Evidence of prey depletion around lesser kestrel *Falco naumanni* colonies and its short term negative consequences

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Predation may reduce prey numbers in such extent that prey may be depleted, which has negative effects on predator populations. Prey depletion would be more likely when the number of predators increase and/or concentrate their activity in a certain area, as is the case of colonial birds. As a matter of fact, food depletion due to intraspecific competition is considered a major cost of coloniality, and several studies have shown indirect evidence of this. However, no direct measures of food depletion have been provided along with its consequences for the fitness of the colony inhabitants. We carried out a field study with the lesser kestrel *Falco naumanni*, a raptor that breeds in colonies ranging from two to dozens of pairs. During the nestling period we sampled the main prey of the kestrels around different sized colonies at increasing distances. At the same time, we recorded hunting distances and prey delivery rates to the nest. In addition, we monitored the reproductive success in colonies of different sizes. Lesser kestrels feed their nestlings mainly with grasshoppers and these prey became depleted through the season in the surroundings of the large colonies. Prey depletion made kestrels fly longer distances to forage and prey delivery rates to the nest decreased. Lower feeding rates were not compensated by bringing larger prey, hence, the net amount of energy provided to the chicks decreased with the date in large colonies. By contrast, none of this occurred around small colonies, where both prey abundance and hunting distance remained constant throughout the season. As a consequence, the seasonal decline in the reproductive success (number of fledglings and fledgling body condition) was greater the larger the colony. Thus, these results evidence that food depletion and its fitness costs are related to colony size, as they are suffered by the kestrels breeding in large colonies but not by those settled at small ones. Finally, the consequences of prey depletion on the demographic dynamics and the regulation of colony size are discussed.

Predators may deplete prey populations, which has subsequent negative consequences on predator fitness and may ultimately regulate predator numbers as well (Begon et al. 1996). Prey depletion is more probable when predation pressure is concentrated on a smaller and specific area. In this context, central place foraging may provoke prey depletion in the areas surrounding the central point; for instance, some studies with solitary breeding birds have shown that prey numbers are significantly reduced in the areas around the nest (Jäättii et al. 2001, Sanz 2001). In the case of colonial birds, prey depletion around the nests is more likely because predation pressure around the colony is stronger due the number of conspecifics foraging in the same area. Therefore, prey depletion is considered a major cost of coloniality (Ashmole 1963, Willklund 1982, Furness and Birkhead 1984, Möller 1987, Hoi et al. 2002).

Most evidence of prey depletion is indirect and includes reduced feeding rates (Lewis et al. 2001) or a worse diet quality in larger colonies (Forero et al. 2002). In some of these cases it cannot be ruled out that prey depletion, and not interference between individuals, is the cause underlying the decrease of feeding rates, as has been proved to happen in oystercatcher foraging flocks (Goss-Custard et al. 2001). Also, it has been argued that food depletion around colonies could take place because prey escape due to the intense predation pressure. This could happen in the case of highly mobile prey, like fish shoals around large gannet *Morus bassanus* colonies (Lewis et al. 2001); however, no measure of prey behaviour or abundance was provided either. Moreover, even in one study in which prey availability was measured directly, it was done just once at the end of the breeding season. Birt et al. (1987) showed that fish population densities increased with distance from two cormorant *Phalacrocorax auritus* colonies. Although this result suggests that cormorants depleted prey, more conclusive evidence would have required a series of samples, both before and after birds began breeding.

Colonial birds can forage close to the colony so as to maximise food delivery to the nest. However, if prey become depleted in the closer areas along the breeding
season they may go to more distant areas to forage, where food availability is higher. Longer foraging trips may reduce prey delivery rates to the nest (Møller 1987, Lewis et al. 2001), but this could be compensated by bringing larger prey to the nestlings (Orians and Pearsons 1979). If the size of the prey delivered is not increased, then the net food intake of the chicks could fall, reducing their body condition and threatening their survival. Prey depletion is predicted to be a density-dependent cost, as it is expected to be more likely the larger the number of breeding pairs in the colony. In this sense, competition for food and prey depletion could regulate colony growth, as the reproductive success could decrease after the colony reaches a certain size (Ashmole 1963).

