THE FEEDING BEHAVIOUR OF BREEDING SHORT-EARED OWLS (*ASIO FLAMMEUS*) AND RELATIONSHIPS WITH COMMUNITIES OF SMALL MAMMAL PREY

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RÉSUMÉ

Le suivi de cinq couples nicheurs de Hibou des marais (*Asio flammeus*) dans le bassin du Drugeon (près de Pontarlier, Haut-Doubs, France) a révélé que leur distribution était liée, dans l'espace et dans le temps, aux variations de densité du Campagnol des champs (*Microtus arvalis*) et du Campagnol terrestre (*Arvicola terrestris*). Les oiseaux sélectionnaient les secteurs où les densités de ces rongeurs prairiaux étaient non seulement les plus élevées mais aussi distribuées de manière la plus homogène. Le succès moyen des tentatives de capture était de 32 %. Les performances de chasse entre mâles dans les différents milieux fréquentés (prairies, pâtures, marais) n'étaient pas significativement différentes. Cependant le nombre de jeunes à l'envol était fortement corrélé (r = 0,89) au succès de capture des mâles. Il semble donc que, compte tenu de l'homogénéité des populations de proies, le succès de reproduction ait bien été déterminé par les performances de chasse des mâles. Le régime alimentaire fut étudié à partir de 192 pelotes, totalisant 297 proies identifiables. La recherche de corrélations entre les tentatives de capture par les mâles et la proportion des différentes espèces de rongeurs dans le régime alimentaire des couples a montré que les proportions de Campagnol des champs et de Campagnol agreste (*Microtus agrestis*) étaient liées à l'effort de chasse des mâles dans l'habitat typique de chaque espèce de rongeur (respectivement r = 0,97 pour la prairie permanente et le Campagnol des champs, et r = 0,96 pour les marais et le Campagnol agreste). Paradoxalement, le ratio de Campagnol terrestre dans le régime alimentaire était corrélé avec l'effort de chasse en marais (r = 0,96) alors que l'espèce était beaucoup plus abondante en prairie permanente.

SUMMARY

Observation of five nesting pairs of Short-Eared Owls (*Asio flammeus*) in a 70 km^2 area, le bassin du Drugeon, Pontarlier Plain (Haut-Doubs, France), revealed a connection between their distribution in space and time and the abundance of Common Voles (*Microtus arvalis*) and Water Voles (*Arvicola terrestris*). The birds selected sectors where the population densities of grassland rodents were not only the highest but also the most evenly distributed. Mean success of capture attempts (capture rate) was 32 %. Differences between males and between habitats (meadows, pastures, marshes) were not statistically significant. However, number of young departing nest and capture rates achieved by the males were closely correlated (r = 0.89). It seems therefore that, given the homogeneity of prey population, reproductive success was determined by male's hunting performance. Diet was studied from

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192 pellets representing 297 prey items. The search for correlations between capture attempts by males and the proportion of the different rodent species in the diet of owl pairs showed that the ratios of Common Voles and Field Voles (*Microtus agrestis*) were related to the males' hunting effort in the habitat typical of each rodent species (permanent grassland $r = 0.97$ and marshland $r = 0.96$ respectively). The ratio of Water Voles in the diet was, however, correlated with the hunting effort in marshland ($r = 0.96$) though the species was more abundant in grassland.

INTRODUCTION

The Short-eared Owl (*Asio flammeus*) is reputed to be a species whose population fluctuations are generally correlated with those of Common Voles (*Microtus arvalis*) and/or Field Voles (*Microtus agrestis*) (Géroudet, 1984; Mikkola, 1983). Relations between vole abundance and Short-eared Owl numbers have been shown in Scotland (Village, 1987), Finland (Korpimaki & Norrdahl, 1991) and Spain (Jubete *et al.*, *in* de Cornulier *et al.*, 1998). In France, de Cornulier *et al.* (1998) have shown that the number of nesting pairs observed in 1996 in the intensively farmed cereal crop plain of Les Deux Sèvres was related to a year of high relative abundance of Common Voles. However, while high vole density usually seems to be necessary, it is not always sufficient. For example, two consecutive years of high vole densities in continental Germany may correspond to one year where the number of nesting pairs of Short-eared Owls is high followed by a year where only a few nesting pairs remain (Holzinger *et al.*, 1973; Mannes, 1975 *in* Glutz von Blotzheim & Bauer, 1980).

