

BREEDING BIOLOGY OF THE SHORT-EARED OWL (*ASIO FLAMMEUS*) IN AGRICULTURAL HABITATS OF SOUTHWESTERN FRANCE

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ABSTRACT.—Long-term studies of the Short-eared Owl (*Asio flammeus*) have been conducted mainly in its central breeding range. We studied its breeding biology in an agricultural habitat in southwestern France, at the southern edge of its breeding range in Europe. The abundance of the main prey species, the common vole (*Microtus arvalis*), varied cyclically. Between 1994–98, breeding was only confirmed in 1996, a peak vole year, when 13–19 pairs bred in cereal crop and rye-grass fields. In that year, breeding success was high ($\bar{x} = 5.7 \pm 0.9$ [\pm SD] fledglings per pair), although some young had to be temporarily removed from fields to avoid mortality due to harvesting or mowing activities. The distribution of breeding pairs was clumped. Land use around Short-eared Owl nests included significantly more cereal and semipermanent crops (the two cover types with the highest vole densities in 1996) than expected from random. The spatial distribution of Short-eared Owls was, however, not entirely explained by vole abundance, as there was an apparent nonrandom spatial association with breeding harriers (*Circus* spp).

KEY WORDS: *Short-eared Owl*; *Asio flammeus*; agricultural habitat; breeding success; conservation.

Biología reproductiva de la lechuza campestre (*Asio flammeus*) en una zona agrícola del sudoeste de Francia

RESUMEN.—La mayoría de los estudios a largo plazo sobre la Lechuza Campestre (*Asio flammeus*) se han realizado en el centro de su área de distribución. En este artículo, describimos la biología reproductiva de esta especie en un hábitat agrícola en el sudoeste de Francia, al límite sur del área de distribución de la especie en Europa. La abundancia de la presa principal, el topillo campestre (*Microtus arvalis*) fluctúa cíclicamente en la zona de estudio. En el periodo 1994–98, la reproducción sólo se confirmó en 1996, un año de sobre-abundancia de topillos, en el que entre 13 y 19 parejas criaron en campos de cereal y de centeno. El éxito reproductor en ese año fue elevado ($\bar{x} = 5.7 \pm 0.9$ [\pm DE] pollos por pareja) aunque algunos pollos tuvieron que retirarse temporalmente para evitar su muerte debido a la siega. La distribución espacial de los nidos no fue aleatoria, sino significativamente agregada. En un radio de 500 m alrededor de los nidos de Lechuza Campestre había significativamente más cereal y cultivos semipermanentes (los dos tipos de cubierta vegetal con mayores densidades de topillo en 1996) que lo esperado según la disponibilidad de ambos. No obstante, la abundancia de topillos no explicaba enteramente la distribución espacial de la Lechuza Campestre, ya que se observó una asociación aparentemente no aleatoria entre los nidos de esa especie y los nidos de aguilucho (*Circus* spp).

[Traducción de Autor]

Short-eared Owls (*Asio flammeus*) usually breed in high arctic to mid-latitudes both in the Old and New Worlds (Cramp 1985, Holt and Leasure 1993). The strong relationship of Short-eared Owls with vole-like mammals in the breeding and wintering range is well-known (Mikkola 1983, Korpimäki 1984, Wiebe 1991, Rau et al. 1992, Holt 1993). Most studies of breeding Short-eared Owls have been conducted within the main breeding range of the species and have concentrated on the relationship between vole abundance and owl breeding numbers, success or territory size (Lockie

1955, Clark 1975, Mikkola 1983, Korpimäki 1984, Village 1987, Korpimäki and Norrdahl 1991, Holt 1992). Nonetheless, Short-eared Owls are nomadic (Mikkola 1983, Holt and Leasure 1993) and may leave their traditional areas to breed elsewhere when prey is scarce and/or when rodent density is high elsewhere (Beske and Champion 1971, Hölzinger et al. 1973, Mikkola 1983). Fluctuations in Short-eared Owl numbers are also marked at the edge of their breeding range, where breeding occurs only irregularly, and data from such areas are very scarce (Beske and Champion 1971, Hölzinger

et al. 1973, Jubete et al. 1996). The comparison of breeding parameters between areas at the center and edge of the breeding range may help to discriminate two hypotheses regarding Short-eared Owl invasions. First, owls invade suboptimal areas as a response to the lack of food in their main area, because it is better to breed in suboptimal areas than not to breed at all (Hölzinger et al. 1973) and second, owls can track changes in vole populations without time lag, thus occupying edge areas because they become optimal at different times (Korpimäki and Norrdahl 1991).