In order to study prey depletion and its related costs in colonial birds we carried out a study with the lesser kestrel *Falco naumanni*, a bird of prey that breeds in colonies ranging from two to some dozens of pairs (González and Merino 1990). We carried out direct measures of prey abundance and recorded adult hunting behaviour along the season in different sized colonies. The main aims of the study were to find out: 1) Where kestrels concentrated their foraging during the breeding season and whether it provoked a progressive prey depletion around the colonies depending on colony size. To do so we measured the seasonal changes in prey abundance at different distances from each colony. 2) In case depletion takes place, we wanted to know if the kestrels flew longer distances to forage the later the date and the effect of hunting distance on prey delivery rates to the nest. 3) Whether kestrel parents may compensate for lower prey delivery rates by bringing larger prey to the nestlings. 4) Regardless of any compensation in foraging behaviour, we wanted to assess whether prey depletion may reduce reproductive success, which could be more probable the larger the colony.

**Material and methods**

**Study area and species**

The study was conducted on a lesser kestrel population located in La Mancha, provinces of Ciudad Real and Toledo, Central Spain (39°20’N, 3°15’W). The study area has an extent of approximately 1,000 km², and was set in a plain used for agriculture, cultivated mainly with barley, wheat, legumes and vineyards. Lesser kestrels form breeding colonies in abandoned field houses and nests are usually placed under tiled roofs or inside holes in the walls. The sizes of the colonies studied ranged from two to sixty pairs, the size of the buildings is rather similar and not related to the number of breeding pairs. Lesser kestrels are migrants in our study area and normally arrive between January and March (depending on the year and age), and lay between three to five eggs (4.08 ± 0.81 SD) in one clutch per year. Egg laying normally takes place between the second fortnights of April and May (range April 15–June 6) (Aparicio and Bonal 2002). Diet is based on insects; grasshoppers and field crickets are the main prey (Franco and Andrada 1974, this study), especially to feed nestlings.

**Observation of hunting behavior**

We recorded hunting behaviour with two purposes. First, to assess in which areas around the colony kestrels focused their foraging and exerted stronger predation pressure. Second, we wanted to know whether kestrels flew longer distances to forage in response to prey depletion in the surroundings of the colony. We monitored hunting behavior in two different seasons (1999 and 2000). Hunting behaviour was quantified throughout the nestling period, so that we could identify any gradual depletion of prey and increased foraging distances over the course of this period. In the first year we monitored a large colony of 60 pairs. In the second year, besides that colony, we also surveyed three small ones with 8, 7 and 3 breeding pairs.

In order to record hunting behavior, the observer chose randomly the order to monitor the kestrels of a colony. Once a certain kestrel was chosen, observation was focused on its nest until it appeared delivering prey. If the kestrel did not appear within 15 min, it was assumed that it was not feeding the nestlings and monitoring continued with the following individual. This waiting time proved to be enough, as data on kestrels hunting for the chicks showed that the average duration of the hunting trips was 5 min 25 s and all trips lasted less than 15 min. The monitoring of hunting behavior was made visually always by the same person placed at elevated points near the colony with a telescope (20–60×). Because the colonies were placed in old field houses surrounded by very large flat areas, the observer was able to follow single kestrels in a radius of up to three kilometers approximately. Observation finished when the kestrel returned to the colony and fed the chicks. We recorded the duration of the whole hunting trip (from leaving the colony until the kestrel returned with a prey). The points where attacks and captures took place were marked on aerial photographs (1:5,000). This method proved to be very accurate in assigning reliable attack points and hunting distances. In fact, the distance from the capture point to the colony measured in the photograph was highly correlated with the time invested by the kestrel flying between these two places ($r^2 = 0.64, P < 0.001$).

