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Landscape and weather determinants of prey availability: implications for the Lesser Kestrel *Falco naumanni*

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Spatial and temporal variation in prey abundance have been shown to impact the time of breeding and breeding success of birds. Understanding the ecological requirements of preferred prey can help develop management measures to improve food supply for target species. For the colonial Lesser Kestrel *Falco naumanni*, mole crickets *Gryllotalpa* spp. are one of the most important prey items during the mate-feeding period. Lesser Kestrel colonies with higher mole cricket consumption had earlier egg-laying dates, suggesting that differences between individuals in the time of breeding could be caused by differences in the diet. Moreover, the mean number of mole crickets in pellets was significantly correlated with clutch size (in one of the studied years) and egg volume. Thus, the impact of environmental variables and land use on mole crickets is likely to be relevant to Lesser Kestrel conservation. Weekly consumption of mole crickets was higher following an increase in either precipitation or minimum temperature values. Furthermore, mole cricket consumption was higher in colonies surrounded by higher quality soils and in wetter areas and years. Predicted probability of mole cricket occurrence in surveyed watercourse margins suggested a positive relationship between soil penetrability and mole cricket occurrence. Among variables that might be the target of management, the presence of riparian vegetation positively influenced the occurrence of mole crickets, whilst tillage and sowing of streambeds were revealed as the most important threats. We suggest that the maintenance of native vegetation in the margins of watercourses could improve soil resilience to erosion, increase water retention, soil penetrability and fertility, and provide a food supply and shelter for mole crickets. Overall, the implementation of such recommendations is likely to benefit other farmland species known to consume mole crickets, including several endangered species.

Keywords: clutch size, conservation, diet, habitat management, laying date, mole crickets, prey availability.

Food availability is probably the ultimate factor influencing avian breeding and most species time their breeding cycle to coincide with periods of peak prey abundance (Lack 1968, Perrins 1970, Newton 1979). Laying date and clutch size are greatly affected by parental condition: birds in better condition typically breed early and produce larger clutches and more offspring (e.g. Perrins 1970, Price *et al.* 1988, Daan *et al.* 1989). Several experimental studies have shown that provisioning extra food at the start of the breeding season advances laying date and increases both clutch and egg size (e.g. Boutin 1990, Magrath 1992, Korpimäki & Wiehn 1998, Aparicio & Bonal 2002, Castro *et al.* 2003, González *et al.* 2006). In contrast, inadequate quantity or quality of food may prevent breeding: food shortages or adverse

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weather prior to laying, limiting foraging activities or prey availability, often prevent female from reaching the body condition necessary for egg production and laying (Carey 1996, Bradley *et al.* 1997, Steenhof *et al.* 1999). From a conservation perspective, identifying the preferred prey items and assessing their dynamics and ecological requirements could help to improve the foraging conditions of target species. Although dietary studies are commonly used to identify the most important prey items, their impact on species' performance is rarely evaluated and most studies lack specific management measures to guarantee the supply of specific prey.

In this study, we investigate the impact of mole cricket *Gryllotalpa* spp. (Gryllotalpidae, Orthoptera) consumption on the time of breeding and clutch size of the Lesser Kestrel *Falco naumanni* in southern Portugal. We also assess the dynamics and habitat requirements of this prey in order to identify potential threats and provide management recommendations to increase its occurrence. The Lesser Kestrel is a small colonial falcon that winters in west Africa (Cramp & Simmons 1980, Catry *et al.* 2011), but breeds in steppe-like habitat, natural and managed grasslands, and low-intensity agricultural areas (BirdLife International 2010). Two of the main causes of Lesser Kestrel population declines in Western Europe have been identified as habitat loss, through urbanization and modification of traditional agricultural practices, and pesticide use (Peet & Gallo-Orsi 2000). Lesser Kestrels are predominantly insectivorous, feeding mainly on Orthoptera, Coleoptera and Scolopendridae (Bijlsma *et al.* 1988, Rocha 1998, Choisy *et al.* 1999).

During the nestling period, chick diet (composition and prey size) has been shown to influence local and annual productivity (Rocha 1998, Lepley *et al.* 2000, Rodríguez *et al.* 2006) but no studies have investigated the impact of prey quality and availability during the pre-laying period on breeding performance. Mole crickets are often a major component of the Lesser Kestrel diet during courtship, when some of the most frequently consumed prey later in the breeding season, such as large grasshoppers, are scarce (Choisy *et al.* 1999, Teodósio 2000, Pilard 2001, Rodríguez *et al.* 2010). As in other raptor species, during the mate-feeding period males may select larger and more energetic prey to feed their mates so they can reach the energy requirements needed for egg production and laying (Newton 1979, Bijlsma *et al.* 1988, Donázar *et al.* 1992). Because mole crickets are large (2.7 ± 0.5 g, $n = 23$, this study) and rich in proteins and lipids (Lepley *et al.* 2000), it has been suggested that they could play an important role in restoring the fat reserves depleted during migration and in the accumulation of reserves necessary for egg production and incubation (Choisy *et al.* 1999), but the actual impact on Lesser Kestrel breeding performance is still unknown.

The main aims of this study were (1) to assess the effect of mole cricket consumption on Lesser Kestrel breeding parameters such as laying date, clutch size and egg volume, (2) to describe temporal (intra- and inter-annual) and spatial (inter-colony) variation in the consumption of mole crickets by Lesser Kestrels and identify the drivers of such variation, (3) to measure habitat selection by mole crickets and (4) to provide management recommendations to improve habitat suitability for mole crickets.