The usual breeding habitats for the Short-eared Owl are open grasslands, moorland heaths, marshes, grassy moorlands, pine plantations and tundra areas (Mikkola 1983, Cramp 1985, Holt and Leasure 1993). However, outside the main breeding range and during vole outbreaks, they also nest in agricultural habitats (Holt and Leasure 1993, Jubete et al. 1996, Yeatman-Berthelot and Jarry 1994, Michelat 1997). The consequences of this habitat choice, in terms of breeding success, are basically unknown. Only Jubete et al. (1996) specified that breeding success in an agricultural habitat was greatly reduced due to harvesting activities.

In this paper, we describe the breeding biology of the Short-eared Owl in an agricultural habitat in southwestern France, at the southern edge of its breeding range. We report on breeding success and behavior, nest dispersion, habitat selection and feeding rates, and compare our results with other published data, discussing the implications for the species of breeding in an edge area and in an agricultural habitat.

STUDY AREA AND METHODS

The study area was located in the Département des Deux Sèvres, westcentral France (46°11'N, 0°28'W) and covered about 340 km² of agricultural habitat. Land use was represented by a mixture of winter cereal crops (ca. 35% of the surface), oil rape-seed crops (ca. 10%), spring-sown crops (sunflower and corn, ca. 25%), pasture (ca. 5%), semipermanent crops dedicated to livestock rearing, such as alfalfa, rye-grass or hay fields (ca. 10%), other crops such as peas, vineyards or flax (ca. 5%) and nonagricultural cover (villages and forest, ca. 10%). From 1994–98, five to 15 people searched the study area daily from April–August for breeding pairs of harrier species (*Circus spp.*), Little Bustards (*Tetrax tetrax*) and Stone Curlews (*Burhinus oedipnemus*). They recorded all observations of Short-eared Owl individuals or pairs.

We defined certain breeding pairs as those for which reproductive behavior was observed: either a nest was found ($N = 6$), a fledged family was observed ($N = 3$), or prey deliveries between males and females were ob-

served ($N = 4$). Observations of pairs in a given area more than once, but where none of these behaviors could be detected, were considered to be possible breeding pairs. All reproductive data (habitat selection, reproductive success and feeding rates) were from 1996, the only year when breeding was confirmed. Nests were located through triangulation. Two observers were placed at different points and they simultaneously watched males or females coming into nests with prey. Nests were subsequently visited by a third person to record clutch or brood size. Nests were visited one to eight times during the breeding season and crop height was measured at the nest during the first visit. We measured egg width and length with vernier calipers to 0.1 mm. Laying date was estimated by backdating from hatching date assuming a 26 d incubation period (Gröndlund and Mikkola 1969). Hatching dates were known in three cases or estimated through nestling age in the others. Prey deliveries were also used to locate and trap nestlings in the field after their dispersal from nests. Nestlings were measured, banded and released at the same spot, except when they were at risk from harvesting activities. If crops were about to be harvested or mowed, we temporarily removed the nestlings, took them to a lab and then released them at the original spot after harvesting. Removals were short (4 to 7 d) and, in most cases, not all nestlings from a brood were removed because we could not find some of them. Parents did not desert the area and kept feeding nestlings after their release from the lab.

Feeding activity rhythm was assessed by means of focal sampling observations on six different pairs for a total of 20 evenings (2100–2300 H) from 29 May–27 July, totaling ca. 20 hr of observations. Two of these pairs were also observed at night (2200–0200 H) with a light amplifier (one night each). At another nest, observations were carried out twice before dawn (0400 H onwards).

The spatial distribution of all pairs found in 1996 was assessed using the nearest neighbor method (Clark and Evans 1954, Krebs 1989). The expected distance to the nearest neighbor in a population with a random spatial pattern is defined by $r_E = 1/2\sqrt{\rho}$ (where $\rho =$ density). The ratio $R (r_A/r_E)$, where r_A is the observed distance to the nearest neighbor) provides an index of aggregation of individuals with R values lower than 1 indicating increasing levels of clumping. The significance of the deviation from randomness was tested from the standard normal deviate $z = (r_A - r_E)/s_r$, where $s_r = 0.26136/\sqrt{n\rho}$ is the standard error of the expected distance to the nearest neighbor (Krebs 1989).