In 61% of the observations it was possible to see the place where the prey was captured; in the rest the kestrel was lost after the attack landing and we did not know whether the attack was successful. In these cases, the place where it was lost was registered as a hunting point. We consider this accurate because, on the numerous occasions when it was possible to observe complete hunting trips (i.e. till the adult came back to the colony with a prey), attack success was over 86%. Thus, the probability of lesser kestrels having captured prey was very high, even for those cases in which we were not able to ascertain the success of an attack. In any case, the distance at which the individual had attacked would reflect both the spatial hunting pressure around the colony and the changes in the spatial distributions of the prey.

**Habitat distribution around the colonies**

There were three main different habitats in the vicinity of the lesser kestrel colonies, namely grasslands, cereal and...
legume fields. Although the habitat is quite uniform in our study area at a large scale, we wanted to make sure that the habitat around the study colonies was similar to control for any potential effect of the type of habitat on the results. We used a map of the area around the colonies in which we sampled prey and recorded hunting behaviour and we visited all the fields to record the type of habitat at each one. We did it in each year, and then we entered these data in a GIS (Geographical Information System) to calculate the proportion of each habitat around each colony. Thus, we assessed a priori that the proportion of each habitat was similar between colonies and that habitat distribution was not biased regarding the distance to the colony.

Prey sampling

We were interested in assessing the temporal changes in prey availability around the colonies through the nestling period, from late May to July. Prey sampling around the colonies was carried out in three different years (1999, 2001 and 2003). The techniques that we used to sample invertebrates changed through the course of the study because the methods needed to evolve as we learned more about our study system and more clearly identified the data that needed to be collected.

In 1999 we performed a pilot sampling around a large colony of 60 pairs. We monitored a large surface, as we had not measured yet the area surrounding the colony in which most hunting was concentrated. We used pitfall traps to sample 17 patches randomly distributed around the colony in a radius of 2,150 m. Such traps have long been used to sample beetles and other walking arthropods, but they can also be employed to trap Orthopterans, other terrestrial arthropods and small vertebrates. In this first year we used this sampling method because we wanted to catch all the potential prey of the kestrels. In the case of saltatorial insects, like grasshoppers, other methods are commonly employed, mainly to increase sample size. Nevertheless, our consistent use of pitfall traps allows as comparing grasshopper abundances between sampling patches too. Sampling patches were placed in three different habitats where the human land use and the vegetation structure were internally uniform (grassland, cereal or legume field). These habitats occupied most of the territory and their distribution was not biased regarding the distance to the colony, avoiding any potential confounding effect on prey abundance and its seasonal changes. Pitfall traps were filled with glycerol to ensure insect preservation and checked every 15 days; between checks traps remained open.

In 2001 we sampled again the same large colony studied in 1999, but we extended the sampling to three small ones with 8, 7 and 3 breeding pairs. Our data from 1999 confirmed that grasshoppers were the main prey (see below), consistent with previous studies on this raptor (Franco and Andrada 1977). Hence, in 2001, we focused on these arthropods and used a methodology (transects) more specific for this taxa. We sampled 10–18 sites around each colony ranging from 170 to 2,100 m. Sampling sites were located at the same habitats (grassland, cereal or legume field) as in 1999. Again, habitat distribution around the colonies was independent of the distance to the colony and did not change substantially among the different colonies, as the agricultural landscape in our study area is quite uniform over a large spatial scale. At each sampling site we sampled five transects of 50 m each one, noting the grasshoppers observed within a band of 1 m. As in the previous year, all patches were sampled every 15 d simultaneously at all colonies. Samplings were done at the time of the day of maximum activity of the grasshoppers (from 12 GTM to 18 GTM) in all cases, moreover, sampling order did not follow a regular pattern with respect to the distance to the colony to avoid any potential biases.

