

Nesting dispersion of a Black Kite population in relation to location of rabbit warrens

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Previous studies have shown that the rabbit (*Oryctolagus cuniculus*) is the main prey of the Black Kite (*Milvus migrans*) in Matagordas (Doñana National Park, southwestern Spain), and that the reproductive success of pairs is enhanced with increasing rabbit consumption. In our study area, rabbits live mainly in large warrens patchily distributed across the breeding area of Black Kites. Rabbit consumption was higher for Black Kite pairs having warren entrances close to their nests. During the 3 years of the study, this population of Black Kites suffered a considerable increase. New pairs in the area selected nesting trees inside areas with a high density of rabbits. The pattern of Black Kite aggregation in our study area, where they breed in a "colony" with a population density among the highest recorded, can be explained, at least partially, by rabbit aggregation. Defense of feeding resources could help to explain the territorial behavior of Black Kites. Coloniality and feeding territoriality are not mutually exclusive.

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Des études antérieures ont démontré que le Lapin de garenne, *Oryctolagus cuniculus*, est la principale proie du Milan noir (*Milvus migrans*) à Matagordas (par national Donana, sud-ouest de l'Espagne) et que le succès des couples d'oiseaux à la reproduction est meilleur lorsque la consommation de lapins est importante. Dans la zone étudiée, les lapins vivent surtout dans de grandes garennes à répartition contagieuse dans l'aire de reproduction de l'oiseau. La consommation de lapins était plus importante chez les couples dont les nids étaient situés près de l'entrée d'une garenne. Au cours des 3 ans qu'a duré notre étude, la population de milans a subi une augmentation importante. Les couples qui ont niché dans la zone d'étude ont construit leurs nids dans les zones de densité élevée de lapins. La répartition contagieuse des Milans noirs dans notre zone d'étude, où ils se reproduisent en une « colonie » au sein d'une population parmi les plus denses jamais rencontrées, s'explique, du moins en partie, par la répartition contagieuse des lapins. La défense des ressources alimentaires peut contribuer à expliquer le comportement territorial des milans. La colonialité et la territorialité reliée à l'alimentation ne sont pas incompatibles.

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Introduction

A wide range of breeding systems has been found in birds, from solitary to colonial nesting (Lack 1968). Food and (or) availability of nesting sites have been suggested as the main factors determining the type of nest dispersion (Perrins and Birkhead 1983). Predictable and uniformly distributed food resources would favor solitary nesting, whereas unpredictable and clumped resources would promote breeding in groups (Krebs and Davies 1978; Tjernerberg 1985). Intermediate stages between these extremes may be found in different populations of a species (Newton 1979). Owing to this close relationship between resource use and spatial aggregation, coloniality and feeding territoriality have been largely considered to be mutually exclusive (Lack 1968; Krebs and Davies 1978; Newton 1979). However, birds living in a colony may defend a feeding territory against conspecific neighbors (Hegner et al. 1982; Adret 1984; Marion 1989).

The Black Kite (*Milvus migrans*) has usually been considered a solitary and territorial raptor, but exhibits all stages between dispersal and colonial nesting (Cramp and Simmons 1980). The reasons why Black Kites aggregate for

breeding are poorly understood, but it has been suggested that colonial nesting is related to the existence of abundant and clumped food sources (Newton 1979).

In our study area, the reproductive performance of Black Kites increased with the proportion of rabbits (*Oryctolagus cuniculus*), their main prey, in the diet (Viñuela 1991; Viñuela and Veiga 1992). Like those in other mediterranean sandy areas (Wood 1980; Rogers 1981), rabbits in Doñana National Park live in large warrens whose distribution and degree of use can be easily detected by predators (Rogers and Myers 1979a, 1979b; Villafuerte 1994). Thus, the main feeding resource for this raptor population is highly concentrated and patchily distributed throughout the study area.

The aims of this study were to determine (i) whether the position of Black Kite nests with respect to warrens influenced rabbit predation by the raptor, and (ii) if this was the case, and provided that there is a relationship between rabbit consumption and reproductive success (Viñuela and Veiga 1992), whether nesting dispersion in this population was associated with warren location.

