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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 France marsh

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Abstract

The results obtained during the seven years of this study on the Saintongeais marshes showed that the population of the common vole, *Microtus arvalis*, displays episodic outbreaks in the study site.

The reproductive biology of the Montagu's harrier, *Circus pygargus*, was studied in close relation to the dynamics of this rodent. All the breeding parameters of harriers showed significant variations from year to year. Some of them (nest density, production of young) were correlated to the available vole densities during the course of the breeding season.

The settlement of nesting pairs was directly correlated with yearly changes in the availability of common voles during spring.

A mean difference of up to two fledglings per nest could be observed between years with a high and low summer vole density. This latter result differs from those reported by certain authors on other harrier species and validates the hypothesis that such cyclic populations of voles directly affect the productivity of specialized populations of this raptor species in this kind of habitats.

Keywords: Breeding success, *Circus pygargus*, *Microtus arvalis*, vole cycle, specialist predator.

Résumé

Les résultats obtenus au cours de ces sept années d'étude dans les marais Saintongeais ont permis de mettre en évidence des explosions démographiques épisodiques de la population de campagnol des champs, *Microtus arvalis*.

La biologie de reproduction du busard cendré, *Circus pygargus*, a été étudiée en étroite relation avec la cinétique de population de ce rongeur. Nous observons des variations interannuelles significatives de tous les paramètres de la reproduction des busards. Certains d'entre eux (densité de nicheurs, production en jeunes) sont corrélables aux densités de campagnols disponibles au cours des diverses phases de la saison de reproduction.

La fixation des couples nicheurs sur le site d'étude était directement corrélable aux variations interannuelles de disponibilité des campagnols au printemps.

Une différence moyenne atteignant deux jeunes à l'envol par nid a pu être observée entre les années de forte et de faible densité estivale de campagnols. Ce dernier résultat diffère des observations rapportées par certains auteurs sur d'autres espèces de busards. Il nous permet de valider l'hypothèse du caractère "spécialiste" de ce rapace et d'une influence directe des populations cycliques de ce campagnol sur le succès reproducteur de ce prédateur dans ce type de milieu.

INTRODUCTION

The French Atlantic marshes cover an area of about 240 000 ha. The small mammal community of these marshes is dominated by the common vole (*Microtus arvalis*) which displays important cyclic variations in population density (SPITZ, 1974; BUTET & LEROUX, 1989, in press). A large community of raptors is also observed and these marshes are one of the most important nesting sites for the French population of the Montagu's harrier, *Circus pygargus* (LEROUX, 1987).

Montagu's harrier has a narrow prey spectrum but particular populations differ sometimes extremely in prey choice (SCHIPPER, 1973; KROGULEC, pers. com.). THIOLLAY (1968) found that this raptor was specialized on small mammals and mainly on common vole in western France marshes. Such predator-prey relationships provide good models for studying food-influenced reproduction since generalist predators are supposed to be less affected by cyclic fluctuations in a single prey. Consequently, diurnal and noctural raptors feeding on microtine species are the most commonly cited avian-mammal examples investigated to evaluate variations in nesting densities as well as breeding success and adaptive behavioural responses to prey fluctuations (LOCKIE, 1955; HAGEN, 1969; GALUSHIN, 1974; HAMERSTROM, 1979; VILLAGE, 1981; SIMMONS *et al.*, 1986).

Main studies on harriers reported no reliable correlation between food availability and the number of young produced (HAMERSTROM, 1979; SIMMONS *et al.*, 1986). During this 7-year field study, we used a large prey sampling scale to obtain reliable local vole density data during successive harrier breeding seasons. Comparative analysis of these data with harrier nesting densities and various other breeding parameters enabled us to test the hypothesis of food-influenced breeding biology in this predator-prey model.

STUDY AREA

The study area (Saintongeais marshes) (45°57' N, 0°55' W) is situated on both sides of the Charente river (Charente-Maritime, France). The sampling area extended over 300 km^2 and its spatial structure comprised parts with different histories: old salting marshes abandoned for several centuries and drained flat marshes. The soil, with this surface heterogeneity and associated differences in hydromorphy, supports various plant communities from reed swamp to grassland. A dense ditch network delimits the parcels where extensive grazing represents the most common land use. Currently both an extension of the fallow land due to the abandonment of pastures and an intensification of wheat cultures on recently drained areas are observed.