In 2003 we changed our data collection protocol, increasing the number of kestrel colonies studied, specifically in order to look at variability in prey depletion with the size of the colonies. We carried out an extensive sampling around 12 different sized colonies, ranging from 4 to 60 breeding pairs. Sampling was concentrated in an area of a radius of 1km around each colony, as in previous years we had found that this is the surface in which 80% of the prey captures take place (see below). We sampled from 10 to 14 patches around the colonies, in the same habitats as in previous years (grassland, cereal or legume field). The number of sampling patches at each habitat was proportional to the surface that it occupied around each colony. Each colony was sampled twice, first at the end of May, when earlier broods hatch, and last at the beginning of July, when most young have just fledged. In previous years the same observer had performed all samplings, but in 2003, due to the magnitude of the field work, more persons participated. Thus, we used a variant of Onsager and Henry’s method to estimate density of rangeland grasshoppers, which yields excellent density estimates when sampling is extensive and carried out by different people (Onsager and Henry 1978). This method consists in putting wire rings of 0.1 m² (35.68 cm in diameter) sufficiently spaced along transects. The wire rings delimit an area inside which the number of grasshoppers can be seen and counted by a person with sufficient clarity to distinguish between motion inside and outside the circle. In each patch we placed 48 rings of 0.1 m² in a net of six lines of eight rings, spaced at approximately four meters intervals along lines. Each patch was sampled by a group of three people, counting the number of grasshopper within the rings, and also the number of grasshopper in transects following the lines between rings. As in 2001, grasshopper censuses were carried out evenly around the colonies and at the time of the day of maximum grasshopper activity (see above).

Prey delivery rates to the nestlings

We wanted to assess the effect of hunting distance on prey delivery rates to the nests. Observations on prey delivery rates were performed at the largest colony (60 pairs) in 1999. We monitored 24 nests noting how often kestrels fed the nestlings at the same time that we were observing hunting behavior. We measured feeding rates by watching randomly chosen nests with a telescope for periods of half an hour. Due to the high frequency of feeding rates (up to 15 in 30 m in some cases) in this time interval is possible to record a sufficient number of prey deliveries and hunting
trips. In fact, for all the individuals used in the analyses we had recorded a minimum of 5 hunting trips. All the observations were made in the hours of maximum hunting activity recorded in our study area, between 7:00 and 11:00 and between 14:00 and 16:00 GTM. In order to control for fledgling age effects, feeding rates were recorded when the chicks were older than 10 d, as the demand of food normally levels off after this age.

**Diet**

We studied nestling diet with two purposes: in first place, to confirm that orthopterans constitute the bulk of the biomass ingested by the chicks; second, we wanted to assess whether a decrease of feeding rates could be compensated by bringing larger prey. Diet was monitored throughout the nestling period at the largest colony (60 pairs), as here the likelihood of prey depletion and any potential compensation by hunting larger prey was more likely to take place. To obtain fresh samples we used a thick and durable paper, which was fitted around the base of the nest at the end of the day. The material regurgitated during the night by the nestlings was collected the following morning, dried and preserved for a later analysis. Each sample included several pellets or pieces of pellets more or less disaggregated. Samples were examined under a binocular microscope (20×). For identification of prey, we used collections of hard parts such as mandibles (for Orthopterans, caterpillars, and beetles), and legs, head, torax and elytros (for beetles), from specimens identified previously. The maximum number of each part (distinguishing taxon, and right and left pieces) found in a pellet was considered as the minimum number of prey items consumed. To estimate their masses, we used regression equations described in Aparicio (2000), which let us obtain reliable estimations on the basis of the length of mandibles for orthopterans and femurs for beetles. In 1999 and 2001 we examined 32 and 71 samples collected at the nests overnight (each one containing several pellets). In total we examined 332 prey items in 1999, and 1,168 in 2001.