Land use of the study area was determined in the field and data were then entered to Geographical Information System software (ArcView 3.0a). To evaluate habitat preference, we used a 500 m circle around the location of each pair and determined the land use in each of the circles (total area of each of the described cover types). These data were compared with the area available in the whole study area using chi-square tests. To evaluate which habitats were preferred or avoided, we assessed how each expected proportion of cover type deviated from the null hypothesis (Neu et al. 1974) by inspecting the standard residuals of each theoretical proportion of occurrence in the chi-square table. As standard residuals follow a normal distribution, standard residuals higher than 1.95 in-

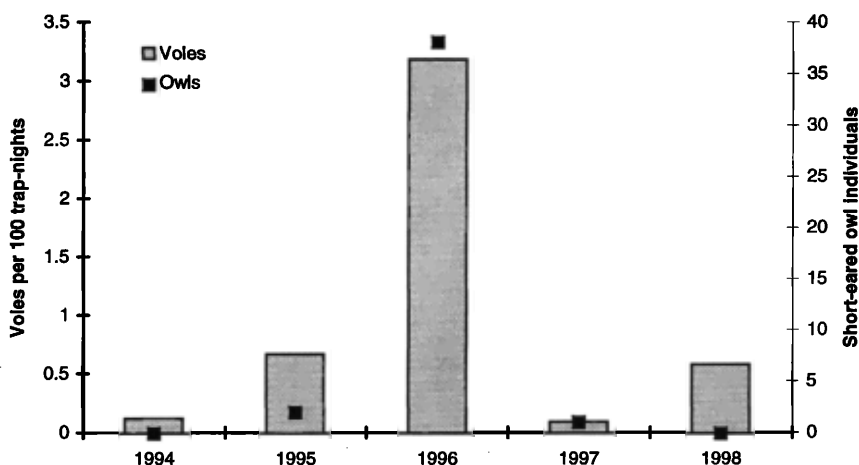


Figure 1. Estimated number of Short-eared Owls recorded during the breeding period (April–August) from 1994–98, and vole abundance in the same period.

indicated that observed proportions deviated significantly from expected values at the 0.05 level.

Vole abundance was estimated in April and July with trap lines, using snap traps. This procedure was considered appropriate for assessing the amplitude of fluctuations of the main prey species, the common vole (*Microtus arvalis*) (Spitz et al. 1974, Spitz 1977, Delattre et al. 1992). Each trap line was 100 m long and had 51 unbaited traps spaced every 2 m (Butet and Leroux 1993). One trap line was placed in each habitat type. The percent of traps in each cover type was similar each year. Traps were checked and removed 24 hr after their set-up. There were approximately 8000 trap-nights each year from 1995–98. In 1994, there were only 1224 trap-nights. Results of trapping are expressed as the number of vole captures per 100 trap-nights.

RESULTS

Variation in Short-eared Owl Numbers. No Short-eared Owls were observed in the study area during the breeding season in 1994 and 1998. An unpaired individual was observed in 1997. A breeding attempt was suspected in 1995 after a pair was observed defending a territory against raptor intruders. Reproduction of Short-eared Owls was verified only in 1996 when 13–19 pairs bred within the study area. That year was a peak vole year and the vole capture rate was five times higher than in intermediate years, and 30 times higher than in low vole years (Fig. 1). Overall, the number of breeding or nonbreeding Short-eared Owls recorded in the study area during breeding seasons from 1994–98 followed the abundance of common voles closely (Fig. 1), but the relationship was not signif-

icant (Spearman rank correlation, $r_s = 0.667$, $N = 5$, $P > 0.1$).

Breeding Habitat and Reproductive Parameters.

Six nests of the 13 breeding pairs detected in 1996 were found. Fledging success and laying dates were also available for three other pairs. Only the locations of the remaining four pairs were known. Of the six nests found, one of them was in a rye-grass field and five in winter cereal crops.

Laying took place between 4 April and 6 May. Median laying date was 20 April ($N = 9$). Fledged young were still fed by their parents up to 61 ± 11 (\pm SD) d after hatching ($N = 5$ broods) but all owls left the area by August. No second broods were observed.