METHODS

Study area

The study was conducted in the Castro Verde Special Protection Area (SPA, Fig. 1), a cereal steppe landscape considered the most important site for Lesser Kestrel conservation in Portugal (Catry *et al.* 2009). The area is characterized by hot dry summers, fairly cold winters and low annual rainfall (500–600 mm; Moreira *et al.* 2005). Soils are mostly derived from schist and their thinness and deficient drainage greatly increase the risk of erosion; only a small percentage of the land area is suitable for agricultural use (Marta-Pedroso *et al.* 2007). For these reasons, cereals are cultivated under a low-intensity rotational system in which after 2 years of cereal cultivation the land is left uncultivated for 3–5 years (fallows) and used only for livestock rearing.

Lesser Kestrels return from their African wintering grounds and occupy their colonies – abandoned rural buildings and artificial nesting structures – mainly in early February (Catry *et al.* 2011) and typically lay four to five eggs in April and May. Previous studies carried out in the Castro Verde SPA (Teodósio 2000, Ventim *et al.* 2004) suggest that, during this period, mole crickets are the most important prey in terms of total biomass.

Data collection

Most raptors produce regurgitated pellets consisting of the indigestible remains of prey; thus pellet analysis is often used to study their diet (Marti *et al.* 2007). Lesser Kestrel pellets were collected every week in 12 colonies from 6 March to 18 April in 2007 and from 27 March to 29 April in 2008, coinciding with the pre-laying period. In each visit and colony, we collected 20 pellets from a pre-selected area comprising 50–100% of all occupied nests (to ensure a representative sample from each colony). To avoid sampling old pellets, the area was then cleared of any other pellets. Furthermore, in one colony (Par in Fig. 5, $n = 65$ pairs), 30 pellets were collected every week from March to June in both years to assess the occurrence of mole crickets throughout the entire breeding season. Overall, we analysed 3370 pellets and the presence and number of mole crickets per pellet were assessed by counting the number of mandibles or other non-digestible pieces with the help of a magnifying glass (Sutherland 2004).

In 2007 and 2008, the 12 Lesser Kestrel colonies were monitored on a weekly basis throughout the breeding season to assess laying date and clutch size. Colony size ranged from 15 to 70 pairs (mean ± se = 29.7 ± 20.3 in 2007 and 28.8 ± 19.9 in 2008). The furthest surveyed colonies were located 35 km apart from each other. In 2007, egg volume was estimated as $Vol(\text{mm}^3) = K \times L\,(\text{mm}) \times B^2(\text{mm})$, where $K = 0.51$ (Ortego *et al.* 2007), and the maximum length (L) and breadth (B) of eggs were measured to the nearest 0.01 mm using a digital calliper from a sub-sample of complete clutches in each colony (mean number of sampled clutches per colony ± sd = 13.8 ± 4.3, range = 7–21, $n = 776$ eggs).

To assess the impact of weather on mole cricket consumption, daily rainfall (available from http://www.snirh.pt) and temperature (available from http://www.ncdc.noaa.gov) data for the study period were obtained for the colonies located in the eastern and western parts of the study area, from the two closest weather stations (Fig. 1). To explain observed differences in the consumption of mole crickets amongst the sampled colonies (spatial variation), we estimated, for an area within a 3-km radius around each colony (the range typically used by foraging Lesser Kestrels; Franco *et al.* 2004), the length of watercourses from 1 : 25 000 military maps, the proportion of each class of soil (according to the Portuguese classification of soil suitability for agriculture) from soil capability maps (SROA 1962) and, in 2008, the current land use from data mapped in the field. All calculations were undertaken using ARCVIEW 3.2 (ESRI 1999).

To assess how habitat characteristics affected the presence of mole crickets we performed 318 point counts at the margins of small watercourses randomly scattered (minimum distance between two points = 600 m) within a 3-km radius around the colonies sampled for pellets (17–25 points per colony). We chose watercourses because in dry landscapes, such as Castro Verde, mole crickets are strongly associated with water sources (Ventim *et al.* 2004, I. Catry unpubl. data). In spring, male mole cricket stridulation attracts conspecific females and can be heard, by humans, from a distance up to 600 m (Bennet-Clark 1970). As males usually stridulate at dusk and throughout the night, all points were surveyed after sunset and the presence or absence of mole crickets was assessed by detecting stridulating males during a 5-min period at each point. Sampling was performed from the beginning of March to the first week of April, avoiding cold or rainy nights (Bennet-Clark 1970, I. Catry pers. obs.). At each point count, we characterized the watercourse in relation to its area of influence, stream width, presence of water, slope of the banks and structure of vegetation cover on both banks (presence of riparian vegetation, mean vegetation height, and percentage of herbaceous and graminaceous plants, rush and bare soil). As soil surface hardness (hereafter penetrability) can be important for subterranean species, we measured mean soil penetrability by dropping a sharpened iron stick from a fixed height and measuring the distance it penetrated the soil (Jones *et al.* 2006). In the field, the habitat in a radius of 300 m around each point was characterized by the percentage of fallows and cereal fields. All explanatory variables are summarized in Table 1.