**Breeding performance**

We wanted to assess whether prey depletion had any effect on reproductive success. Therefore, we monitored breeding performance in 24 different sized colonies, ranging from 5 to 65 breeding pairs. At each colony we located all potential nests before the onset of egg-laying and regularly monitored them to determine clutch size, the number of fledglings and their body condition (for more details on field routines, see Aparicio 1997). We used pectoral thickness as an estimator of fledgling body condition (Aparicio 1997, Aparicio and Cordero 2001). This trait has been used in previous studies as a measure of body condition on several bird species (Sears 1988, Newton 1993, Aparicio 1998) and is considered to be more reliable than residuals of body mass on tarsus length (Gosler and Harper 2000). In addition, it is easy to be taken accurately on live birds by using a portable ultrasonic meter, in this case a Krautkrämer Branson USK7B device (see Sears 1988, Newton 1993). Pectoral thickness was measured in arbitrary units, which reveal individual variation (Newton 1993), since measurements are highly repeatable (Aparicio 1997). In the analyses we used only one measure of fledgling pectoral thickness, taken when wings were at least 160 mm long (the nestlings are able to fly with wing lengths around 175 mm), at this stage fledglings are between 29 and 32 d old. Pectoral thickness levels off when wings reach a length of 150 mm (Aparicio unpublished data), thus, the measure of body condition we used is age independent and more stable over the time than other measures such as body mass.

**Statistical analyses**

**Hunting distance, date and colony size**

We analysed whether hunting distance from the colony changed with the date and colony size (i.e. number of breeding pairs). We performed a general linear model (GLM) with hunting distance as the dependent variable and the date and colony size as continuous predictors. The relationship between hunting distance and the continuous predictors was hypothesized to be linear, all effects were tested using a whole model test. We wanted to assess the pure effects of the date and colony size on hunting distance. Besides that, we also tested for an interaction between both continuous predictors; hunting distance could increase more with the date the larger the colony, as the seasonal prey depletion around large colonies could be stronger too.

**Prey depletion, distance to the colony and colony size**

We wanted to know whether seasonal prey depletion depended on the distance to the colony and colony size. For 1999 we had data from a single large colony and performed a GLM in which the dependent variable was the seasonal change in grasshopper abundance at each sampling site (i.e. the slope of the regression between the number of grasshoppers and the date at that sampling site). As continuous predictor we included the distance from the sampling site to the colony, we expected the relationship between the dependent variable and the continuous predictor to be linear. We included the type of habitat where the sampling site was placed (grassland, cereal or legume field) as a fixed factor in the analysis. We included the type of habitat because we wanted to assess the effect of the distance to the colony on prey depletion controlling for any potential effect that the type of habitat might have. We were not interested in the interaction between the fixed factor and the continuous predictor for the purposes of this study. For 2001 we performed exactly the same analysis (GLM) with the difference that, besides the distance to the colony, we also included colony size as continuous predictor, as we sampled several different sized colonies. Moreover, we analysed the interaction between both continuous predictors, as the changes in grasshopper abundance relative to distance for the colony could be affected by colony size. As in the previous case, we controlled for the effects of the type of habitat including it as fixed factor. Both in 1999 and 2001 we fit only a single statistical model (whole model test). For 2003, when the number of colonies was largest, we performed a different kind of analysis. We had sampled 1km around each colony both at the the beginning and the end of the breeding season. We performed a Spearman correlation to see whether the
changes in the number of grasshoppers during the breeding season in that area were correlated with colony size (i.e. number of breeding pairs in the colony).

Prey delivery rates, hunting distance and date
We performed Pearson correlations to assess whether prey delivery rates to the nest were related to hunting distance, and to analyse whether there was any relationship between prey delivery rates and the date.