There is also a correlation between the Short-eared Owl local and regional population numbers and the proportion of Common Voles and Field Voles in their diet (Mikkola & Sulkova, 1969; Glue, 1977). However, interpretation of this is usually made difficult by the absence of parallel monitoring of prey densities in the field (Cramp *et al.*, 1985). At European scale, comparatively few studies focus on summertime diet (Mikkola, 1983). Thus Cramp *et al.* (1985) mention just a single study of diet during the breeding season: the work of Mikkola & Sulkova (1969) in Finland. Glutz von Blotzheim & Bauer (1980) cite three other studies conducted in Norway (Hagen, 1952 *in* Mikkola, 1983) and in the British Isles (Lockie, 1955; Glue, 1977). Baudvin *et al.* (1991) do not quote any. The reason for this scarcity is simple enough: it is usually difficult to locate pellets during the nesting period because the adults scatter them around their territory. The young produce their first pellet only 8 or 9 days after birth and as they generally leave the nest aged 12-16 days only few pellets may be found on the nesting site (Mikkola, 1983). These difficulties are compounded for Central Europe by the rarity of nesting (Mikkola, 1983). In France a few studies of the species' diet outside the nesting period have been made (Martin & Saint-Girons, 1973; Chartier & Chartier, 1986).

Five out of six pairs of Short-eared Owls were monitored in the Haut-Doubs during the nesting period in 1993 (Michelat, 1997). This study sets out to report on correlations between prey density, male hunting performance and reproductive success. It seeks to answer the following questions in particular:

— Is there a connection between the spatial and temporal distribution of nesting pairs and the abundance of rodent populations?

— What is the success rate of capture attempts, and is this rate dependent on the hunting environment and/or weather conditions?

— How does the capture success rate affect reproductive success?

— What are the connections between Short-eared Owl hunting behaviour and diet and the distribution of grassland rodent populations?

MATERIAL AND METHODS

At an elevation of 850 metres, the Bassin du Drugeon is a plain stretching over 20 kilometres between Frasne (46° 51' N, 6° 10' E) and Pontarlier (46° 54' N, 6° 22' E). The low-lying areas are occupied by varied wetland features: a number of ponds and lakes, streams, marshes and peat bogs. Grassland is distributed throughout the valley, with a few copses and very few hedgerows (GNFC, 1984). All the pairs nested in marsh or peat areas in the immediate vicinity of meadows and pastures (Fig. 1).

SMALL MAMMAL POPULATION

Each rodent species corresponds to a specific habitat in this region: the Common Vole (*Microtus arvalis*) and Water Vole (*Arvicola terrestris*) frequent permanent grassland while the Field Vole (*Microtus agrestis*) inhabits abandoned agricultural land (Giraudoux, 1991; Giraudoux *et al.*, 1994) and marshland. The

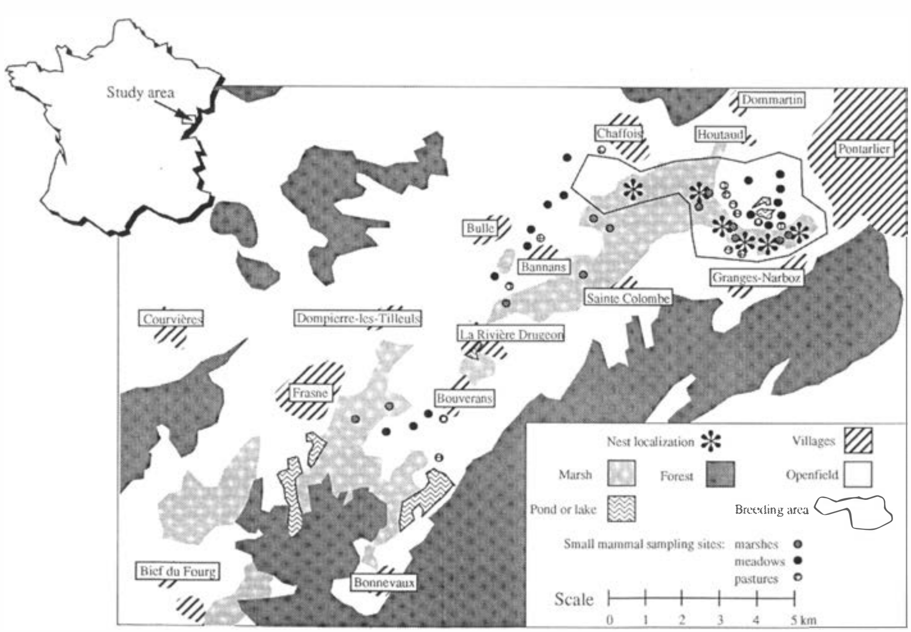

Figure 1. — Map of Pontarlier plain, nesting sites of the different pairs and rodent population sampling zone.

abundance levels of other species were not systematically investigated in their specific habitats (hedgerows, etc.) because they feature less in the diet of the owl.