Data analysis

For each colony, mean annual laying date and mean clutch size were calculated. We excluded second clutches and pairs known to include yearling birds, as these would have smaller clutches (I. Catry unpubl. data). We used simple linear regressions to test the relationship between breeding parameters and frequencies of occurrence (calculated as the

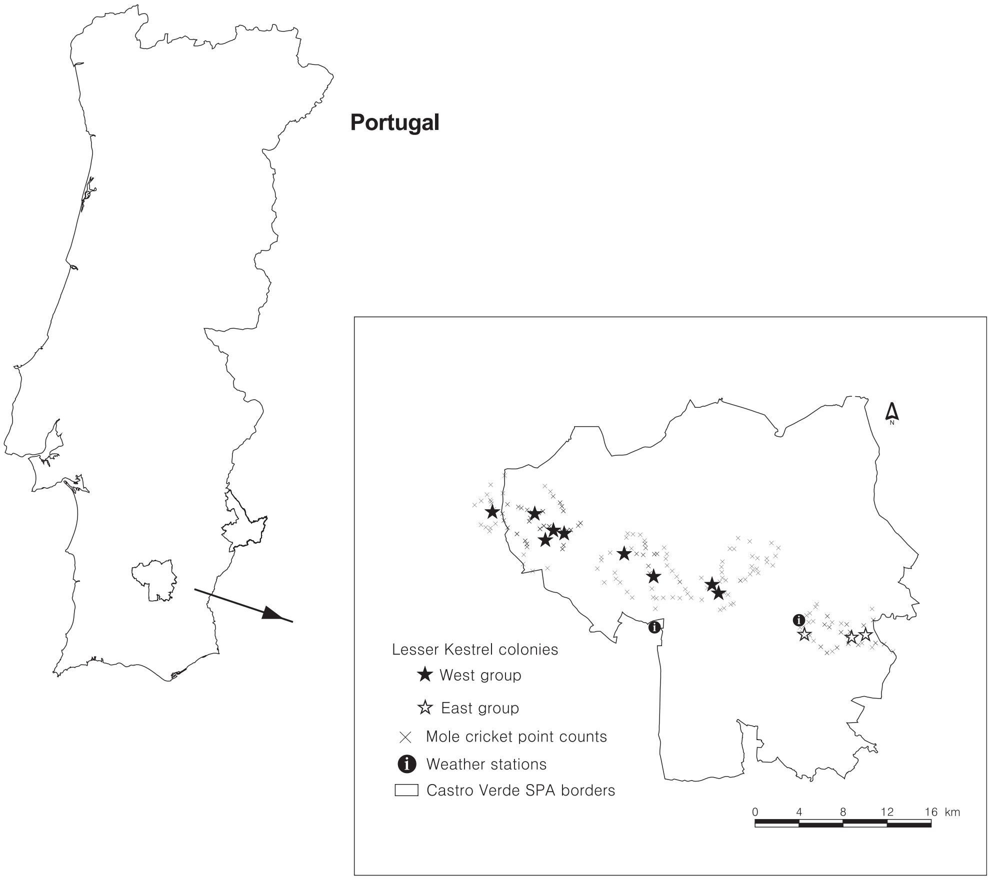

Figure 1. Spatial distribution of Lesser Kestrel colonies sampled for pellets (stars) and mole cricket point counts (crosses) in the study area. Black and white stars represent colonies included in the western and eastern part of the study area, respectively. The closest weather station for each group is shown.

percentage of pellets containing mole crickets) or abundance (mean number of mole crickets per pellet) of mole crickets in the diet of Lesser Kestrels during mate-feeding. The mate-feeding period started 30 days before the mean laying date (I. Catry unpubl. data; Franco 2003), when females significantly increase body mass for egg production and laying (Donázar *et al.* 1992). In 2008, one colony was excluded from the analysis due to its small size ($n = 7$ pairs) and the difficulty of accessing all nests to measure breeding parameters.

The consumption rates of mole crickets (number of individuals per pellet) across the breeding season reflect their availability in the areas around the colonies. For our study area, Ventim *et al.* (2004) found a correlation coefficient of 0.96 between the abundance of mole crickets in field samples and its occurrence in Lesser Kestrel pellets. Thus, we examined the relationship between temporal variation in mole cricket consumption in March and April and possible predictors of this variation (precipitation, daily minimum temperature and week of sampling) using a generalized linear mixed model (GLMM). Changes in mole cricket abundance were defined as

$$r = \ln(N_t + 1) - \ln(N_{t-1} + 1)$$

where N_t and N_{t-1} represented the mean number of mole crickets found in pellets at one colony in weeks t and t–1. Weekly changes in mean precipitation and average daily minimum temperature were calculated using the same approach. Colony and year were fitted as random factors. To assess the observed spatial variation in mole cricket consumption among the 12 sampled colonies, we used a GLMM to test the relationship between mean number of mole crickets per pellet and two variables: proportion of soil classes A, B and Ch and total length of watercourses within a 3-km radius around each colony. Soil classes A, B and Ch are the most suitable classes for agriculture and are characterized by a lower risk of erosion and a higher capacity to retain water; classes D and E have high risk of erosion and low or no suitability for agriculture. We grouped together classes A, B and Ch because of their low occurrence in the study area. Because annual precipitation may play an important role in terms of the amount of water retained in the soil and streambeds, we also tested the interaction between year (2007 and 2008, a drier and wetter year, respectively) and each of the predictors. Colony was fitted as a random factor. For both GLMM models we assumed a Gaussian error distribution and an identity link function. Correlation coefficients between the explanatory variables were not large ($|r| < 0.5$), thus all variables were included in the analyses. Model selection procedures followed Burnham & Anderson (2002) using Akaike's information criterion (AIC). In both datasets, the ratio between the number of observations and parameters (n/k) was < 40, so we calculated the bias-adjusted AIC (AICc) for the performed analysis. For each model we calculated the Akaike weight (ωi), which is the probability that model *i* would be selected as the best-fitting model if the data were collected again under identical circumstances (Burnham & Anderson 2002). The relative importance of each predictor variable was estimated by adding ωi across all the models in the set where that variable occurs. The fit of the model was assessed using model deviance, representing the percentage of deviance explained by the model.