Prey size and the date
We wanted to know whether prey size increased with the date, thus compensating for a potential decrease of prey delivery rates. We analysed the data from 1999 and 2001 separately. For each year we performed a GLM with the mean prey size recorded at each nest in each sample as the dependent variable. The continuous predictor was the date and we also included the nest as a random factor. We were not interested in knowing the effect of the nest identity on prey size, but we included it just to control for any effect that it might have and thus avoid pseudoreplication, as the data coming from the same nest might not be independent. We performed whole model tests, and the relationship between prey size and the date was treated as a linear covariate.

Seasonal changes in reproductive parameters
Prey depletion could arise gradually through the season at large colonies, hence, its negative effect on reproductive parameters could appear progressively too. We performed three separate GLMs to analyse how the seasonal changes in clutch size, fledgling number per nest and fledgling body condition (i.e. pectoral thickness) were related with colony size. We used data from 24 different colonies collected in different years; as a whole, in the analyses we used 74 colony-years. The dependent variable for each GLM was the seasonal change of those reproductive parameters, more concretely, the slopes of the regressions between the date and clutch size, fledgling number and fledgling body condition, respectively. The continuous predictor was colony size (i.e. number of breeding pairs). We also included colony identity as random factor. Again, we were not interested in the pure effect of colony identity, but we included it to control and avoid pseudoreplication because the data coming from the same colony might not be independent. We performed a whole model test for each GLM and the relationships between the reproductive parameters and the continuous predictor (colony size) were predicted to be linear. All statistical analyses were done with SPSS 7.5.

Results

Hunting distance
During the nestling period most prey captures (80%) took place within a radius of 1 km from the colony (Fig. 1). Hunting distances (log-transformed) were significantly shorter the smaller the colony (F = 4.74, df = 1,179, P = 0.03). The date itself had no effect on hunting distance

(F = 0.60, df = 1,179, P = 0.44); however, the interaction between the date and colony size was significant (F = 5.75, df = 1,179, P = 0.017), as hunting distance increased later in the breeding season in the large colonies while it did not in the small ones (Fig. 2).

Changes in grasshopper abundance
Prey were depleted in the areas close to the larger colonies. In 1999, when just the largest colony was sampled, we found that grasshopper abundance was higher at greater distances from the colony (F = 5.89, df = 1,12, P = 0.036). This effect was significant after controlling for the type of habitat, although habitat type did not have a statistically significant main effect on grasshopper abundance (F = 1.04, df = 3,12, P = 0.41). In 2001, when different sized colonies were included in the analyses, we found a statistically significant main effect of colony size on

![Fig. 1. Cumulative percentage of kestrel attacks in relation to the distance to the colony (m) in two years, 1999 (dotted line) and 2001 (solid line).](image1)

![Fig. 2. Temporal changes in hunting distance around the largest colony (60 pairs; open circles) and around three small ones (less than 10 pairs; filled squares) along the nestling period (late May to early July). The date is given as the number of weeks after January 1st. For the small colonies hunting distance at each week is the average for the three colonies.](image2)
grasshopper numbers, with fewer grasshoppers around larger colonies (F = 4.73; df = 1.47, P = 0.03). The distance to the colony itself did not have an effect on the temporal variation in grasshopper abundance (F = 3.01, df = 1.47, P = 0.09). However, the interaction between the distance to the colony and the size of the colony was significant (F = 4.58, df = 1.47, P = 0.03) after controlling for the type of habitat, which had a significant effect too (F = 5.91, df = 3.47, P < 0.001). The interaction between the distance to the colony and colony size was significant because there were temporal declines in grasshopper abundance near large colonies (r = -0.55, P = 0.018, n = 18), but not statistically significant declines by small colonies (r = -0.17, P = 0.34, n = 36).

In 2003 we confirmed that prey depletion depended on colony size. The number of grasshoppers increased later in the season around small colonies, while numbers decreased around larger colonies (Fig. 3). The extensive samplings around 12 different sized colonies showed that the temporal changes in grasshopper abundance around the colony ranged from increases in abundance around small colonies to decreases around large colonies (r = -0.64, P = 0.025, n = 12; Fig. 3).

