

RESPONSES OF AN AVIAN PREDATOR TO VARIATIONS IN PREY DENSITY AT A TEMPERATE LATITUDE

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Abstract. Fluctuating prey populations and their effects on avian predator population dynamics have been studied particularly at high latitudes, where prey populations, especially microtines, are known to be cyclic; raptors show both numerical and functional responses to variations in their prey. In this paper, we investigate the response of a migratory raptor (Montagu's Harrier, *Circus pygargus*) to variations in abundance of its main prey (common vole, *Microtus arvalis*) in France. We document multiannual fluctuation in the abundance of common voles. The numerical response of Montagu's Harrier to this variable food supply was studied using breeding parameters (breeding density, breeding phenology, and various measures of breeding success). Breeding density and mean clutch size were strongly correlated with spring vole abundance, whereas mean brood size at fledging was correlated positively with summer vole abundance. The mechanism involved in the numerical response of Montagu's Harrier indicates that dispersal and colonization by yearlings may be more important than natality per se. Pellets collected between 1986 and 1997 were used to determine the functional response of Montagu's Harrier to variations in vole abundance. In terms of biomass, Montagu's Harrier diet consisted mainly of voles (33.7–86.6%, between 1986 and 1997). Vole biomass in pellets was closely related to vole abundance estimated by trapping. A type II functional response was detected, with satiation at high prey density, as the shapes of many relationships between breeding parameters and vole abundance were more curvilinear than linear. Our results fit the pattern of relationships between predators and cyclic prey found in Fennoscandia, in which specialist predators show a strong numerical response, although at such a temperate latitude, a more pronounced functional response might have been expected.

Key words: *Circus pygargus*; common vole; cyclic prey; Fennoscandia; functional response; microtine rodent; *Microtus arvalis*; Montagu's Harrier; numerical response; predator; small-mammal cycles; variable prey density.

INTRODUCTION

The relationships between predators and variations in prey density have been the subject of many studies. Solomon (1949) suggested that these relationships were of two types, numerical and functional. The numerical response is the relationship between the numbers of predators and the numbers of their prey, whereas the functional response describes how the rate of prey capture varies with prey abundance (Andersson and Erlinge 1977). Under a numerical response, the predator adapts its breeding effort or its numbers to the numbers of the prey, through differential natality or emigration (usually without time lags). The functional response is determined by other life history traits of the predator, or its foraging or social behaviors (Andersson and Erlinge 1977, Village 1981, Korpimäki and Norrdahl 1991). Empirical and experimental studies have revealed that three types of functional response exist,

according to the nature of the relationship between predation rate and prey density (Holling 1959): linear (type I), convex (type II), and concave or sigmoid (type III). Studies of invertebrates have shown that predators that can switch to alternative prey are more likely to produce sigmoidal functional responses; this has also been shown in vertebrates (Keith et al. 1977). Functional response curves of avian and mammalian predators are usually convex (Murdoch and Oaten 1975, Keith et al. 1977, Linden and Wikman 1983, Korpimäki and Norrdahl 1991, Dale et al. 1994), although linear responses have sometimes been documented (Korpimäki and Norrdahl 1989, 1991; review in Boutin 1995).

Raptors show both numerical (Newton 1976, Phelan and Robertson 1978, Smith et al. 1981, Korpimäki and Norrdahl 1989, 1991) and functional responses (review in Sonnerud 1992) to variations in food supply. Interestingly, both response types have been recorded in the same species, either at different times in the same area, or in different localities (Luttich et al. 1971, Phelan and Robertson 1978). Two predator strategies have been identified that differ in their reaction to variations of prey densities, and possibly in their effects on prey

Manuscript received 20 July 1998; revised 15 September 1999; accepted 30 September 1999.

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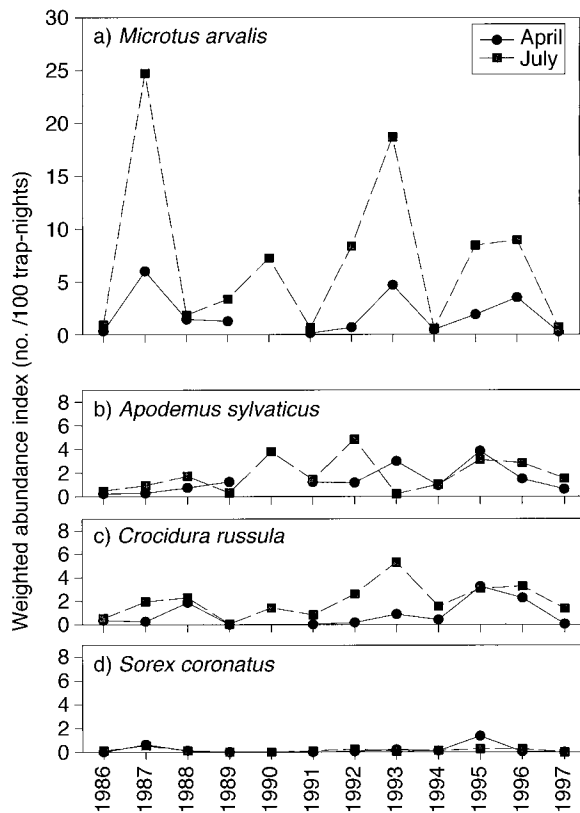