The relative densities of Common Voles and Water Voles were evaluated by index methods on 100 m transects. These correspond to the number of 10 pace intervals where an indicator of the species is found (feaces or earth mound) over the total distance walked (Delattre *et al.*, 1990; Giraudoux *et al.*, 1995). Relative densities of Field Vole populations were evaluated by setting 34 INRA trap lines (Aubry, 1950) spaced three metres apart and checked each morning for three days. Each line therefore corresponds to a sampling effort of 102 trap nights (Spitz *et al.*, 1974). The relative density is then measured as the number of animals captured for 102 trap nights. Coefficients for specific lines (proportional to the extent of the range of each species) yield a rough order of magnitude of the densities of the different species of rodents captured (Spitz *et al.*, 1974; Giraudoux *et al.*, 1994).

Six trap lines were laid in marshland and 30 index transects walked in meadows and pastures within the owl territories (Fig. 1).

Small mammal density was also investigated in sites that were *a priori* favourable to the species but where no nests were observed. Eight small mammal trap lines were set in various marshes, at increasing distances from the zone where the nesting pairs were concentrated. Fifteen transects were walked to estimate relative densities of Common Vole and Water Vole populations in meadows and pastures in the vicinity of the marshes, along the same distance gradient.

This work was repeated in 1994 and 1995, during which years no Short-eared Owls were observed on the nest sites occupied in 1993, nor elsewhere in the Bassin du Drugeon.

The small mammal population studies were conducted each year in early July.

SHORT-EARED OWL

Observation of individuals

Information on owl behaviour was based on direct observation of individuals in the hours before nightfall. Sixty-four sessions, lasting two hours on average, were held between April 30th and July 20th. Observations were made whenever possible from two high and unobstructed vantage points where the owls could be watched from a great distance. Six observation points were used, allowing five pairs to be watched. These points were all outside the marshland and several hundred metres from the supposed nest sites. Observations were made with a Kowa TS1 telescope (× 25 magnification).

Precise observation of all ten adults (numbered by pairs A to E) meant individuals could be recognized from their plumage (Michelat, 1998).

During the observation sessions, information was recorded about:

— the habitat where captures were attempted (pair A to D only). Three types of habitat were identified: (i) marsh and peat bog, (ii) mowing meadow, (iii) pasture;

— the number of capture attempts by each individual (pairs A to E). A capture attempt was defined as any hunting action leading the owl to land on the ground. When hunting by soaring like buzzards or hovering, the birds regularly feint attacks. These actions (in the course of which the bird does not actually attempt a capture) were not included in the capture attempts;

— the number of successful attempts for each individual (pairs A to E). A capture attempt was counted as successful if prey was captured and killed. The capture rate was defined as the number of successful attempts divided by the total number of attempts;

— the identity of the prey taken (small mammal or bird) and its fate (immediate consumption or transport) (pairs A to E).

Four sessions were carried out in the rain on pairs B, C and D, in order to evaluate the impact of weather conditions on hunting behaviour and the capture rate.

Analysis of diet

Diet was studied from pellet analysis. This is the best method for quantifying predation of small mammals (Holt & Leasure, 1993). The observation sessions meant the favourite perching spots of each pair were identified. So as not to disturb nesting, pellets were collected only after the young had flown the nest. The pasture fence posts and bushes of the different territories were also examined.

STATISTICS

The chi-square test was used to evaluate differences in contingency tables (possibly with Yates' correction for 2×2 tables). Differences between relative density indices were tested by Mann-Whitney or Kruskal-Wallis tests (Siegel & Castellan, 1988). If necessary, the variances were compared by using a permutation test based upon 500 random rearrangements (Good, 1994). Pearson's linear correlation coefficient was used to measure the relationship between variables (Scherrer, 1984).

RESULTS

SMALL MAMMAL POPULATION

Within territories occupied by Short-eared Owls in 1993

In summer 1993, rodent population densities were very high throughout the zone occupied by the owl pairs; Common Vole density approached 250 individuals per hectare and Water Vole density 300 individuals per hectare (Table I). The marshland population was dominated by Field Voles, with a high density for that species (more than 50 ind./ha on average). Marked differences were observed, however: Field Vole densities were less than 35 ind./ha within the territories occupied by pairs A and C as opposed to 70 ind./ha in the other three territories (Mann-Whitney test, $p = 0.05$). At the scale of the total zone frequented by owls, divided into five geographical sectors, the population was dominated largely in biomass by the two grassland rodent species. Population density comparisons of the five sectors revealed no significant difference for Common Voles or Water Voles (Kruskal-Wallis test, $p = 0.4$ and $p = 0.35$ respectively).