**Hunting distance and feeding rates**

We found that the greater the hunting distance the lower the feeding rates to the nestlings. There were twenty individuals for which we had recorded at least five hunting trips at the same time that we recorded their prey delivery rates. In these cases, we found that a higher mean distance of prey capture was correlated with a lower mean feeding rate for nestlings (r = -0.54, P = 0.01, n = 20). We monitored feeding rates in a large colony where hunting distance increased progressively with the date and we found that, accordingly, feeding rates declined significantly through the season too (r = -0.18, P < 0.001, n = 98).

**Diet composition and prey size**

The progressive decrease of feeding rates was not compensated by bringing larger prey. Nestling diet was based on orthopterans (grasshoppers and field crickets), which amounted for 45–70% of prey items, and secondarily by beetles (15–35%), whereas small vertebrates were only a small proportion of nestling diets (<1%). In 1999, prey size decreased significantly with the date rather than increasing (B = -0.067 ± 0.026 SE, F = 4.71, df = 1.17, P = 0.04), and in 2001 prey size remained practically the same throughout the whole nesting period (B = -0.009 ± 0.089 SE; F = 0.01, df = 1.57, P = 0.92).

**Seasonal pattern of reproductive parameters in relation to colony size**

Larger colonies had both fewer fledglings per nest and lower fledgling body condition. Both the number of fledglings and fledgling body condition tended to decrease with later laying date; however, and after controlling for the effects of colony identity, the GLM showed that the decrease was significantly sharper the larger the colony (F = 6.38, df = 1.30, P = 0.02; for fledgling number, Fig. 4B and F = 5.36, df = 1.33, P = 0.03 for fledgling body condition, Fig. 4C). Clutch size also tended to decrease with the date, but there was not any relationship between those changes and colony size (F = 0.09, df = 1.26, P = 0.77; Fig. 4A).

**Discussion**

Lesser kestrels hunting to feed the nestlings foraged close to the colony, where most prey captures took place. Prey depletion was sharper around the larger colonies, as predation pressure was also stronger due to the large number of breeding pairs. Prey depletion made the kestrels fly longer distances to forage and delivery rates to the nest decreased; moreover, lower delivery rates were not compensated by providing larger prey. Thus, nestlings from larger colonies generally suffered from food shortage and, additionally, in large colonies later-starting nests had poorer reproductive success than later nests from smaller colonies.

**Hunting distance, prey depletion and colony size**

Kestrels may forage within a radius of 5–11 km from the colony when they hunt for themselves (Donázar, et al. 1993, Bonal and Aparicio 2001), and may stay in those areas for several hours. However, during the breeding season lesser kestrels behave as central place foragers which bring only one prey item to the nest per hunting trip (see Orians and Pearsons 1979); hence, adults hunt close to the colony to maximise the amount of food delivered to the nestlings. Therefore, predation pressure is very strong in the vicinity of the colony, with most prey captures made within a radius of 1,500 m. These hunting distances recorded by direct observation do not differ from those obtained using radio tracking in the same time of the year and study area (Bonal and Aparicio 2001). Hunting pressure had a negative effect on prey abundance in the
areas close to the larger colonies, while no prey depletion was found in the surroundings of the smaller ones. Our study provides direct evidence of prey depletion, something that has been rarely measured in studies on avian coloniality in spite of its major importance (Brown and Brown 1999). It also shows that prey depletion can take place in terrestrial colonial birds like kestrels, whose colonies are much smaller than those of seabirds, for which prey depletion has usually been hypothesized (Ashmole 1963, Lewis et al. 2001). The present results constitute a more solid evidence of prey depletion compared to other study of colonial birds, in which prey abundance was measured just once at the end of the season (Birt et al. 1987). These previous studies cannot rule out the possibility that the observed distribution of prey was not related to the activity of predators; in contrast, our study found changes in prey abundance across the kestrel’s nesting period, confirming prey depletion in areas closer to the large colonies.