Two logistic regression models (with a binomial error distribution and a logit link function) were used to investigate habitat selection by mole crickets in the study area. The first model aimed to identify the habitat variables that most influenced the probability of occurrence of mole crickets at sampled watercourses and included all variables. The second model included only variables that can be manipulated in a management programme (Table 3). A Spearman correlation matrix was generated to assess colinearity between variables; if a pair of variables had a correlation coefficient > 0.5 the variable that yielded the highest AICc value from univariate models was removed. Moreover, to reduce the number of possible explanatory variable combinations to a manageable level, we removed two more variables from different categories of variables (soil cover and land use, Table 1) based on AIC rank from univariate models. We constructed a set of alternative models from all linear combinations of the remaining predictors and fitted each model to the presence/absence data. Again, we used information-theoretic methods with AICc to rank all possible parameter subset models and assessed the Akaike weight (ωi) for all models. Because no single model was clearly superior to others in the set, we adopted a multi-model inference approach for estimating the standardized coefficient of each variable using the weighted average of the corresponding coefficient in all of the candidate models (Burnham & Anderson 2002). The accuracy of the predictions was evaluated using the area under the curve (AUC, Manel *et al.* 2001), which represents the probability that a random chosen observation will be correctly classified. Values of AUC of 0.5–0.7 indicate low accuracy, 0.7–0.9 useful applications and > 0.9 high accuracy (Manel *et al.* 2001).

All analyses were performed with R 2.11.1 (R Development Core Team 2010).

RESULTS

Mole cricket consumption and breeding parameters of Lesser Kestrels

Mole cricket consumption (mean number of mole crickets per pellet) by Lesser Kestrels during the mate-feeding period was negatively correlated with colony laying date in both years ($F_{1,10} = 5.6$, $P = 0.039$, $r^2 = 0.36$ and $F_{1,9} = 12.5$, $P = 0.006$, $r^2 = 0.58$, for 2007 and 2008, respectively; Fig. 2). The same relationship was found when comparing the proportion of pellets containing mole crickets with laying date ($F_{1,10} = 6.3$, $P = 0.03$, $r^2 = 0.39$ for 2007 and $F_{1,9} = 7.7$, $P = 0.02$ $r^2 = 0.46$ for 2008). Furthermore, we found a positive relationship between mole cricket consumption and clutch size in 2008 ($F_{1,9} = 5.5$, $P = 0.04$, $r^2 = 0.38$) but not in 2007 ($F_{1,10} = 0.8$, $P > 0.05$, $r^2 = 0.07$). Egg size (mean volume), estimated only in 2007, was positively correlated with mean number of mole crickets per pellet ($F_{1,10} = 5.5$, $P = 0.04$, $r^2 = 0.36$).

Mean laying dates of surveyed colonies in 2007 and 2008 did not differ significantly (mean laying date = 118.4 ± 3.0 and 119.3 ± 2.8 for 2007 and 2008, respectively; Mann–Whitney U-test for

Table 1. Independent variables analysed to investigate habitat selection by mole crickets.

Variable	Description	Units/class
Water course variables		
Width of the area of influence	Distance from the streambed to the beginning of the closest habitat (fallow or cereal) (< 1, 1–2, 2–4, 4–6, 6–9, > 9 m)	1–6
Stream width	Measured within a set area of the point count (< 1, 1–2, 2–4, 4–6, 6–9, > 9 m)	1–6
Water	Absent, present	0–1
Water depth	Average of 10 measurements taken along the water course	cm
Soil penetrability	Average of five samples	cm
Human intervention level	Streambed: no intervention, ploughed or cultivated	0–1
Margin slope	Flat to steep	0–3
Soil cover variables		
Vegetation height	Average of 50 measurements in a 1 × 300 m strip along both margins of water courses (0–10, 11–20, 21–30, 31–40, > 40 cm)	1–5
Presence of riparian vegetation	Absent; present	0–1
Percentage of herbaceous plants	Estimated in a 1 × 300 m strip along the margins of water courses (< 1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–100%)	0–5
Percentage of graminaceous plants		
Percentage of rush		
Percentage of bare soil		
Land-use variables		
Percentage of fallow	Estimated in the field in a radius of 300 m around the point count (< 1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–100%)	0–5
Percentage of cereal		

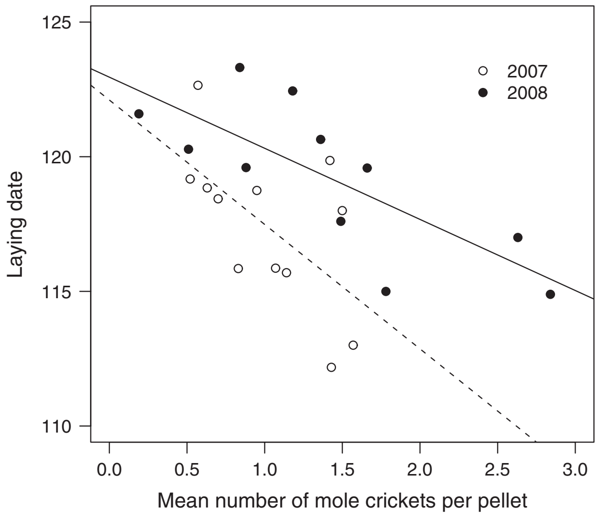

Figure 2. Effect of mole cricket consumption (mean number of individuals per pellet) during mate-feeding on Lesser Kestrel laying date in 2007 ($P < 0.05$) and 2008 ($P < 0.01$). Each circle corresponds to one colony; laying dates refer to day of the year (e.g. day 120 corresponds to 30 April in 2007 and 29 April in 2008 given the different length of February in the two years).

paired data, $V = 16$, $P = 0.15$), nor did mole cricket consumption during the 30-day mate-feeding period (mean number of mole crickets per pellet = 1.03 ± 0.38 and 1.41 ± 0.78 for 2007 and 2008, respectively; $V = 15$, $P = 0.12$).