This heterogeneity of land use offers various nesting sites for raptors characterized by dense and tall herbaceous communities (*Carex spp., Scirpus spp....*) and ungrazed or old abandoned pastures. Wheat fields constitute new nesting sites.

METHODS

The dynamics of the vole population was sampled by the line live trapping method using the live traps model (INRA, AUBRY, 1950). We used 20 trap lines randomly located on different parcels respecting the relative importance of agricultural land use within the study area. In practice, there were 4 trap lines in cultivated fields, 4 in herbaceous fallows and 12 distributed on both grazed and ungrazed pastures. Trap lines were about 2 kilometers apart to avoid problems of variations in local prey abundance and comprised 51 traps spaced 2 meters of each others and placed for 48 hours (equivalent to 2040 trap nights per trapping session). The number of trapping sessions varied between years but sampling was always maintained during spring (end of April or early in May) at the arrival of harriers, during summer (July) corresponding to the intensive provisioning phase, in autumn (October) when generally the vole population is at its yearly peak and in winter to appreciate the winter decline. A mean local relative abundance of the vole population can then be expressed by the trap night index (*i.e.* number of animals caught per 100 trap nights) which is commonly used. For the common vole, the number of captures can be converted into density per hectare using a standardized method (SPITZ *et al.*, 1974), based on different conversion factors of capture numbers. These correction factors were obtained from differences in vole activity according to season, sex, age for both sexes, and sexual activity of females. We collected these biological parameters to use these trap line coefficients which, for the western French common vole population, have been previously tested and described by SPITZ (1977). Vole age was estimated using the lens weight method (MARTINET, 1966). The sex-ratio and the sexual activity of females was estimated during autopsies.

164 potential nesting sites were recorded over the 300 km^2 of the study area by an air survey. They were visited one to three times during the breeding season. The nest searching method has been described in detail by LEROUX (1987). Depending on searching difficulties, the areas prospected ranged from 0.5 to 10 km^2 per half-day. Nesting densities were recorded by the general census method for raptors (THIOLLAY, 1968; LEROUX, 1987) and expressed as the number of nesting pairs per 10 km^2 including both located nests and settled oairs exhibiting typical nesting behaviour such as male food provisioning and/or territorial defence. Clutch size, hatching and fledging success were noted for each located nest. The fledging success was assessed both from the mean fledging success of all nests and mean fledging success of successful pairs (*i.e.* raising at least one fledgling). A one way analysis of variance was used to analyse the yearly variations of the various breeding parameters and their relationship with the vole density fluctuations was assessed by a Spearman rank correlation (r_s) using a two-tailed hypothesis.

We considered that only food conditions in spring (May) could influence the first events of breeding and may be related to nest numbers as well as to laying and hatching efficiency. On the other hand, fledging success should be more closely related with prey availability in summer (July), since breeding pairs of harriers had large nestlings dependent on provisioning conditions at that time (SIMMONS *et al.*, 1986).

RESULTS

Variations in vole density

Figure 1 shows vole densities during successive harrier breeding seasons. When harriers arrived in the study site in spring (end of April), the estimated mean vole densities varied between 1 (spring 1986) and 85 (spring 1990) voles/ha. The changes in vole density also differed between the seven breeding seasons. The outbreaks observed in 1987 and 1992 were characterized by a rapid increase in mean local density. During these two years densities increased up to 325 ind./ha and 170 ind./ha at the autumn peaks. In contrast, low vole densities were observed in 1986, 1988, 1989 and 1991, autumn peaks being between 30 and 70 voles per hectare. We observed an intermediate vole density in 1990 with an autumn density around 120 voles per hectare. These results indicate that the vole population in this region displays periodic fluctuations and may be considered a cyclic one. The mean increase rates of the vole population differed between years and there was no significant correlation between vole density in spring and autumn ($r_s=0.61$, $n=7$). This indicates that sampling must be maintained in spring and summer to evaluate food conditions for harriers during their breeding season. The necessity for large scale sampling on the various types of land was confirmed by the differences in density observed within trapping sessions. For example in October 1987 density varied from 560 voles per hectare in one abandoned old field to 150 voles per hectare in the least populated parcel.