**Hunting distance, prey delivery rates and seasonal changes in prey size**

The progressive prey depletion in the vicinity of the large colonies made the kestrels fly longer distances to forage in areas where food availability was still high. This fact had a negative effect on prey delivery rates to the nest, which decreased significantly in large colonies while they did not change in the smaller ones, where no prey depletion took place. Longer hunting trip duration (Lewis et al. 2001), and lower prey delivery rates to the nest (e.g. Möller 1987) have been found before and attributed to prey depletion around the colony, although no prey sampling was carried out. With respect to these studies our results provide measures of prey depletion and its direct link to foraging distance and prey delivery rates to the nest. We examined whether lower prey delivery rates were compensated by providing larger prey. However, prey size decreased rather than increased with the date, just when feeding rates also declined, so, the net energy delivered to the nestlings decreased with the date too. Lesser kestrels feed mainly upon grasshoppers (Franco and Andrada 1977, this study) and, in absolute terms, the range of weigh variation among these insects is very small for a bird of this size. Thus, in any case, it may be generally very difficult to obtain prey large enough to compensate a low delivery rate.

**Prey depletion, colony size and reproductive success**

Prey depletion around the larger colonies was not compensated by providing larger prey and, consequently, nestlings suffered food shortage and their survival and body condition decreased. We found a negative effect of prey depletion on the number of fledglings per nest and their pectoral thickness (i.e. body condition). Reproductive success decreased with the date in most colonies, which is a general trend in birds (e.g. Lack 1966, Klomp 1970, Aparicio 1994), generally attributed to differences in age and/or parental quality and independent of any seasonal decline in food supply (Aparicio 1994, 1998, but see Norris 1993). However, the decline of the number of fledglings and their body condition was sharper at larger colonies, where preys were progressively depleted and the amount of food provided to the chicks decreased along the season more sharply. In contrast, clutch size did not vary with colony size, probably because food depletion does not take place during the pre-laying period and negative consequences of lower prey abundance in previous years do not carry over to the clutch laying period of the current year.

**Prey depletion and colonial demographic dynamics**

Food depletion around avian colonies has been argued as a density dependent mechanism that regulates colony size and growth (Ashmole 1963, Lewis et al. 2001). The poorer
body condition of lesser kestrel fledglings in larger colonies would reduce their chances of surviving (Aparicio 1997) and joining the colony in the following year. In addition, according to recent findings in the study of coloniality, the decrease of reproductive success in larger colonies may reduce the number of immigrants (Brown et al. 2000). Conspicuous breeding success has been proposed as a main cue for settling decisions, as it integrates the fitness costs and benefits at a given place (Brown and Brown 1996, Danchin and Wagner 1997). Inspection of nests by young birds or adults failing to reproduce has been observed in several species (e.g. Cadiou et al. 1994, Rannala 1995) and has been demonstrated to influence their settlement decisions in the following breeding season (Danchin et al. 1998, Brown et al. 2000, Doligez et al. 2002) and to improve future reproductive success (Schørring et al. 1999). In fact, inspecting behaviour has been recorded for lesser kestrels in our study area too (pers. obs.), and it has been found that increasing experimentally conspicuous reproductive success attracts immigrants and increases the number of breeding pairs in the future (Aparicio et al. 2007). Thus, poor reproductive performance in large colonies may prevent inmigrant arrival and reduce colony growth as well.

Conclusion

The present results provide direct evidence of prey depletion around lesser kestrel colonies and show that it is more likely the larger the colony. Progressive prey depletion made the kestrels fly longer distances to forage and prey delivery rates decreased, what could not be compensated by providing larger prey. Thus, the net amount of food provided to the nestlings decreased and, as a consequence, reproductive success declined more strongly through the season the larger the colony. This study shows that prey depletion is a density-dependent cost which has to be considered in the study of the evolution of coloniality, as it may regulate colony size and demographic dynamics.

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