Outside territories occupied by Short-eared Owls in 1993

Population densities were also high: 150 to 200 ind./ha for Common Voles (Table I), a figure very slightly lower than that in the nesting zones (Mann-Whitney test, p = 0.01). Water and Field Vole densities were of the same order of magnitude as in the nesting zones (Mann-Whitney test, p = 0.24 and p = 0.4 respectively). However, for the three species, generally higher standard deviations were associated with these values. Differences were statistically significant for the Common Vole, (permutation test on the variance ratio, p =0.006), but not for the Field Vole (p = 0.65) and the Water Vole (p = 0.52). The Common Vole population therefore appeared as a mosaic of patches of very high population density (close to that recorded in the owl nesting zone) separated by sectors with lower densities (though still high values).

TABLE I

Estimated relative densities of small mammal populations. Means are given as a percentage of positive intervals in meadows. SD, standard deviation; Abs Dens, absolute density, given as a guide in number of individuals per hectare for species where estimation is possible; this is only a rough order of magnitude.

YEAR 1993		Inside territories			Outside territories		
		Mean	SD	Abs. dens.	Mean	SD	Abs. dens.
Pastures (N = 7 and 6)	*Microtus arvalis*	24.63	4.63	*246*	18.50	8.24	*185*
	Arvicola terrestris	14.87	3.64	*300*	15.00	4.20	*300*
Meadows (N = 8 and 9)	*Microtus arvalis*	27.71	3.04	*277*	19.11	13.44	*191*
	Arvicola terrestris	15.43	4.61	*300*	17.78	3.03	*300*
Marshes (N = 6 and 6)	*Microtus agrestis*	11.00	5.69	*55*	9.00	8.49	*45*
	Clethrionomys glareolus	0.50	0.84	*2*	0.17	0.41	*1*
	Microtus arvalis	0.17	0.41	*2*	4.83	8.73	*48*
	Apodemus sp.	0.00	0.00	*0*	0.83	0.75	*2*
	Arvicola terrestris	0.50	0.84	—	2.00	3.03	—
	Sorex araneus	2.33	1.37	—	1.50	1.38	—
	Neomys fodiens	0.17	0.41	—	0.33	0.82	—
	Mustela nivalis	0.33	0.52	—	0.00	0.00	—

YEAR 1994		Inside territories			Outside territories		
		Mean	SD	Abs. dens.	Mean	SD	Abs. dens
Pastures (N = 7 and 6)	*Microtus arvalis*	0.75	0.71	*8*	0.67	1.03	*7*
	Arvicola terrestris	2.13	1.81	*20*	1.00	1.55	*20*
Meadows (N = 8 and 9)	*Microtus arvalis*	1.57	0.97	*16*	3.89	8.49	*39*
	Arvicola terrestris	4.00	3.42	*20*	2.00	2.92	*20*

YEAR 1994		Inside territories			Outside territories		
		Mean	SD	Abs. dens.	Mean	SD	Abs. dens
Marshes (N = 6 and 6)	*Microtus agrestis*	0.70	1.22	*4*	1.50	0.55	*8*
	Clethrionomys glareolus	0.30	0.55	*1*	0.00	0.00	*0*
	Microtus arvalis	0.00	0.00	*0*	0.00	0.00	*0*
	Apodemus sp.	0.00	0.00	*0*	0.00	0.00	*0*
	Arvicola terrestris	0.00	0.00	—	0.00	0.00	—
	Sorex araneus	0.50	0.55	—	1.30	0.84	—
	Neomys fodiens	0.20	0.45	—	0.20	0.45	—
	Mustela nivalis	0.00	0.00	—	0.00	0.00	—

YEAR 1995		Inside territories			Outside territories		
		Mean	SD	Abs. dens.	Mean	SD	Abs. dens.
Pastures (N = 7 and 6)	*Microtus arvalis*	0.63	0.74	*6*	0.50	0.84	*5*
	Arvicola terrestris	0.50	0.75	*0-10*	0.83	1.60	*0-10*
Meadows (N = 8 and 9)	*Microtus arvalis*	0.71	0.75	*7*	1.11	0.71	*11*
	Arvicola terrestris	0.29	0.49	*0-10*	0.56	1.13	*0-10*
Marshes (N = 6 and 6)	*Microtus agrestis*	0.30	0.55	*2*	0.80	0.45	*4*
	Clethrionomys glareolus	0.00	0.00	*0*	0.50	1.22	*2*
	Microtus arvalis	0.00	0.00	*0*	0.70	1.05	*7*
	Apodemus sp.	0.00	0.00	*0*	0.00	0.00	*0*
	Arvicola terrestris	0.00	0.00	—	0.00	0.00	—
	Sorex araneus	0.30	0.84	—	2.20	2.28	—
	Neomys fodiens	0.20	0.45	—	0.00	0.00	—
	Mustela nivalis	0.00	0.00	—	0.00	0.00	—

Over the entire study area in 1994 and 1995

In the summers of 1994 and 1995 the rodent population densities were well below 50 ind./ha for all rodent species.