Drivers of temporal and spatial variation in mole cricket consumption

Figure 3 shows the variation of mole cricket abundance in the diet of Lesser Kestrels from March to June. Despite the inter-annual variation, there was a pattern of decreasing abundance of mole crickets across the breeding season (GLMM: $t = -0.20$, $P < 0.001$). Mole cricket abundance in Lesser Kestrel pellets declined markedly from May onwards. Results of the GLMM analysis show that observed changes in mole cricket consumption were positively and significantly associated with temporal changes in mean precipitation and average daily minimum temperature in two consecutive weeks (Table 2). Both predictors entered the model with the lowest AICc value with very high selection probabilities ($\Sigma\omega i > 0.99$), explaining 42% of the observed variance (Table 2). More mole crickets were eaten following an increase in either precipitation or minimum temperature from 1 week to the next (Fig. 4a,b).

Figure 5 shows the spatial variation of mole cricket consumption in the 12 Lesser Kestrel colo-

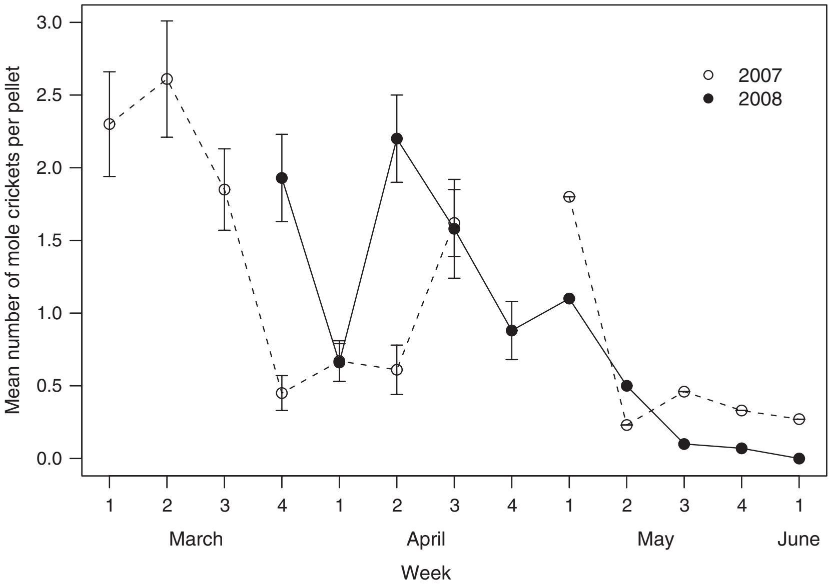

Figure 3. Temporal variation in mole cricket consumption by Lesser Kestrels along the 2007 and 2008 breeding seasons. Mean values (circles) and standard errors (bars) are shown for 12 colonies ($n = 250$ pellets/week/year); from May onwards pellets were collected in a single colony (Par, $n = 30$ pellets/week/year).

nies for the coincident sampling period in 2007 and 2008. Overall, more mole crickets were consumed in 2008 than in 2007 (mean number of mole crickets per pellet = 1.67 ± 0.73 and 0.89 ± 0.31 for 2008 and 2007, respectively; Mann–Whitney U-test for paired data $V = 6$, $P = 0.007$), coinciding with a generally higher total rainfall in 2008. Nonetheless, in 2008, three colonies (Psm, Bel, Boi, Fig. 5) had significantly lower intake (Mann–Whitney U-test $U = 366$, $P < 0.001$), standing at similar levels to 2007. The three colonies were located in the eastern part of the study area and in 2008 there were marked spatial differences in rainfall pattern (Fig. 4c). Results from the GLMM model to investigate the spatial (inter-colony) variation of mole cricket consumption revealed a strong positive effect of the interaction between year and the presence of soil classes A, B and Ch in explaining the variation of mole cricket consumption in the sampled colonies (Table 2); significantly more mole crickets were eaten in colonies surrounded by a higher proportion of these soil classes in 2008 (Fig. 4d). In contrast, the density of watercourses around the colonies and its interaction with year did not enter the best models, showing very low selection probabilities ($\Sigma\omega i < 0.001$; Table 2). Finally, land use around the colonies (assessed in 2008) was not associated with mole cricket consumption by Lesser Kestrels ($F_{1,10} = 0.35$, $P = 0.56$ and $F_{1,10} = 2.45$, $P = 0.15$ for proportion of cereal and fallow fields, respectively).

Habitat selection by mole crickets

Correlations exceeding 0.5 were found between the following pairs of variables: area of influence and stream width ($r = 0.52$), soil penetrability and presence of water ($r = 0.63$), water depth ($r = 0.60$) and presence of riparian vegetation ($r = 0.52$), and between presence of riparian vegetation and percentage of rush ($r = 0.51$). To reduce the effect of multicolinearity, we removed (based on AIC comparisons of the univariate models) the variables stream width, presence of water, water depth, presence of riparian vegetation and percentage of rush from further analysis (presence of riparian vegetation was included in the model only with manageable variables because soil penetrability was not considered in this approach). Moreover, we removed the variables percentage of fallow and percentage of graminaceous plants from the sets of soil cover and land-use variables as they were not included in the most parsimonious univariate models for all explanatory variables within each set.