Study area

The study was carried out in Matagordas, north of Doñana National Park in southwestern Spain (37°N, 6°5'W). The study area is a 300-ha sandy grassland zone on the northern edge of a large

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marsh. Vegetation includes scrub patches, pastures, and dispersed cork oaks (*Quercus suber*). This area has been heavily grazed by cattle and deer. The Black Kite population in this area increased from 21 pairs in 1987 through 40 in 1988 to 45 in 1989 (Viñuela 1991). Every year, all nesting trees were located on 1:3000 aerial photographs.

Methods

In our study area, female Black Kites establish a nesting territory and rarely leave it during practically the whole of the early breeding period (March–May), as has been previously described (Cramp and Simmons 1980). Furthermore, the pair spend considerable time perching near their future nest. Both behaviors, as observed during daily controls, allowed us to determine the arrival dates during 1988 and 1989 for a total of 85 pairs.

Warren locations and rabbit predation rate

To examine whether nest location with respect to warrens influenced the proportion of rabbits in the diet, we selected a small zone (125 ha) that included one of the high rabbit density areas described below. During August 1989, i.e., outside the rabbit breeding season, we located all the warrens and mapped their positions on aerial photographs. For each warren we considered the following variables: (1) total number of entrances, including those that were not used or had collapsed, and (2) active entrances, as noted from the presence of fresh tracks and fecal pellets (Parer and Wood 1986).

Three pairs of Black Kites fledged young inside this focal area during 1987, eight during 1988, and seven during 1989. Nest checks, including recording of prey remains, were carried out every 4–7 days (see Viñuela and Veiga 1992). For each pair that fledged young, the mean number of rabbits found per nest visit was calculated (see Viñuela and Veiga 1992).

Using aerial photographs we counted the warren entrances included within each of four circles drawn around each nest at a radius of 50, 100, 150, and 200 m.

Spearman correlation coefficients were computed between the mean number of rabbits found per nest and the total number of warren entrances within each circle. Correlations with the number of active entrances were also computed, but only for 1989, when warrens and nests were checked simultaneously.

Nest-site selection in relation to warren locations

In the aerial photographs we could easily delineate the areas used intensively by rabbits to build warrens. These areas were identifiable in the photographs as light zones wherein the sand had been removed as a result of burrowing (these areas were previously detected during fieldwork). This, as well as the low shrub cover, allowed us to differentiate four areas of high rabbit density. These areas measured 18.1, 18.1, 10.2, and 27.7 ha, corresponding to 24.7% of the total study area. High rabbit density areas were measured using a planimeter, and a peripheral strip measuring 150 m was added outside the limit of the sandy area. This strip was considered to be slightly longer than the distance defended by Black Kite pairs around their nests (about 3 ha, or 100 m radius circles; see Bustamante and Hiraldo 1990). The rest of the study area was considered to be an area of low rabbit density. Each Black Kite nest was classified as being in either a high or a low rabbit density area. As we included the 150-m strip bordering the high rabbit density areas, some nests outside these areas were also considered to be inside them. The number of trees in each area was also noted. We considered only the trees that could be used for nesting, and excluded burnt or dead trees. Also, we noted the occurrence of rabbit warrens in proximity to each nest (50 m).

Distance to the nearest-neighbor nest was recorded for each nest, and yearly means were computed separately for high and low rabbit density areas. Log-transformation was used to standardize this variable. A two-way ANOVA was performed to test for differences in the distance to the nearest neighbor between nest locations and years. The results are given as the mean \pm standard deviation.

TABLE 1. Spearman correlation coefficients between the mean number of rabbit prey found per nest visit from hatching to fledging of chicks (NRV) for each Black Kite nest and the total number of warren entrances located within circles around each nest

	Warren entrances			
	50 m	100 m	150 m	200 m
1988 (8)	0.68 ^a	0.71 ^a	0.62	0.62
1989 (7)	0.87*	0.63 ^a	0.56	0.53
1987–1989 (18)	0.42 ^a	0.55*	0.39	0.36

NOTE: Numbers in parentheses show the number of nests. An asterisk denotes a significant correlation ($p < 0.05$).

^aCorrelation coefficients with $p < 0.1$.

Results

Distance from the nest to warrens and rabbit predation rate

A total of 108 warrens were inspected and plotted on the map. The mean number of entrances per warren was 29.2 (range 1–275).