SHORT-EARED OWL PREDATION BEHAVIOUR

All told, 453 capture attempts were observed during the study period. Of these, 435 were made by the males of the five different pairs. In this sample, the hunting habitats were recorded for 428 attempts.

Hunting habitats

53 % (227/428) of capture attempts made by all adults were in marshes, 30 % (128/428) in meadows and 17 % (73/428) in pastures. Figure 2 shows wide variations between individuals.

Capture rate

Of the 453 capture attempts, 143 were successful, giving a capture rate of 32 %. The capture rate of the different males varied from 26 % to 42 % (Table II),

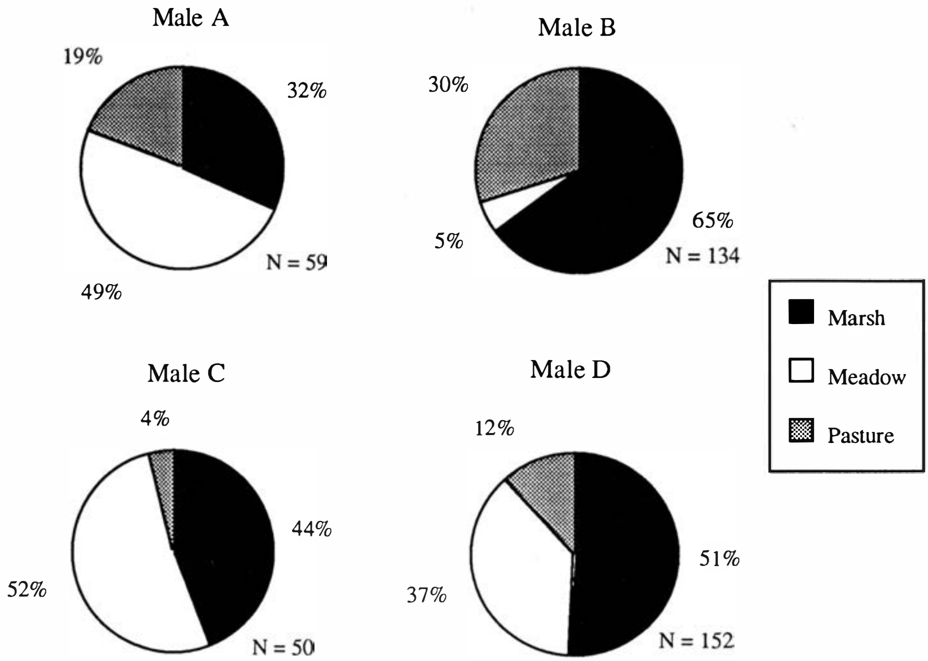

Figure 2. — Number of attempted captures by type of environment.

but these differences were not statistically significant (chi-square = 5.27; df = 4; p = 0.26). However, the reproductive success of each pair (Fig. 3) was significantly correlated with the capture rate of the males (r = 0.89; p = 0.04).

TABLE II

Capture rate of the different Short-eared Owl males.

Males	Number of attempted captures	Success ratio %
A	59	42
B	134	32
C	50	26
D	152	28
E	40	38
Total	435	32

r = 0.89
p = 0.04

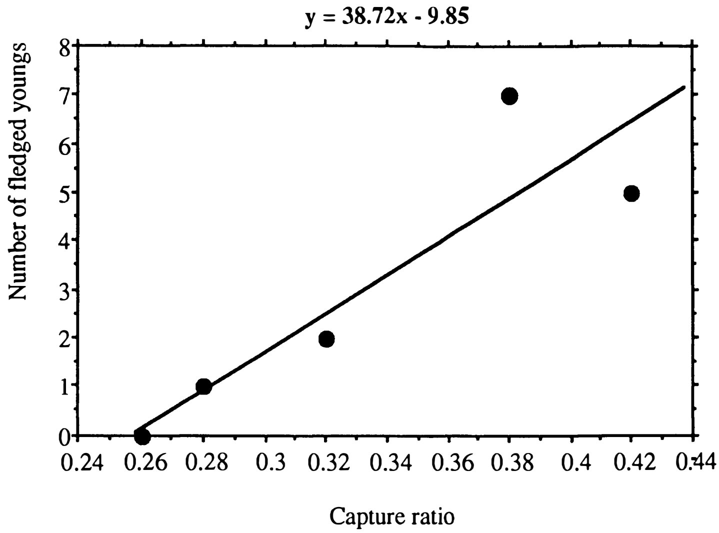

Figure 3. — Number of juveniles flying the nest and male capture rate.