Mean clutch size was 8.0 ± 1.1 for nests visited at egg stage ($N = 4$). Mean egg length was 39.0 ± 0.8 mm, and mean egg width 31.4 ± 0.6 mm ($N = 8$ eggs). Brood size in these four nests was 7.5 ± 1.3 . Brood size at first visit for the other two nests was six and seven. Young apparently hatched at 1- or 2-d intervals based on nestling measurements. They dispersed from nests at 13 ± 2 d of age (range = 9–16 d, $N = 16$ young) so we found young ≤ 100 m from nests when eggs were still being incubated. Because nestlings dispersed in all directions, successive prey deliveries to very different sites allowed us to quantify the minimum number of living young. One clutch was collected because of mowing activities and incubated artificially. The five young that were raised were

released when they reached normal fledging age. Additionally, a minimum of 46 young fledged in the study area, 16 of which were temporarily removed before harvesting. Thus, mean productivity ranged between 5.7 ± 0.9 – 3.9 ± 2.6 ($N = 9$) young per pair, the latter value obtained by assuming that all nestlings temporarily removed during harvesting or eggs incubated artificially would have died without intervention.

Feeding Rates. Nestlings were fed by males when females were still incubating or brooding, and by both parents thereafter, although we could not gather data on the relative contribution of each sex. In general, feeding took place just after sunset (93% of 77 observed prey deliveries). Four other prey deliveries were observed in the hour immediately before sunset in only three of the 20 focal nest observations. Mean feeding rates at sunset during the nestling period were 5.76 ± 1.9 prey deliveries per hour. We never observed any feeding or hunting activity in daylight, and therefore could not report on hunting distances or territory sizes. However, the short interval between prey deliveries (ca. 10 min.) suggested that most of the hunting was done very close to nests. After 2300 H, prey deliveries were very rare and only one prey delivery was seen during observations at night. Similarly, we did not see any food delivery early in the morning indicating that young were fed exclusively in the evening when each young received on average 1.14 ± 0.63 voles per hour. Assuming that the total hunting time of adults was limited to 2 hr each day from sunset to 2300 H, each nestling received a total of 2–3 voles per day.

Nest Spacing and Habitat Selection. Short-eared Owl pairs in 1996 were not randomly distributed, but significantly clumped ($R = 0.44$, $z = -3.85$, $P = 0.001$; Fig. 2). All breeding pairs were concentrated in an area of about 125 km², where density reached 0.10–0.15 pairs/km², and where vole abundance in April was high relative to the whole study area (Fig. 2). Clumped nest distribution was marginally significant if the test was conducted only with data from the highest density area ($R = 0.73$, $z = -1.88$, $P = 0.06$). Mean distance to the nearest neighbor was 1120 ± 883 m ($N = 13$, range = 350–2700 m), or 1692 ± 1666 m if we included the six probable breeding pairs.

Overall, the distribution of breeding sites was apparently related to food abundance. The western side of the study area, where Short-eared Owls were absent, showed the lowest values of vole cap-

ture rate in April (Fig. 2). Furthermore, the average proportion of different crop types within 500 m of breeding sites was significantly different from that available in the study area ($\chi^2_6 = 144$, $P < 0.001$). Cereal and semipermanent crops, where voles were highly abundant, were significantly more frequent around nests than expected based on their availability (Table 1). In contrast, pasture and spring-sown crops, where voles were very scarce, were significantly avoided together with inhabited areas (Table 1). Land use varied significantly among Short-eared Owl nest areas ($\chi^2_{72} = 5326$, $P < 0.0001$), but cereal and semipermanent crops were more represented than expected by random in 10 and 11, respectively, of the 13 nest areas. This suggested that nest location was mainly influenced by food abundance and availability.

There was an apparently nonrandom link between Short-eared Owl and harrier nest locations. At least one harrier nest was located within 500 m of owl nests in 10 of 13 cases. For these 10 pairs, mean number of nearby breeding harriers was 2.6 ± 1.3 (range = 1–4) and mean minimum distance to a harrier nest was 230 ± 156 m. Harriers breeding near Short-eared Owls were mainly Montagu's Harriers (*Circus pygargus*), which were particularly abundant in the study area in 1996, but Marsh Harriers (*C. aeruginosus*) and Hen Harriers (*C. cyaneus*) bred nearby on one and two occasions, respectively. Interspecific agonistic contacts between Short-eared Owls and harriers were frequently observed at seven of the 10 nests. In contrast, intraspecific agonistic behavior was rarely observed, even in the areas where several owl nests were located within 500 m of each other, although the owls seemed to avoid each other by hunting in opposite directions from their nests.