The mean number of rabbits found per nest visit (NRV) was 1.1 ± 0.9 (means of the averages for each nest ranged from 0 to 2.9). NRV was significantly correlated with the total number of warren entrances within the 50-m circle around the nests in 1989, but no other correlation was significant (Table 1). When years were pooled, NRV was significantly correlated only with the total number of warren entrances within the 100-m circle around the nests (Table 1). In 1989, NRV was significantly correlated with the number of active warren entrances within the 50-m circle around the nests ($r_s = 0.87$, $n = 7$, $p = 0.03$). We did not find any significant correlation between NRV and the number of entrances (total or active) within the 150- and 200-m circles.

Nest-site selection in relation to warren locations

During the 3 years of the study we located 106 pairs of Black Kites, 44 and 62 inside high and low rabbit density areas, respectively. The number of trees available for nesting was 181 and 528 in high and low rabbit density areas, respectively. Considering that high rabbit density areas represented 24.7% of the total, there were no differences between the numbers of trees observed and expected in the two zones ($\chi^2 = 1.76$; $df = 1$, $p = 0.18$). However, the number of breeding pairs inside high rabbit density areas was higher than that expected from a homogeneous distribution ($\chi^2 = 15.4$, $df = 1$, $p < 0.001$).

Distances to the nearest neighbor differed significantly between high and low rabbit density areas (high density: 140.2 m, $n = 44$; low density: 182.4 m, $n = 62$; two-way ANOVA partial $F = 10.74$, $df = 1$, $p = 0.001$; Fig. 1) and varied among years (partial $F = 5.71$, $df = 2$, $p = 0.004$; Fig. 1). Interaction between the two factors was not significant ($F = 1.8$, $df = 2$, $p = 0.16$).

Nesting territories in high rabbit density areas were occupied earlier than in the low rabbit density ones, but the difference was not significant (high density: 11.25 ± 10.1 , $n = 36$; low density: 14.7 ± 11.7 , $n = 49$; Kruskal–Wallis test, $p = 0.19$; day 1 was 15 March in both years). The pairs having warren entrances within 50 m of the nest tree arrived earlier than the pairs without warrens within that distance (with warrens: 11.3 ± 10.7 , $n = 62$; without warrens < 50 m: 18.3 ± 10.8 , $n = 23$; Kruskal–Wallis test, $p = 0.008$).

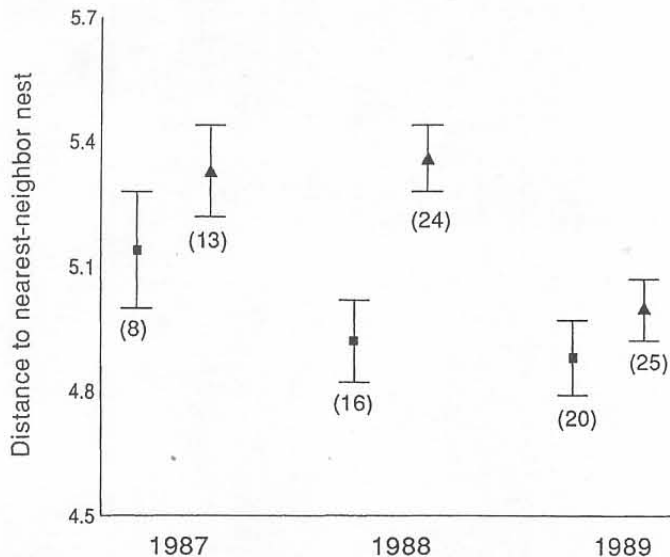


FIG. 1. Distance to nearest-neighbor nest (in logarithm of metres) in the Black Kite population studied, showing variation among years and between high (■) and low (▲) rabbit density areas (see text for definitions of types of area). Numbers in parentheses show the number of nests. Values are given as the mean \pm SD.

Discussion

We found that Black Kite pairs nesting near warrens consumed more rabbits. At least three factors may contribute to this result: (1) Young rabbits, which are selected by Black Kites (Viñuela and Veiga 1992), do not usually move far from the warren entrances (Myers et al. 1975; Richardson and Wood 1982). (2) Black Kite pairs defend a nesting territory around the nesting tree of about 3 ha (or a circle of 100 m radius), repelling other kites entering this area (Bustamante and Hiraldo 1993), so that they may gain exclusive access to warren entrances inside that area. The population density of this breeding population of Black Kites was among the highest recorded for this species (15 pairs/km² during 1989; Viñuela 1991). In such a dense population, a Black Kite pair may have access only to the warren entrances near its nest, because other warrens are likely to be inside the territory defended by other pairs. The fact that a correlation between rabbit predation and the number of warren entrances was found when circles of 50 or 100 m around the nests, but not circles of 150 or 200 m, were considered, gives support to this hypothesis. (3) Female Black Kites do not move away from the nesting tree, at least during the two first thirds of the nesting period, and perform almost all hunting flights in the vicinity of the nest (Cramp and Simmons 1980; Viñuela 1991).