FIG. 1. The weighted abundance (see Table 1) of the four species of small mammals trapped in April (circles) and July (squares) at Rochefort, during the period 1986–1997: (a) common voles, *Microtus arvalis*; (b) wood mice, *Apodemus sylvaticus*; (c) white-toothed shrews, *Crocidura russula*; (d) French shrews, *Sorex coronatus*.

dynamics (Andersson and Erlinge 1977, Korpimäki and Krebs 1996). Resident generalist predators respond numerically to increases in prey abundance with a time lag (e.g., Ryszkowski et al. 1973, Goszczynski 1977), through higher natality, lower mortality, and immigration (Erlinge et al. 1983). They usually show a type II functional response to increases in their preferred prey (Keith et al. 1977, Linden and Wikman 1983). In contrast, the numerical response of nomadic specialists seems to be based on mobility, as these predators track changes in prey density without a time lag (Korpimäki and Norrdahl 1991). It has been suggested that the response strategy of raptors varies with latitude, being mainly numerical at high latitudes and functional at lower latitudes (e.g., Korpimäki 1986b). However, it is sometimes difficult to separate raptors that show numerical response from those with functional response. Common Kestrels *Falco tinnunculus*, for example, can adopt either strategy, depending on prey availability (Village 1987). Numerical responses have also been documented in non-arctic or boreal ecosystems (Pierce and Maloney 1989).

Cyclic prey populations and their effects on avian

predator populations have been studied in particular at high latitudes (Newton 1979, Norrdahl and Korpimäki 1996; see Silva et al. 1995, Jedrzejewski et al. 1996, for studies conducted at lower latitudes). Cyclicity in microtine populations is clinal with respect to latitude in Fennoscandia (Hanski and Henttonen 1996), and the different response of raptors could be a consequence of this cline (Luttich et al. 1971, Phelan and Robertson 1978). In this paper, we investigate the response of a migratory raptor, the Montagu's Harrier *Circus pygargus*, to variations in densities of its main prey in a temperate region. In our area, this species is semicolonial (i.e., it does not defend feeding territories), and feeds principally on the common vole, *Microtus arvalis*, which is highly variable in density (Butet and Leroux 1989). Based on a seven-year study, several parameters of this harrier population have already been shown to be positively correlated with vole density (Butet and Leroux 1993), whereas others are not, e.g., fledging sex ratios (Leroux and Bretagnolle 1996). Our aims were to investigate fluctuations in small-mammal abundance, and the numerical (abundance) vs. the functional responses (diet) of Montagu's Harriers to these fluctuations. We compare Montagu's Harrier–common vole relationships to the predator–microtine patterns found in Fennoscandia, and discuss the mechanism involved in the numerical response.

MATERIALS AND METHODS

Study area and species

Montagu's Harriers have been studied since 1986 in marshes north of the estuary of the Charente (Charente-Maritime, France, 45°57' N, 0°55' W). The study area extends over 170 km² (for details, see Butet and Leroux 1993), and is dominated by drained lowland marshes with a few cultivated patches on higher grounds. The study area is surrounded by intensely cultivated fields. Grasslands and pastures, delimited by ditches, were the predominant land type when the study began. Grasslands have been progressively converted into cultivated fields, the latter representing 12% of the total area in 1987 and increasing to 49% in 1994. These changes resulted not only in the disappearance of some permanent pastures, but also in an increase in field size and a reduction in the number of ditches.

The Montagu's Harrier is one of the smallest of its genus (Nieboer 1973, Leroux and Bretagnolle 1996). The breeding range of this strictly migratory bird is from North Africa, and West and Central Europe across to India, but it winters only in Africa and India (Cramp and Simmons 1980, Clarke 1996). It is semicolonial, at least in some regions, with a flexible pattern of nest distribution, ranging from solitary to colonial (up to 28 pairs on a 22-ha plot; Krogulec and Leroux 1994).

Nests were sought systematically each year by following adult females after a food pass. Once discovered, they were visited 2–4 times during the breeding

TABLE 1. Spring and summer abundance of common voles (*Microtus arvalis*) at Rochefort during the period 1986–1997.