Variation in capture rate with type of habitat

Capture rates of 27 % (62/227), 34 % (43/128) and 36 % (26/73) were observed in marsh, meadow and pasture respectively (non significant differences, chi-square = 2.56; df = 2; p = 0.3). A 35 % capture rate (24/69) in meadowland after mowing as against 29 % (15/52) before mowing was also recorded (non significant differences, chi-square with Yates' correction = 0.48; df = 1; p = 0.45). Finally, comparison of capture rates in open environments with tall vegetation (unmown meadows and marshes) of 28.7 % (82/286) versus 35.5 % (50/142) in environments with short vegetation (mown meadows and pastures) reveals no statistically significant differences (chi-square with Yates' correction = 1.68; df = 1; p = 0.2).

Effect of weather conditions on hunting

Four observation sessions were carried out in rainy weather. In every case (male B, D on June 9th, male A and both adults C on June 14th, male D on June 29th, male D on July 10th) the owls remained perched in the rain and foraging began only when the rain stopped.

DIET

A total of 192 pellets were collected. Analysis allowed identification of 297 prey items. The results are reported in Table III.

For each of the five owl pairs, Common Vole was the dominant prey totalling at least two-thirds of the number of preys. Field and Water Vole came next at about 1/5 of the number of preys. Differences in diet between the five pairs were

TABLE III

Diets of the five pairs of Short-eared Owl.

Prey	Pair A	Pair B	Pair C	Pair D	Pair E	All pairs
Microtus arvalis	87.8	57.7	77.8	75.3	61.4	71.4
Arvicola terrestris	6.1	14.1	11.1	11.3	20.5	12.5
Microtus agrestis	6.1	26.8	11.1	13.4	13.6	15.2
Clethrionomys glareolus	0.0	0.0	0.0	0.0	4.5	0.7
Birds (passerine)	0.0	1.4	0.0	0.0	0.0	0.3
Number of prey items	49	71	36	97	44	297

statistically significant (chi-square = 18.45; df = 8; p = 0.01). Twe two pairs (A and C) that nested in the marshes with fewest Field Voles were those with the lowest proportion of the species in their diet (6.1 and 11.1 % respectively).

When diets are compared with the hunting effort of the different pairs, some discrepancy can be observed. The number of prey captured in marshes might suggest there should be a higher proportion of Field Voles in the diet. However, though 65 % of male B's capture attempts were in marshes, Field Vole made up only 26.8 % of this pair's prey. Nevertheless significant correlations were obtained between the number of attempted captures in marshes and the proportions of Field Voles and Water Voles in diet (Figs 4 & 5; r = 0.97; p = 0.35 and r = 0.96; p = 0.05

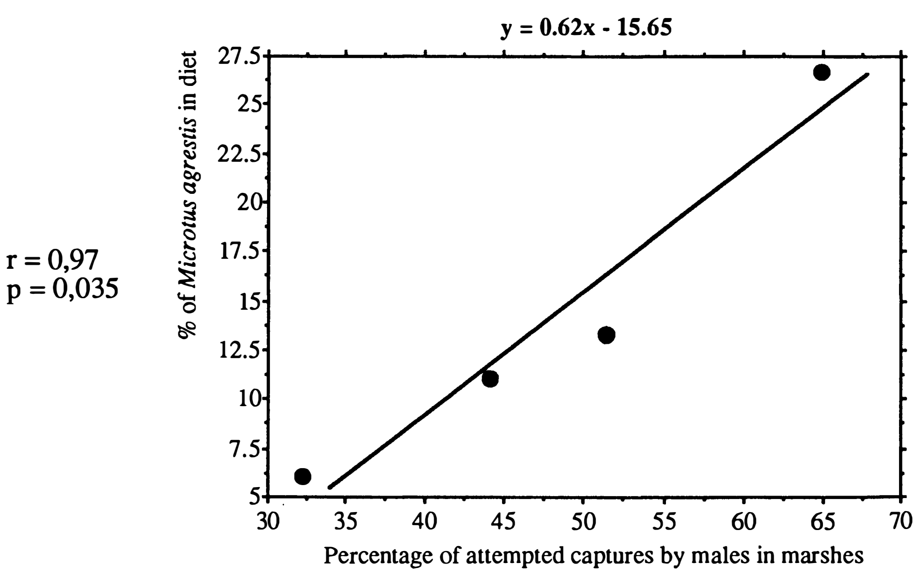

Figure 4. — Male capture rate in marshes and ratio of Field Voles in diet.