Trees adequate for nesting are abundant at Doñana National Park, but Black Kites selected those located near rabbit warrens, as expected. We also expected less favorable habitats to be occupied secondarily (Svårdson 1949; Fretwell 1972). At Matasgordas, the nests with warrens within a radius of 50 m were occupied earlier in the season. Furthermore, as the population increased between 1987 and 1988, Black Kites selected more favorable places, as indicated by the decrease of internest distance in the high rabbit density areas. On the other hand, as the Black Kite population increased between 1988 and 1989, internest distance in low rabbit density areas also decreased (Fig. 1). This can be accounted for by saturation of the seemingly optimal area (which contained an

exceptional density of 27 pairs/km²) and subsequent occupation of suboptimal areas by newly arrived pairs. In fact, most new pairs during 1989 occupied a territory in which practically no rabbit warrens were found. Therefore, their addition to the "colony" may be due to conspecific attraction (Stamps 1988), e.g., taking advantage of kleptoparasitism, a common behavior in this species (Sunyer 1988). Consequently, an important factor constraining the pattern of breeding dispersion in Black Kites in our study area seems to be the clumped distribution of the main feeding resource, as suggested by Newton (1979), and this supports Horn's (1968) hypothesis about the origin of colonial breeding.

Territorial behavior in the Black Kite has been explained as a defence against predators or intruding fledglings from neighboring nests (Bustamante and Hiraldo 1993). In the population studied by those authors, the defence of feeding resources could not be associated with territorial behavior because those Black Kites obtained most of their food far from the nesting trees. However, in our case the birds gathered their main prey only in the vicinity of the nest, consequently our results suggest that territorial behavior could also be related to the defence of feeding resources. Other observations made from blinds during the study period support this hypothesis: one pair of Black Kites repelled any individual flying low above the roof of a nearby house, where there was a House Sparrow (*Passer domesticus*) colony. House Sparrows were among the main prey of that pair. Also, other pairs chased away any kite flying above the rush (*Juncus* sp.) patches near the nesting trees. Rush patches were hunting areas for these pairs, where they preyed on dung beetles (these areas are often used by cattle as resting places), spiders, and songbirds. If we consider that this population of Black Kites behaves as a colony, then territoriality and colonialism are not mutually exclusive as was previously assumed (Lack 1968; Krebs and Davies 1978). Our results therefore support recent work reporting the existence of feeding territoriality in colonial species that search for their food far from the colony (Hegner et al. 1982; Adret 1984; Hegner and Emlen 1987; Marion 1989).

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Presence of rodlet cells in the intrahepatic biliary ducts of the brown trout, *Salmo trutta fario* Linnaeus, 1758 (Teleostei, Salmonidae)

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We report for the first time rodlet cells in the epithelium of intrahepatic biliary ducts of the brown trout (*Salmo trutta fario* Linnaeus 1758). Such cells have not been described in the liver of any salmonid. Several developmental stages of the rodlet cells were found, including mature, discharging elements. The number of rodlet cells decreased from June to April. Intra-epithelial macrophages were found in close proximity to rodlet cells, suggesting a mild pathological reaction.

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Nous avons découvert la présence de cellules à bâtonnets dans l'épithélium des canaux biliaires intrahépatiques de la Truite brune (*Salmo trutta fario* Linnaeus, 1758). Jamais de telles cellules n'ont été décrites auparavant dans le foie d'un salmonidé. Les cellules à bâtonnets ont été observées à plusieurs stades de développement, notamment des cellules à maturité en train de libérer leurs inclusions. Le nombre de cellules à bâtonnets a diminué de juin à avril. Des macrophages intraépithéliaux ont été aperçus dans le voisinage immédiat de ces cellules à bâtonnets, peut-être à la suite d'une légère réaction pathologique.

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