Table 2. Top two competing models (GLMM) of factors affecting the temporal and spatial variation of mole cricket consumption by Lesser Kestrels. In the first approach (temporal variation), colony and year were fitted as random terms. Models are ranked according to the Akaike Information Criterion, corrected for small sample sizes (AICc). The ΔAICc indicates AICc differences between a particular model and the best-fitting model. Akaike weights (ωi) indicate the contribution of each model to the average of all candidate models. Coefficients (± se) are shown for variables included in a particular model while blank spaces represent the exclusion of variables. Σωi for each predictor variable shows the sums of Akaike weights for all possible models in which the predictor variable was included. Σωi reflects the relative importance of each variable. Dev is the total amount of deviance explained by each model.

Temporal variation

	Variables						
Model	Precipitation	Min. temperature	Week	AICc	ΔAICc	ωi	Dev
1	0.36 ± 0.04	0.92 ± 0.13		112.9	0	0.971	0.42
2	0.36 ± 0.04	0.91 ± 0.14	0.02 ± 0.02	120.3	7.42	0.024	0.37
Σωi	> 0.99	> 0.99	0.02				

Spatial variation

	Variables								
Model	Soil quality	Year	Soil quality × Year	Water courses	Water courses × Year	AICc	ΔAICc	ωi	Dev
1	−0.21 ± 1.47	−0.3 ± 0.17	7.7 ± 1.3			35.5	0	0.999	0.63
2	3.67 ± 1.33	0.52 ± 0.23				51.47	15.96	< 0.001	0.24
Σωi	> 0.99	> 0.99	> 0.99	< 0.001	< 0.001				

The multi-model inference approach for the analysis of mole cricket habitat selection was justified by the relatively large number of candidate models where $\Delta\text{AICc} < 2$ (Supporting Information Table S1). Multi-model averaged estimates are summarized in Table 3. The first model, which considered all variables, suggested that soil penetrability had the largest relative importance ($\Sigma\omega i > 0.99$) compared with all other variables, showing a positive relationship with the occurrence of mole crickets (Table 3). The 95% confidence intervals surrounding multi-model weighted coefficients for all predictor variables other than soil penetrability spanned zero, indicating that these factors had limited effect in predicting the occurrence of mole crickets (Table 3). The second model, based only on variables amenable to management, suggests that the probability of occurrence of mole crickets increases with the presence of riparian vegetation and decreases if streambeds are ploughed or cultivated (Table 3). These variables had larger selection probabilities ($\Sigma\omega i > 0.99$ and 0.97, respectively) compared with other manageable variables (Table 3).

The models had good overall predictive ability according to the AUC value (0.80 and 0.71 for the first and second models, respectively), showing a useful application of the model predictions.

DISCUSSION

Mole crickets and Lesser Kestrel breeding success

Colonies with higher frequency of occurrence and greater consumption of mole crickets laid earlier, suggesting that inter-individual differences in the time of breeding could be caused by differential acquisition of food and so supporting previous experimental studies showing that females provided with extra food lay earlier (Aparicio & Bonal 2002). Mole cricket consumption in the mate-feeding period was also found to be positively associated with clutch size and egg size. Larger clutches can produce a higher number of hatchlings and larger eggs contain a greater absolute amount of nutrients than do smaller eggs and may play an important role in hatching survival (Nisbet 1973, Valkama *et al.* 2002).

Mole cricket abundance in pellets may also conceal gender variation, as it was not possible to differentiate between pellets produced by males and