DISCUSSION

Owl Outbreaks, Vole Abundance and Breeding Success. Hölzinger et al. (1973) suggested that Short-eared Owls leave their regular breeding quarters in northern Europe when prey supply is scarce, moving to southwestern areas with high vole populations and returning northwards in subsequent breeding seasons. Alternatively, owls may track high density vole areas without a time lag and establish territories in areas where expected breeding success is highest (Korpimäki and Norrdahl 1991).

Short-eared Owls winter regularly in western France (Yeatman-Berthelot and Jarry 1991), in-

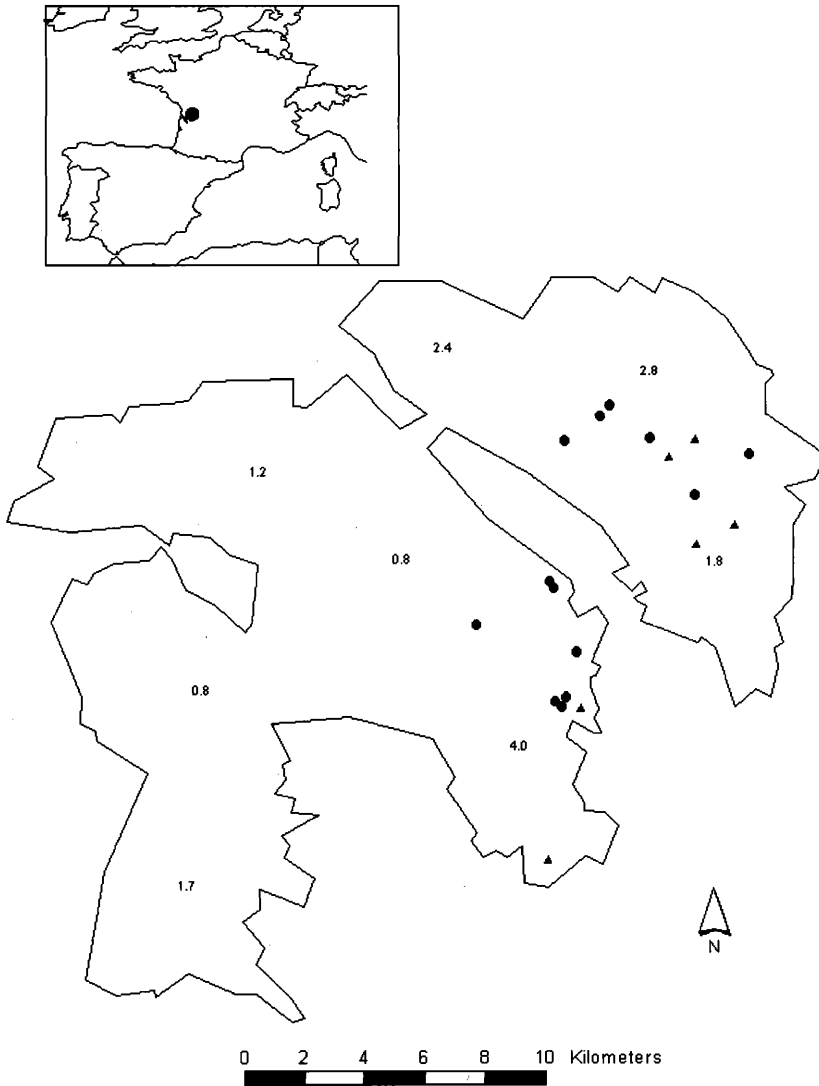


Figure 2. Distribution of breeding pairs of Short-eared Owls in 1996. Circles show confirmed breeding pairs and triangles show probable breeding pairs. Numbers refer to the average vole abundance (captures/100 traps) in April in different sectors of the study area.

cluding our study area, but they remained to breed only in 1996, a peak vole year. In France, another outbreak of breeding Short-eared Owls was observed in 1993 which was also a vole peak year (Michelat 1997, pers. obs.). In that year, 48–134 pairs nested in France, sometimes inland, which was atypical (Michelat 1997). Similarly, in Spain, where the species rarely nests (Asensio et al. 1992), ≤ 400 pairs were estimated to breed in 1993–94 when a vole irruption occurred (Jubete et al.

1996). In Spain, breeding areas also corresponded to regular wintering areas (Asensio et al. 1992, Jubete et al. 1996). These results suggested that Short-eared Owls may remain near their wintering areas if conditions for nesting are good, rather than dispersing from northern breeding areas when prey is low as proposed by Hölzinger et al. (1973).