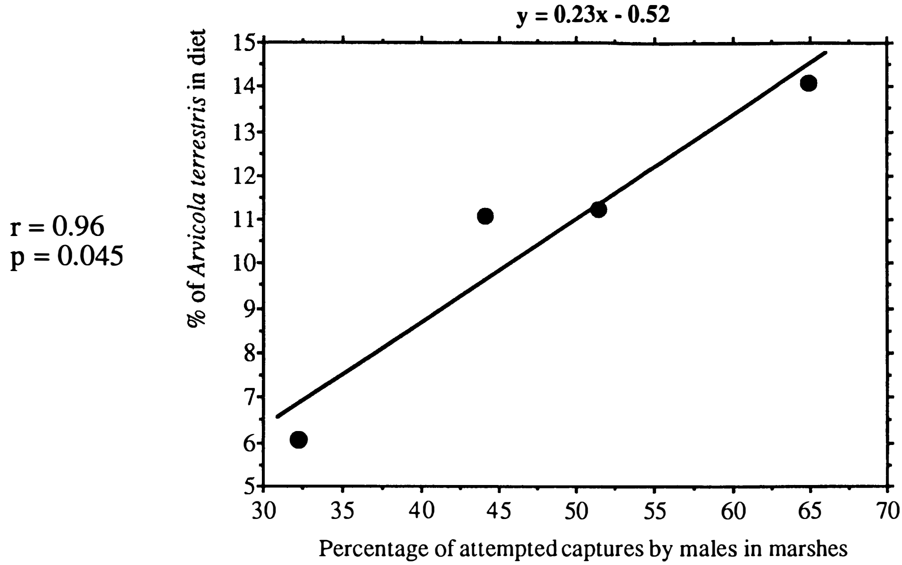

Figure 5. — Male capture rate in marshes and ratio of Water Voles in diet.

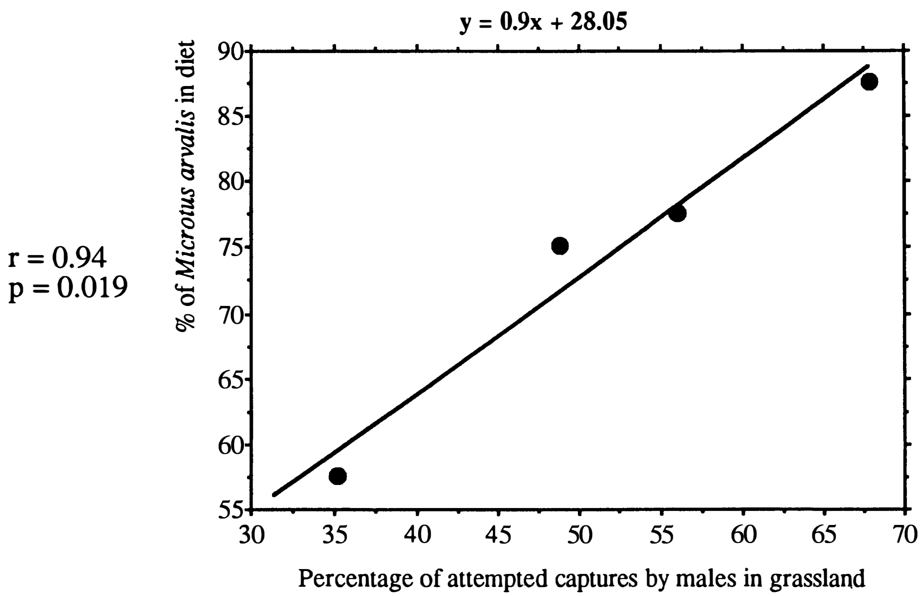

Figure 6. — Male capture rate in meadows and pastures and ratio of Common Voles in diet.

respectively), as well as between the proportion of Common Voles in the diet and the number of capture attempts made in meadows and pastures (Fig. 6; $r = 0.98$, $p = 0.019$).

DISCUSSION

The arrival of six nesting pairs of Small-eared Owls in the Bassin du Drugeon corresponded to a surge of grassland rodents (Common Voles and Water Voles). The disappearance of the owls from the study zone in the following years coincided with the rodent population crash. These results are consistent with the bird's reputation as nomadic, tracking Common Vole outbreaks (Glutz von Blotzheim & Bauer, 1980; Mikkola, 1983; Géroudet, 1984; Cramp *et al.*, 1985, Boyer & Hume, 1991; de Cornulier *et al.*, 1998).

