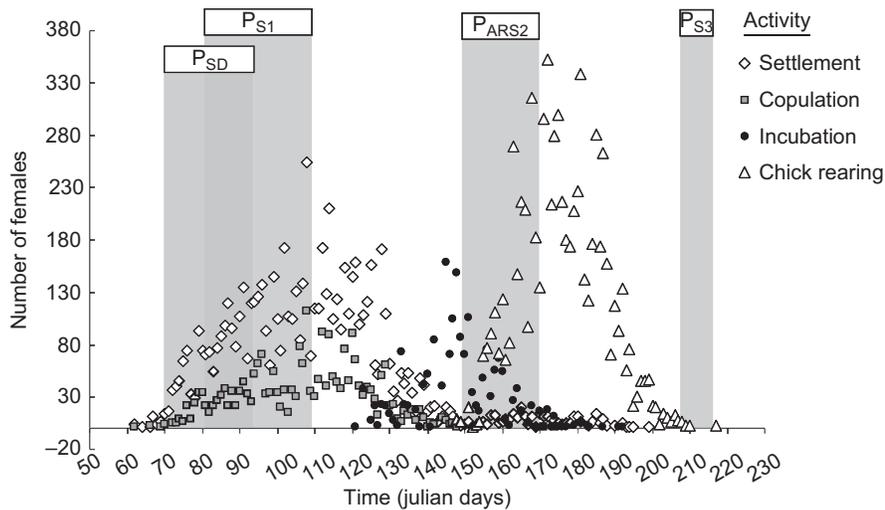
Figure 3. Timing of breeding activities along the breeding season (1 = 1 January) as recorded by the number of adult females performing a specific behaviour on a given day over all the years of the study. Relative to temperature time windows are also presented with $P_{SD}$ = settlement date time window, $P_{ARS2}$ = reproductive success time window, $P_{S1and3}$ = selection for earlier settlement (see text for more details) from 1994 to 2008. Symbols refer to census data of specific reproductive activities on given days. Shaded areas represent time windows where temperature was significantly correlated with settlement and reproduction.

to adjust their arrival and onset of breeding with the local temperatures of their breeding area.

Plasticity of settlement dates (almost 4 d per 1°C) in the lesser kestrel was stronger than plasticity of breeding dates in other raptors: common buzzard *Buteo buteo* bred 10 d earlier for an increase of 8 degrees in April (Lehikoinen et al. 2009) and the sparrowhawk *Accipiter nisus* showed very little (1.7 d for a change in 2.65°C, (Nielsen and Møller 2006) if any (Both et al. 2009)) response to temperature. This plasticity in settlement date is a rather strong response and can may have important consequences for population dynamics; for example in pied flycatchers, populations in which laying date was advanced by 2 d per 1°C were stable, while populations with lower responses were declining (Both et al. 2006).

The main impact of changing climatic conditions on reproductive success in lesser kestrels breeding in the Crau occurred in early summer, when increased temperature improved reproductive success. In contrast with what was found by Rodriguez and Bustamante (2003) in the Spanish lesser kestrel population, we did not find a positive effect of rainfall on breeding success. As warmer early summer temperatures and rainfall can speed up insect life-cycles, so that food availability is greater during the nestling stage (Frampton et al. 2000, Rodriguez et al. 2010), each population maybe more sensitive to the most limiting climatic factor of their respective habitats (minimum amount of annual accumulated rain: 225 mm in Guadalquivir [Rodriguez and Bustamante 2003], 337 mm in the Crau [this study]; average annual temperature: 18°C in Guadalquivir [Sevilla, Cordoba], 15°C in the Crau).

Increased breeding success when temperatures were warmer is contrary to expectations if the population is lagging behind a temperature-induced advancement in the timing of peak food availability. This suggests that increasing temperatures may not have significant negative consequences for this population. Perhaps the fact that these

lesser kestrels are at the northern edge of their distribution, and hence may be well adapted to warmer climates, is why they respond to small temperature increases in a positive way.

## Selection and response to temperature

We found a significant impact of temperature on selection intensity for settlement date in females but not in males. Since selection coefficients were uncorrelated in males and females, the differences in patterns could be best explained by different advantages in early arrival between sexes: an absolute advantage to arrive early in females that is influenced by temperature (e.g. rate of gathering the energy needed for egg laying and incubation depending on environmental quality) and instead, a relative advantage of being early compared to other nest competitors in males (e.g. benefit of securing a nest in a good quality colony) independent of temperature. Indeed lesser kestrels exhibit strong despotic behaviours, and males usually arrive on the breeding ground earlier than females in order to secure a nesting site in a good quality colony (Serrano and Tella 2007). Females may also benefit from arriving early to find a male able to secure a good quality nest, but may also need time to replenish energy reserves after migration before investing in breeding.

In adult females, selection strength decreased as early spring temperatures increased; meaning that there were strong benefits to arrive early in a cool spring, but these benefits largely disappeared for warm springs. This pattern is the opposite to that expected in passerines struggling to match the food peak to the timing of reproduction: in Dutch pied flycatchers and great tits, selection increased as temperature increased (Visser et al. 1998, Both and Visser 2001). Furthermore, if selection was linked to the impact of settling dates on performance during chick feeding, we would expect selection to be mostly affected

by temperatures during chick rearing and not, as is the case here, by temperatures experienced during the settling period. One interpretation for the strength of selection on settling dates being lower during warmer springs in this population is that food could be more abundant in warm years, relaxing food constraints on all females and resulting in lower variation in reproductive success. However in cooler years, if food is less abundant, selection will favour females who arrive earlier because they will be able to select territories with greater food resources and will have more time to reach breeding condition, resulting in greater breeding success for early settlers.

## Conclusions

In contrast with studies showing that changes in breeding phenology can be maladaptive in raptors (Lehikoinen et al. 2009, Senapathi et al. 2011), we found a general positive impact of warmer climate on lesser kestrels. This could be best explained by lesser kestrels in France being at the northern edge of their breeding area, so that position of a population within its distribution area would also be an crucial parameter in understanding effects of climate change, calling for more between population comparisons. Climate scenario predict an increase in mean temperatures in the future (IPCC 2007), which could have positive impacts on this population of lesser kestrels, but caution is still needed as such predictions also need to integrate the impact of climate change on the abundance and timing of their prey (Devictor et al. 2012).

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