Nesting success in edge areas is generally low. In Germany, breeding success was 27% with an average of 1.94 fledglings per pair ($N = 17$, Hölzinger

Table 1. Mean (\pm SD) height (cm), and vole abundance (captures/100 trap-nights) of different cover types measured in April 1996. Sample size (number of fields sampled) is shown in brackets. Cover type availability (% of total surface) in the study area and mean (\pm SD) proportion in 13 Short-eared Owl nesting locations is also expressed. The standard residuals of each theoretical proportion of occurrence (from the chi-square table) indicate how observed data deviate from the null hypothesis (proportion observed = expected).

COVER TYPE	HEIGHT	VOLE ABUNDANCE	AVAILABILITY	PRESENCE IN SHORT-EARED OWL TERRITORIES	STANDARD RESIDUALS
Winter cereal	46.7 \pm 10.9 (15)	9.1 \pm 12.3 (17)	35	43.5 \pm 13.6	4.12
Oil rape-seed	127.3 \pm 13.5 (8)	6.8 \pm 4.8 (8)	10	10.8 \pm 8.7	0.83
Spring-sown crops	3.9 \pm 10.8 (9)	1.6 \pm 2.4 (9)	26	20.4 \pm 15.7	-2.87
Pasture	29.2 \pm 13.0 (11)	1.9 \pm 3.0 (10)	5	0.6 \pm 1.5	-5.35
Semipermanent crops	33.2 \pm 16.3 (40)	12.9 \pm 5.5 (42)	10	17.1 \pm 9.7	6.22
Other crops	—	—	5	5.4 \pm 8.3	0.51
Nonagricultural cover	—	—	10	2.1 \pm 3.8	-6.89

et al. 1973). In Wales, clutch size was low at 5.8 \pm 0.8 eggs ($N = 5$); average fledging success per successful pair was 3.0 young and few pairs produced fledglings due to heavy losses between laying and fledging (Lawton and Bowman 1986). In Spain, productivity was also low averaging only 1.87 fledged young per pair (range 1–10, $N = 39$; Jubete et al. 1996). Mean fledged brood size in France in 1993 was 2.7 \pm 1.2 ($N = 30$), but that figure did not include nests that failed before fledging (Michelat 1997). In contrast, breeding success in areas located within the main breeding range is much higher. In western Finland, mean productivity was 3.1 \pm 2.3 young (range = 1.3–4.1, $N = 78$ pairs over 5 yr, Korpimäki 1984). In the northeastern U.S., mean fledging success was 3.2 \pm 2.2 ($N = 9$, Holt 1992). This indicates that owls do not track the best areas. However, in our study area, breeding success in 1996 was much higher than that reported for other southern edge areas and similar to that found in the main breeding areas. Similarly, breeding success was also high in another southern edge area, the Buena Vista Marsh (Beske and Champion 1971), with an average of five fledglings per pair and up to 10 fledged from a single nest (70 young from 14 successful pairs). The latter study took place in a year when the vole population was particularly high compared with other vole peaks (Beske and Champion 1971). Therefore, we suggest that breeding at edge areas may be sub-

optimal given the low average breeding success in these areas unless food conditions are exceptionally good, and are not preferred unless prey abundance in wintering areas is so exceptional that expected breeding success is high. It should be noted that the latter explanation does not rely on knowing prey levels in usual breeding areas. Data on between-year movements of individual birds would be needed to validate this hypothesis.

Breeding in Agricultural Habitats and Conservation. The use of agricultural habitats by breeding Short-eared Owls is relatively uncommon except during vole outbreaks (Mikkola 1983, Holt and Leasure 1993). It seems more common outside than inside the main breeding range (Holt and Leasure 1993, Jubete et al. 1996, Yeatman-Berthelot and Jarry 1994, Michelat 1997). Even so, during the 1993 outbreak in France, most nests were in marshes or humid areas and only 10% of pairs nested in crops (Michelat 1997). In Spain, 55% of 76 pairs monitored nested in agricultural fields (of which 20 were in cereal crops), and some nests were even found in ploughed fields without vegetation cover (Jubete et al. 1996). In our study, all pairs nested in agricultural fields, possibly due to the scarcity of alternative habitats.