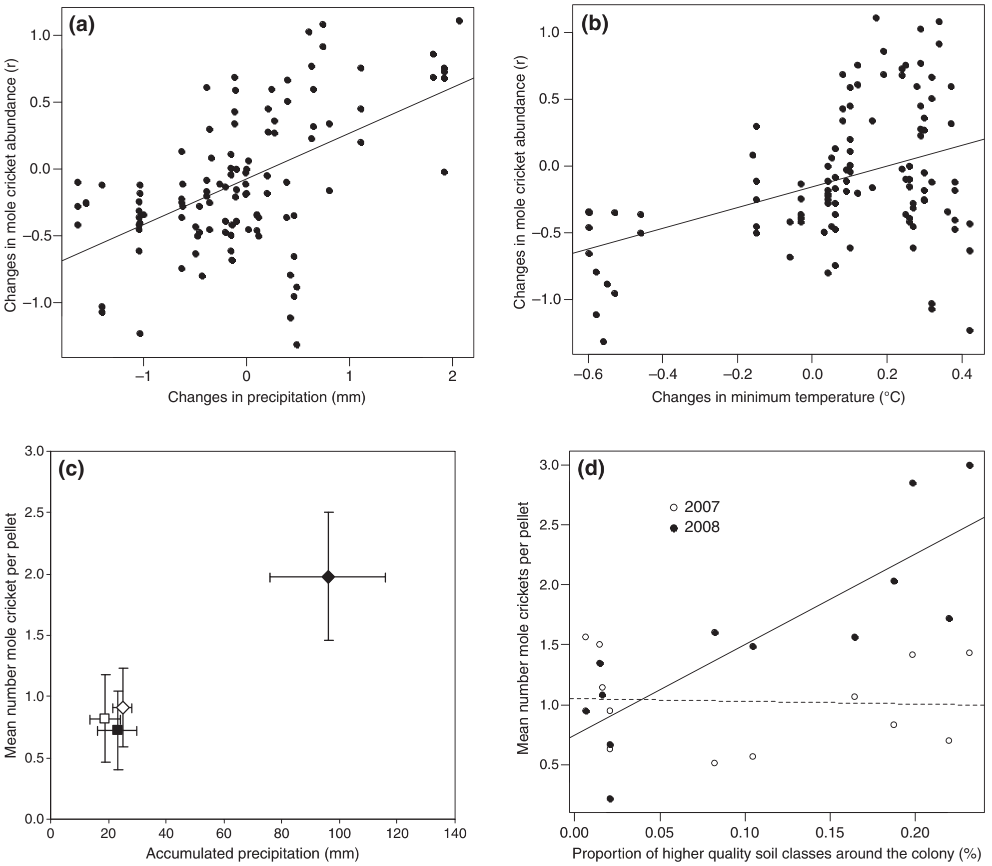

Figure 4. Effect of weekly (a) changes in mean precipitation (mm) and (b) changes in mean daily minimum temperature (ºC) on mole cricket consumption by Lesser Kestrels; (c) comparison between mole cricket consumption in eastern (squares) and western (diamonds) Lesser Kestrel colonies in 2007 (white shapes) and 2008 (black shapes) in relation to accumulated precipitation (mm) registered during pellet sampling in the closest weather stations and (d) influence of higher quality soils (classes A, B and Ch) on mole cricket consumption by Lesser Kestrels in the sampled colonies in 2007 (white dots and dashed line, $P > 0.05$) and 2008 (black dots and solid line, $P < 0.05$).

females. The average diet of Lesser Kestrels, across males and females, is thought to consist mainly of smaller prey items, but during the mate-feeding period, females are generally fed larger prey by their mate (Bijlsma *et al.* 1988). Mole cricket consumption by females may therefore be greater than the value we present, highlighting the importance of this prey in a period of high energy demand for both egg production and laying. Finally, the high abundance of mole crickets found in pellets in early March (also observed by Ventim *et al.* 2004), after Lesser Kestrels return from Africa, reinforces the potential role of this prey in restoring the fat reserves depleted during migration, as previously suggested by Choisy *et al.* (1999).

Temporal and spatial variation of mole cricket consumption

The occurrence of mole crickets in the diet of Lesser Kestrels among our studied colonies can be explained by prey phenology, physiology and ecological requirements. Mole crickets spend most of their lives underground, inaccessible to avian predators. During spring, however, the male's courtship song is produced from the entrance of a burrow to attract flying females (Bennet-Clark 1970), causing a peak in mole cricket accessibility for avian predators. Variation in mole cricket consumption in March and April was strongly associated with weather conditions (mean values of

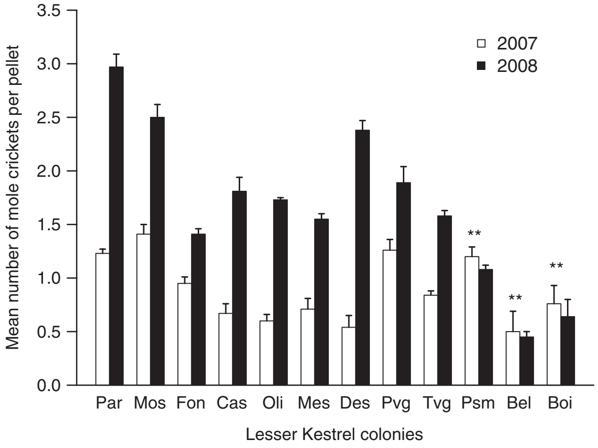

Figure 5. Spatial variation in mole cricket consumption by Lesser Kestrels in 12 colonies in 2007 and 2008 in Castro Verde. Mean values and standard errors reported for the period between the last week of March and the third week of April (*n* = 80 pellets/colony/year except for Par colony, where *n* = 120). In contrast to the general pattern of higher mole cricket consumption in 2008, Lesser Kestrels from three colonies (**) consumed fewer mole crickets in 2008.

minimum daily temperature and rainfall), which affect both habitat suitability for mole crickets and their activity. Mole crickets are cold-blooded and remain dormant underground during cold periods (Potter 1998). Previous studies showed that pulse rates of calling songs are a function of soil temperature (Bennet-Clark 1970, Ulagaraj 1976), suggesting that small increases in air temperature are likely to influence mole cricket activity, as shown by the increase in the mean number of individuals found in pellets. On the other hand, rainfall influences the amount of water in the streambeds and soil penetrability, an important ecological requirement for mole crickets, as revealed by the habitat selection analysis. Mole crickets require damp, but not waterlogged, soil to build galleries (HMSO 1995). In wet weather the male insect digs openings from the main burrow system to the surface (Bennet-Clark 1970). When the air is very dry or during drought, mole crickets risk dehydration and will dig deeper into the soil to find moisture until rain softens the soil (Potter 1998). Therefore, in an arid area such as Castro Verde (around 500 mm annual precipitation, mainly between November and March), a small increase in precipitation is predicted to have a positive influence on mole cricket availability and their consumption by Lesser Kestrels. The annual decline of rainfall from May onwards and the drying up of many water courses lead to a decline in mole cricket accessibility and therefore a reduction in consumption by Lesser Kestrels. Moreover, annual and site-specific climatic conditions impacted mole cricket availability, as shown by the comparison between the eastern and western colonies in 2007 and 2008.