However, in 1993 the precise location of the six pairs in accordance with rodent abundance does not seem to be a chance event. Results clearly show that Short-eared Owls settled in the sector where populations of those rodents most regularly consumed by the owls were not only very high but also most evenly distributed. This observation suggests that Short-eared Owls may have been capable of selecting from a comparatively extensive geographical zone (approximately 7 000 hectares) those sectors where rodent densities were most homogeneous, despite the entire zone being subject to a Common Vole and Water Vole surge with population densities of about 200 ind./ha and 300 ind./ha respectively.

Short-eared Owls hunted exclusively in open habitats: marshes, mowing meadows and pastures. These results are consistent with what is already known of the biology of the species (Glutz von Blotzheim & Bauer, 1980; Mikkola, 1983; Géroudet, 1984; Cramp *et al.*, 1985; Boyet & Hume, 1991).

As with most nocturnal birds of prey, male provides female with food (Glutz von Blotzheim & Bauer, 1980; Holt & Leasure, 1993). The scarcity of female hunting behaviour is explained by the fact that females do not participate in the hunting effort from the start of egg laying until the young are about 15 days old. Subsequently, the male continues to forage alone for the entire family if food is plentiful (Cramp *et al.*, 1985; Boyer & Hume, 1991). Densities of about 250 Common Voles per hectare, 300 Water Voles per hectare and 50 Field Voles per hectare may then be considered high enough for the female not to have been needed to contribute to the hunting effort.

Studies of capture rates are rare for this species. Lockie (1955) found a capture rate of 18 % (5/28) for a supposed female and 13 % (6/45) for a supposed male. Clark (1975) reported a capture rate of 24 % (42/192) for a male. Marr & MacWhirter (1982) provide very variable rates for three individuals of a family group: 71 % (12/17) and 44 % (7/16) for the adults, and 15 % (2/13) for the immature bird. The capture rate of 32 % (143/453) for the five males in this study is therefore an intermediate value. No significant difference in the capture success rate has been highlighted for the habitats where owls hunted, although the values reported suggest that habitats with short vegetation facilitate capture.

Heavy rainfall interfered with Short-eared Owl hunting to the extent of halting foraging even when they had young to feed. At the start of showers, the birds could opt for a hunting technique that probably favours sight, but when the rain persisted, they quickly stopped any foraging and went to perch. Géroudet (1984) reports that wind and rain entail difficulties in supplying the nestlings and can lead to them dying. A reduction in the number of prey items brought to young birds during rainy nights was reported for the Little Owl (*Athene noctua*) (Juillard, 1984) and Tawny Owl (*Strix aluco*) (Baudvin & Dessolin, 1987). Diminished hunting performances during rain have also been observed for the Long-Eared Owl (*Asio otus*) (Wijnants, 1984), Kestrel (*Falco tinnunculus*) (Masman, 1986), and even a halt in hunting for the Barn Owl (*Tyto alba*) (Michelat & Giraudoux, 1991). The rain seems therefore to be a factor restricting the hunting performances of many birds of prey, notably here, owls.

Counts of rodents in the nesting zone of the six pairs of owls indicate that small mammal populations were at comparable levels in the territories of the different pairs, particularly with regard to those rodents making up a large proportion of the diet. It seems that the hunting capabilities of the males were decisive for reproductive success.

The diets of the different owl pairs of the Bassin du Drugeon show a preference for Microtinae (Common and Field Voles), a result consistent with the literature quoted above. The proportion of Water Voles in the diet is high here and is to be related to the very high density of this rodent in the study zone.

Erkinaro (1973) reports that the Short-eared Owl's hunting activity coincides with periods when prey is active. Clark (1975) reports that in winter owls hunt mainly at dusk.

The differences in hunting efforts in the various habitats (measured by the percentage of attempted captures) are difficult to interpret without exact knowledge of the range of each individual. As these could be observed only at dusk the nocturnal part of their activity completely escaped observation. In addition, the males increased the size of their crepuscular territory as breeding advanced. Individuals with nestlings annexed part of the adjacent territories after the neighbours' young fledged or nesting failed. The hunting territories observed at dusk included almost equal proportions of marsh and grassland (Michelat, 1998). From the hunting frequency of Short-eared Owls, a larger proportion of Field Voles could be expected in the diet. The apparent under-representation of Field Voles may result from the observational bias mentioned above i.e. the activity of birds during the hours of darkness being unknown. Our results could therefore be interpreted as follows: males apparently hunted in marshes close to the nest at dusk (when observations were made) and switched to the grassland areas later in the night.

The correlation between the percentage of Water Voles in the diet and the marshland capture rate is surprising as it is in meadows that the species is by far the most abundant. It can be hypothezised that Water Voles are more vulnerable in marshes than in grassland where they lead a mainly underground existence (Saucy, 1988).

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