Breeding inside crops potentially results in the destruction of many nests due to mowing and harvesting. For instance, in Spain, 43% of 39 nests failed and 53% of the failures were due to har-

vesting activities. The remainder were due to predation (Jubete et al. 1996). Similarly, 31% of young in our study had to be protected at the time of harvesting and 11–44% of nests would have failed without our intervention. The lack of natural habitat might be an important factor limiting the distribution and breeding success of the Short-eared Owls and may also explain why edge areas are suboptimal except in occasional circumstances when prey abundance is particularly high.

Nest Spacing, Territoriality and Habitat Selection. Short-eared Owls are believed to be strongly territorial, establishing and maintaining territories through intraspecific agonistic behavior (Lockie 1955, Holt and Leasure 1993). Hunting takes place within the defended territory, and consequently, territory size depends on prey abundance (Lockie 1955, Clark 1975, Village 1987). Territory size is highly variable ranging from 15–200 ha in Europe (Mikkola 1983) and 20–126 ha in North America (Holt and Leasure 1993). In areas where owls do not hunt microtines, they hunt far away from nests (Lawton and Bowman 1986) and hunting ranges are as big as 286 ha in southern Chile, where birds also form an important part of Short-eared Owl diets (Martínez et al. 1998). Territory sizes and between-nest distances are particularly small in areas and years with vole superabundance (Village 1987).

In our study, distribution of nests did not match that of a typical territorial raptor, and nests were clumped similar to raptors that use open habitats such as harriers (Krogulec and Leroux 1993, Arroyo 1995). Only Holt and Leasure (1993) describe Short-eared Owls as facultatively breeding in loose colonies in North America. Such clumped distribution might result from the clumping of voles. This is possible, given that Short-eared Owls in our study nested in the area where voles were most abundant and crops with high vole abundance were selected. However, the association with harriers that we observed may indicate that other factors influence the choice of nest sites, given that harriers usually hunt far away from the nests (Salamolard 1997). Associations between Short-eared Owls and harriers have also been described by Urner (1925) and in the Buena Vista Marsh (Beske and Champion 1971), where all of the 17 owl territories overlapped with harrier territories. The aggregation of Short-eared Owl nests and association with harriers may be related to predator detection and defense, as predation has been shown to be

an important factor explaining Short-eared Owl breeding success in other areas (Lockie 1955). Similarly, the rapid rate of growth shown by Short-eared Owl young and their early dispersal from nests is also likely related to predator avoidance. Holt et al. (1992) found that the most rapid weight increase in Short-eared Owls occurred between 11–15 d and coincided with pre fledging dispersal from nests which takes place at about 14–17 d (Holt and Leasure 1993). We found a slightly earlier pre fledging dispersal and that dispersal distances were higher than those previously reported (55 m in Holt and Leasure 1993). These differences may have been due to habitat characteristics related to vegetation density and predation risk between crops and natural habitats, although more data are needed to verify the latter.

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LITERATURE CITED

- ARROYO, B.E. 1995. Breeding ecology and nest dispersion in the Montagu's Harrier *Circus pygargus* in central Spain. Ph.D. dissertation, Oxford Univ., Oxford, U.K.
- ASENSIO, B., F. CANTOS, A. FERNANDEZ AND I. FAJARDO 1992. La lechuza campestre en España. *Quercus* 1992 18–24.
- BESKE, A. AND J. CHAMPION. 1971. Prolific nesting of Short-eared Owls on Buena Vista marsh. *Passenger Pigeon* 33:99–103.
- BUTET, A. AND A. LEROUX. 1993. Effect of prey on a predator's breeding success. A 7-year study on common vole (*Microtus arvalis*) and Montagu's Harrier (*Circus pygargus*) in a west of France marsh. *Acta Oecol.* 14: 857–865.
- CLARK, P.J. AND F.C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.
- CLARK, R.J. 1975. A field study of the Short-eared Owl, *Asio flammeus* (Pontoppidan), in North America. *Wildl. Monogr.* 47:1–67.
- CRAMP, S. [ED.]. 1985. The birds of the western Palearctic. Vol. 4. Oxford Univ. Press, Oxford, U.K.
- DELATTRE, P., P. GIRAUDOUX, J. BAUDRY, D. TRUCHETET, P. MUSARD, M. TOUSSAINT, P. STAHL, M.L. POULE, M. ARTOIS, J.P. DAMANGE AND J.P. QUÉRÉ. 1992. Land use patterns and types of common vole (*Microtus arvalis*)