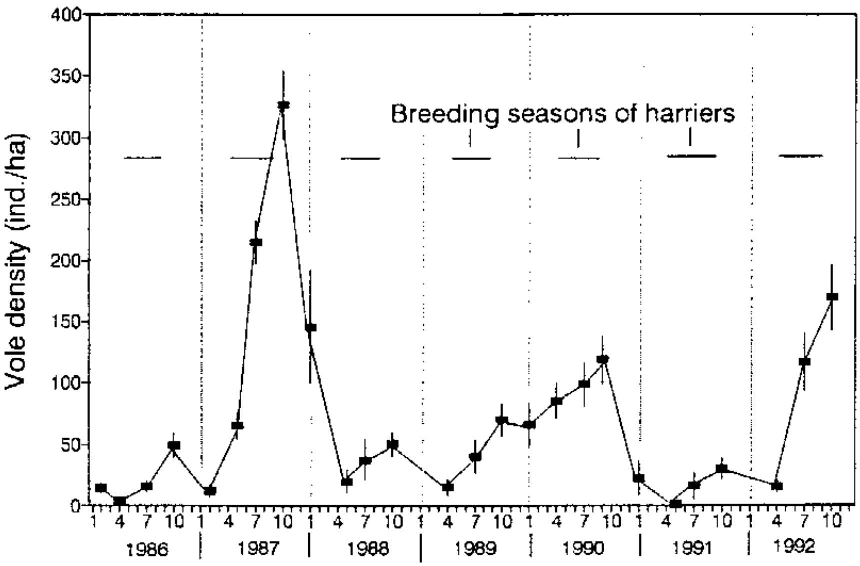

FIG. 1. – General pattern in fluctuations of the mean vole density during seven successive years (1986-1992) in the "Saintongeais marshes". Plotted values with standard error were obtained at the end of April or early in May, July, October and some winter values in January or February.

Harrier breeding parameters

217 nests were used for analysis during the seven years of the study. The nesting density ranged between 0.6 and 3.0 nests / 10 km^2 (table I). Fluctuations in nest numbers were correlated with spring vole densities over 7 years ($r_s=0.88$, $n=7$, $p<0.05$, fig. 2 *a*).

During the seven years of the study 162 nests were inspected for clutch size (table I). The mean values ranged from 2.8 eggs to 4 eggs and varied significantly between breeding seasons ($F_{6,40}=2.82$, $p < 0.05$). Mean clutch size was not correlated with spring vole density ($r_s=0.67$, $n=7$).