Mole cricket consumption in the two study years was higher in colonies surrounded by a higher proportion of good quality soils (classes A, B and Ch). Within the Castro Verde area, more than 80% of

Table 3. Logistic regression results for all variables and variables amenable to management considered in predicting occurrence of mole crickets in margins of water courses around Lesser Kestrel colonies. We derived coefficients and associated confidence intervals for each predictor variable from multimodel inferences using all possible parameter subsets and Akaike weights (ωi). The sum of Akaike weights (Σωi) for each predictor across all candidate models containing that predictor is provided as a measure of relative variable importance. Factors are deemed to have a significant influence on effect size where 95% confidence intervals for estimated coefficients do not span zero; these cases are indicated in bold.

Model	Variable	Coefficient	95% CI		Σ ωi
All variables	Intercept	−3.760	−4.910	−2.610	
	Area of influence	−0.0064	−0.110	0.098	0.27
	Soil penetrability	**0.676**	**0.489**	**0.863**	**> 0.99**
	Margin slope	0.0325	−0.119	0.184	0.31
	Vegetation height	0.0264	−0.075	0.128	0.34
	Percentage of herbaceous plants	0.011	−0.044	0.066	0.30
	Percentage of bare soil	0.072	−0.154	0.298	0.42
	Percentage of cereal	−0.146	−0.340	0.049	0.81
	Human intervention level	−0.767	−2.830	1.300	0.53
Variables amenable to management	Intercept	−1.13	−1.680	−0.578	
	Riparian vegetation	**1.54**	**0.959**	**2.120**	**> 0.99**
	Vegetation height	0.002	−0.008	0.012	0.32
	Percentage of cereal	−0.05	−0.189	0.088	0.49
	Human intervention level	**−2.24**	**−4.38**	**−0.099**	**0.97**

soils belong to classes D or E, with either no or very low suitability for agriculture and very high erosion risks (SROA 1962). More suitable soils for agriculture are less prone to severe erosion and are more likely to keep some moisture and to have higher penetrability and thus higher suitability for mole crickets. However, a strong interaction between soil quality and year suggests that mole cricket availability is likely to be dependent on the combination of soil quality and annual precipitation. In contrast, the density of watercourses around colonies was not a good predictor of mole cricket availability for Lesser Kestrels. Small watercourses are very frequent around all colonies (range of length = 75–95 km) and other variables, such as presence of water, soil penetrability, presence of riparian vegetation and human intervention level of streambeds, are likely to be better indicators of probability of occurrence of mole crickets.

Threats to mole cricket occurrence and management implications

Among variables amenable to management intervention, the probability of occurrence of mole crickets was positively influenced by the presence of riparian vegetation and negatively influenced by the human intervention level in streambeds. While the presence of riparian vegetation might reflect higher penetrability soils (the two variables are positively correlated), tillage and sowing of streambeds may destroy tunnels and galleries, causing mortality of mole crickets. Moreover, the mechanical cultivation of streambeds can lead to a rapid degradation of soil organic matter, a reduction of water retention and fertility losses. Thus, the prohibition of ploughing streambeds and the promotion of buffer zones (uncultivated strips with riparian vegetation) along watercourses could increase water and nutrient retention, with direct benefits to soil penetrability and food supply for mole crickets and hence Lesser Kestrels. The implementation of these recommendations is crucial in areas such as Castro Verde, where most soils have already high risks of erosion (SROA 1962). The establishment of buffer strips along watercourses is currently being implemented under the CAP Pillar 1 in some countries (Cooper *et al.* 2009) and is promoted, among other measures, in the Castro Verde agri-environmental scheme. Nonetheless, a decline in financial support to farmers under this scheme led to a significant decline in the area affected, from 61% in 1999 to < 15% by 2007 (CMCV 2010), jeopardizing the conservation of watercourses and their suitability for mole crickets. We recommend that further studies should focus on assessing the suitability of both natural temporary and artificial ponds for mole crickets (point counts performed at 25 ponds revealed that mole crickets were present in the margins of 54% of surveyed ponds), as these water bodies might enhance prey availability around Lesser Kestrel colonies and play an important role in water retention in drier years.

Land-use management can play a crucial role in improving soil resilience not only under present agricultural practices but with the predicted future increase in the frequency of climatic events such as droughts and floods. As a consequence, this would increase habitat suitability for mole crickets with likely benefits for Lesser Kestrels and many other steppe-bird species known to consume this prey, such as Great Bustard O*tis tarda* and Little Bustard *Tetrax tetrax* (Jiguet 2002, Rocha 2006), Montagu's Harrier *Circus pygargus* (Salamolard *et al.* 2000), Little Owl *Athene noctua* (Tomé *et al.* 2008) and Woodchat Shrike *Lanius senator* (Sandor *et al.* 2004).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Best logistic regression model subsets (ΔAICc < 2 and < 7 for all variables and manageable variable models, respectively) of factors affecting the occurrence of mole crickets in Castro Verde, Portugal. Models are ranked according to the Akaike information criterion, corrected for small sample sizes (AICc). The ΔAICc indicates AICc differences between a particular model and the best-fitting model that had the smallest AICc. Akaike weights (ωi) indicate the contribution of each model to the average of all candidate models. Variables included and not included in a particular model are indicated with ones and zeros, respectively. Area – width of the area of influence; Pen – soil penetrability; Slop – margins slope; Vegh – vegetation height; Herb – percentage of herbaceous plants; Rip Veg – presence of riparian vegetation; Bar Soil – percentage of bare soil; Cer – percentage of cereal; Hil – human intervention level.