- population kinetics. *Agric. Ecosyst. & Environ.* 39:153–169.
- GRÖNDLUND, S. AND H. MIKKOLA. 1969. On the ecology of the Short-eared Owl in Lapua Alajoki in 1969. *Suomenselan Linnut* 4:68–76.
- HOLT, D.W. 1992. Notes on Short-eared Owl, *Asio flammeus*, nest sites, reproduction, and territory sizes in coastal Massachusetts. *Can. Field-Nat.* 106:352–356.
- . 1993. Trophic niche of nearctic Short-eared Owls. *Wilson Bull.* 105:497–503.
- AND S.M. LEASURE. 1993. Short-eared Owl. In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 62. The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.
- , M. MELVIN AND B. STEELE. 1992. Nestling growth rates of Short-eared Owls. *Wilson Bull.* 104:326–333.
- HOLZINGER, J., M. MICKLEY AND K. SCHILHAUSL. 1973. Untersuchungen zur brut-und ernährungs-biologie der Sumpfohreule (*Asio flammeus*) in einem suddeutschen brutgebiet mit bemerkungen zum auftreten der art in Mitteleuropa. *Anz. Ornithol. Ges. Bayern* 12:176–197.
- JUBETE, F., A. ONRUBIA AND J. ROMÁN. 1996. La lechuza campestre en España: de invernante a reproductor. *Quercus* 1996:19–22.
- KORPIMÄKI, E. 1984. Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. *Ann. Zool. Fenn.* 21:287–293.
- AND K. NORRDAHL. 1991. Numerical and functional responses of kestrels, Short-eared Owls and Long-eared Owls to vole densities. *Ecology* 72:814–826.
- KREBS, C. 1989. *Ecological methodology*. Harper and Row, New York, NY U.S.A.
- KROGULEC, J. AND A. LEROUX. 1993. Breeding ecology of Montagu's Harrier *Circus pygargus* on natural and reclaimed marshes in Poland and France. In B.-U. Meyburg and R.D. Chancellor [EDS.], *Raptor conservation today*. Pica Press, Cornwall, U.K.
- LAWTON, J. AND N. BOWMAN. 1986. Diet and ecology of Short-eared Owls *Asio flammeus* breeding on heather moor. *Bird Study* 33:12–17.
- LOCKIE, J.D. 1955. The breeding habits and food of Short-eared Owls after a vole plague. *Bird Study* 2:63–69.
- MARTÍNEZ, D.R., R.A. FIGUEROA, C.L. OCAMPO AND F.M. JAKSIC. 1998. Food habits and hunting ranges of Short-eared Owls (*Asio flammeus*) in agricultural landscapes of southern Chile. *J. Raptor Res.* 32:111–115.
- MICHELAT, D. 1997. La nidification du Hibou des marais *Asio flammeus* en France en 1993. *Ornithos* 4:35–40.
- MIKKOLA, H. 1983. *Owls of Europe*. T & A.D. Poyser Ltd, Calton, U.K.
- NEU, C.W., C. RANDALL BYERS AND J.M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541–545.
- RAU, J.R., M.C. VILLAGRA, M.L. MORA, D.R. MARTÍNEZ AND M.S. TILLERIA. 1992. Food habits of the Short-eared Owl (*Asio flammeus*) in southern South America. *J. Raptor Res.* 26:35–36.
- SALAMOLARD, M. 1997. Utilisation de l'espace par le Busard cendré *Circus pygargus*. Superficie et distribution des zones de chasse. *Alauda* 65:307–320.
- SPITZ, F. 1977. Développement d'un modèle de prévision des pullulations du campagnol des champs. *Bull. OEPP* 7:341–347.
- , H. LE LOUARN, A. POULET AND B. DASSONVILLE. 1974. Standardisation des piégeages en ligne pour quelques espèces de rongeurs. *Terre Vie* 28:564–578.
- URNER, C.A. 1925. Notes on two ground-nesting birds of prey. *Auk* 42:31–41.
- VILLAGE, A. 1987. Numbers, territory size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. *Ornis Scand.* 18:198–204.
- WIEBE, K.L. 1991. Food habits of breeding Short-eared Owls in southwestern British Columbia. *J. Raptor Res.* 25:143–145.
- YEATMAN-BERTHELOT, D. AND G. JARRY. 1991. *Atlas des oiseaux de France en hiver*. S.O.F., Paris, France.
- . 1994. *Nouvel atlas des oiseaux nicheurs*. S.O.F., Paris, France.

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