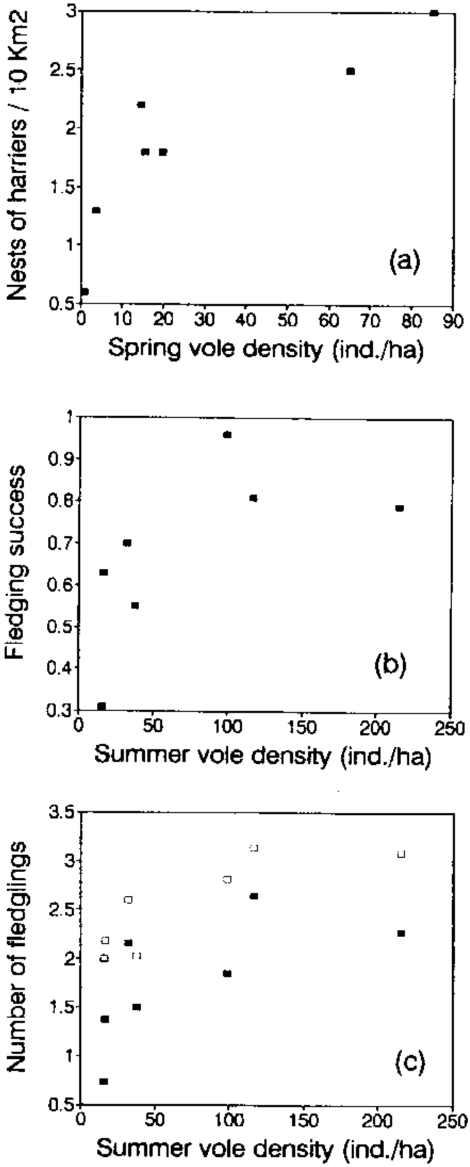

FIG. 2. – Various breeding parameters of harriers plotted against vole density during 1986-1992. (*a*) Nests/10 km^2 versus spring vole density ($r_s = 0.88$, $p < 0.05$). (*b*) Fledging success versus summer vole density ($r_s = 0.75$, $p < 0.05$). (*c*) Number of fledglings versus summer vole density, on all nests (black squares, $r_s = 0.85$, $p < 0.05$), on successful nests (empty squares, $r_s = 0.85$, $p < 0.05$).

As for clutch, we observed a significant variation in the mean number of hatchlings during the seven years of the study ($F_{6,38} = 3.5$, $p < 0.05$). Differences between breeding seasons exceeded one hatched young per nest (table I). The mean number of hatchlings was not significantly correlated with spring vole densities ($r_s = 0.18$, $n = 7$).

Hatching and fledging success varied significantly (table I) between years ($F_{6,43} = 2.28$, $p < 0.05$ and $F_{6,37} = 5.17$, $p < 0.05$, respectively). Hatching success was neither correlated with spring vole density ($r_s = -0.04$, $n = 7$) nor summer vole density ($r_s = 0.43$, $n = 7$). Only fledging success showed a significant correlation with summer vole density ($r_s = 0.75$, $n = 7$, $p < 0.05$, fig. 2 *b*).

The mean number of fledglings calculated with all breeding pairs or with only successful nests showed significant variation over the seven breeding seasons ($F_{6,60} = 4.45$ and $F_{6,44} = 5.76$ respectively, $p < 0.05$). The difference in the mean production of youngs by all pairs could reach two birds. There was a significant relationship of these two parameters with summer vole densities ($r_s = 0.86$, $n = 7$, $p < 0.05$, fig. 2 *c*).

Nest failures varied greatly from year to year (table I) but were not correlated with summer vole density ($r_s = -0.27$, $n = 7$).

TABLE I. – *Variations in breeding density, nest failures and mean values of clutch, hatch and young harriers produced during 1986-1992. Mean values with standard error and sample size.*

	1986	1987	1988	1989	1990	1991	1992
Nests/10 km²	1.3	2.5	1.8	2.2	3.0	0.6	1.8
Clutch size	3.43	3.80	3.48	3.61	3.80	2.81	4.05
	0.16 (23)	0.15 (40)	0.17 (25)	0.14 (18)	0.21 (25)	0.40 (11)	0.18 (20)
Nb. of hatchlings	2.37	3.26	2.71	3.46	2.25	2.09	3.65
	0.33 (27)	0.24 (38)	0.32 (24)	0.19 (15)	0.34 (20)	0.48 (11)	0.27 (20)
Nb. of fledglings							
– all nests	1.37	2.27	1.50	2.16	1.85	0.73	2.64
	0.21 (35)	0.22 (60)	0.18 (42)	0.29 (18)	0.29 (26)	0.38 (11)	0.29 (25)
–successfull nests	2.18	3.09	2.03	2.60	2.82	2.00	3.14
	0.17 (22)	0.17 (44)	0.16 (31)	0.21 (15)	0.20 (17)	0.70 (04)	0.20 (21)
Hatching success	0.68	0.77	0.73	0.89	0.61	0.64	0.96
	0.08 (24)	0.05 (43)	0.07 (29)	0.07 (15)	0.09 (18)	0.13 (11)	0.02 (18)
Fledging success	0.63	0.79	0.55	0.70	0.96	0.31	0.81
	0.11 (19)	0.05 (37)	0.07 (24)	0.09 (14)	0.03 (14)	0.12 (08)	0.06 (18)
Nest failures (%)	9.1	15.4	19.3	16.6	33.3	84	16.6

DISCUSSION

NEWTON (1979) mentioned several studies reporting that vole cycles influenced certain breeding parameters of various raptor species (*Circus cyaneus, Falco tinnunculus, Buteo buteo*). For example, BALFOUR (1962), CAVÉ (1968), HAMERSTROM (1979), ROCKENBAUCH (1969), VILLAGE (1979) and SIMMONS *et al.* (1986) reported that prey abundance affected nesting density in different raptor species. Our data suggest that density of harriers in our study area was also influenced by yearly variations in vole abundance at the onset of harrier breeding. HAMERSTROM (1979) pointed out that nesting of harriers (*Circus cyaneus*) in central Wisconsin was strongly linked to vole (*Microtus pennsylvanicus*) abundance during 3 out of 4 peak years within a 16-year period. This strong relationship is surprising considering the more eclectic diet of this harrier species (Hamerstrom, 1979; Simmons *et al.*, 1986). The frequency of presentation of prey to females by males may be an important explaining mechanism. When voles are abundant, males often present females with small tidbits. When voles are scarce, harriers turn to larger quarry (birds) and the female is less often stimulated (Hamerstrom, 1979). Sexual urge and provisioning rate should be interrelated (Balfour, 1963, *in* Hamerstrom, 1979).

The clutch size in the Saintongeais marshes is one of the smallest observed in Europe (5.15 in Great Britain, Brown, 1976; 4.25 in Poland and 4.13 in Andalusia, Kroguleс, pers. com.; 4.24 in the Netherlands, Schipper, 1978; 3.6, Cormier, 1985 at Noirmoutier France; 3.64 for 162 nests in the present study). Prey-dependent clutch size variations were found in the European buzzard *Buteo buteo* (Mebs, 1964). On the other hand, Simmons *et al.* (1986) reported that harrier females appeared to be in a better condition for egg laying in years with high food abundance. We observed important variations of the clutch size between years but differences were not significantly correlated with prey abundance and the small clutch size in our study area is probably dependent on other factors than prey availability.

Simmons *et al.* (1986) reported that breeding success of northern harriers was positively, but not significantly, related to availability of meadow voles. Hamerstrom (1979) reported no reliable correlation when studying the same species in Wisconsin. Simmons *et al.* (1986) explained this trend by a prey shift at harrier hatch. Northern harriers in New Brunswick fed mainly on voles during the breeding season, but nestling and fledgling birds in mid-June constitute a new available prey source and have a boosting effect on harrier reproduction, especially when voles are scarce. This prey shift confers a more generalistic character to northern harriers and consequently disturbs the expected vole-related effects. A similar explanation can be given for Hamerstrom's (1979) findings.

Our preliminary observations on nest provisioning after hatching (Butet & Leroux, 1989), showed that voles remained the main prey even when density was low and only feeding rates seemed to vary slightly according to microtine availability. This agrees with Thiollay (1968) who observed that Montagu's harrier fed almost exclusively upon the common vole in another nearby breeding site. The significant vole-related fledging success observed in the Saintongeais marshes probably reflects this single prey dependency.

Simmons *et al.* (1986) reported that predation rates on nests were lower when vole densities were high. Within the Saintongeais marshes, predation is responsible for about 45% of nest failures (Leroux, 1989) but we did not observe a close relationship between prey availability and nest failures.

Newton (1979) mentioned several studies showing that breeding parameters affected by voles cycles varied according to raptor species. For example, an increase of young productivity has been demonstrated in the case of *Buteo buteo* (Rockenbauch, 1975) and *Falco tinnunculus* (Village, 1979) but never reported for harrier species. Recently, Korpimäki (1992) studied the breeding success of long-eared owls in west Finland. This raptor appeared to be specialized on common vole *Microtus epiroticus* and its density, clutch size and production of youngs was clearly dependent on spring density of this rodent. This demonstrates that Montagu's harriers are food-specialized raptors in west France marshes and supports the idea of a food-influenced breeding success in this kind of habitat where the common vole is the most dominant and cycling prey species.

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