Habitat and measurement	1986		1987		1988		1989		1990†	1991	
	April	July	April	July	April	July	April	July	July	April	July
Cereals											
No. ind.	0.00	1.47	3.92	19.26‡	0.49	0.49	2.45	3.92	4.57	0.00	0.00
No. lines	2	4	4	0	4	4	4	1	3	3	2
Fallowes											
No. ind.	0.00	0.00	10.78	37.24	9.80	3.27	0.00	3.92	15.68	0.49	5.23
No. lines	2	1	2	1	1	3	1	3	1	4	3
Pastures											
No. ind.	0.37	0.91	5.88	25.58	0.90	2.11	0.78	3.01	8.23	0.16	0.52
No. lines	16	15	13	19	13	13	15	15	15	12	15
Weighting coefficient§											
Cereals				0.12					0.41		
Fallowes				0.07					0.07		
Pastures				0.81					0.52		
Weighted abundance for the study area											
No. ind.	0.30	0.92	5.99	24.66	1.44	1.84	1.26	3.36	7.24	0.12	0.63
No. lines	20	20	19	20	18	20	20	19	19	19	20

Notes: Data are expressed as “no. ind.,” the number of individuals trapped per 100 trap-nights and “no. lines,” the number of trap lines (see *Methods*) and are then weighted by the relative proportions of habitat types.

† No data available for spring 1990.

‡ Missing value estimated using the regression of vole abundance in July and that in April ($r = 0.773$, $n = 9$, $P = 0.014$).

§ Weighting coefficients have been estimated from relative proportions of the different crops, which were mapped in 1987, 1990, and 1994. Values between these dates were estimated by interpolation. Proportions of the different types of habitat are considered to have been constant before 1987 and after 1994.

season to record clutch size, hatching, and fledging success. However, some nests were found at a later stage (e.g., chick rearing); thus, we could have missed some nests that failed early. Each year, the same effort was put into monitoring harriers and the same area was covered. Laying dates were estimated by direct observation in some cases, and by back-calculation from the wing length of fledglings in other cases (Arroyo 1995, Brignon 1997). At the start of the breeding season (April and early May), pairs defend small territories around nests, but some may fail to breed. We distinguished between settled pairs (showing territorial behavior) and breeding pairs (laying eggs). Density (of settled or breeding pairs) is defined as the number of pairs/10 km². The “decade” (a 10-d period) of laying was defined as the date by which 75% of first eggs were laid (decade 1 was the first decade of March). A 10-d interval was chosen because eggs are laid on average every two days, and the range in clutch sizes is 2–8 eggs. Numbers of eggs laid and fledglings produced were obtained for each nest checked and were averaged for each year. Breeding success was calculated by brood size/clutch size for each nest (brood sizes of zero included), and was averaged for each breeding season.

Analysis of diet

Three methods traditionally have been used to analyze breeding-season diets of raptors: observations of prey deliveries to nests, identification of prey remains at nest or perch sites, and pellet analysis. We used the

latter, although all techniques have advantages and disadvantages (Collopy 1983, Simmons et al. 1991, Real 1996). Prey remains may better represent bird remains than pellet analysis (Sanchez-Zapata and Calvo 1998), but Montagu's Harriers mostly eat small prey, and remains of this kind were rare (<1% of the total number of prey in this study). In total, 1216 pellets (8817 prey items) were collected and analyzed between 1986 and 1997 ($n = 11$ years, 1987 excluded). The number of pellets varied between years according to harrier breeding density. We converted totals of each identified prey type to biomass, using mean values. Mammal remains were identified from teeth, from which we calculated the number of individuals per pellet. When only fur was present, we assumed that there was only one “undetermined mammal” per pellet. Undetermined mammals were attributed to different groups based on their relative percentages per year and period ($16.6 \pm 10.6\%$ of the diet; range 0–38.1%). Mean biomass values were: common vole (*Microtus arvalis*), 20 g ($n = 700$; M. Salamolard, A. Butet, A. Leroux, and V. Bretagnolle, unpublished data); wood mouse (*Apodemus sylvaticus*), 20 g; and shrews (*Sorex* and *Crocidura*), 8 g. Bird prey could not be identified to species; pellets contained only small feathers and occasionally mandibles or breast bone pieces (mean biomass 20 g). Frogs and reptiles (exclusively lizards, 10 g) were recognized by mandibles and other bones. We used only mandibles to identify families of large insects (mean biomass 0.8 g): Gryllotalpidae (solely *Gryllotalpa gryllotalpa*), Gryllidae (mainly the cricket *Gryllus campestris*), and

TABLE 1. Extended.

1992		1993		1994		1995		1996		1997	
April	July	April	July	April	July	April	July	April	July	April	July
0.00 1	5.88 3	3.92 1	25.48 1	0.00‡ 0	0.00 2	1.47 4	10.29 4	2.61 12	9.80 12	0.16 12	0.49 12
1.96 2	23.52 1	5.88 3	22.21 3	0.00 3	6.86 2	4.41 4	10.78 4	3.92 4	9.02 5	0.00 4	1.63 6
1.10 16	8.45 16	5.27 16	11.20 14	0.98 8	0.15 13	1.96 12	6.06 11	4.41 20	8.05 19	0.31 19	0.65 18
				0.49 0.07 0.44							
0.67 19	8.35 20	4.68 20	18.67 18	0.46 11	0.55 17	1.89 20	8.45 19	3.50 36	8.97 36	0.22 35	0.64 36

species in Odonata, Acrididae, and Tettigoniidae. Mean biomass was 0.5 g for Coleoptera and 0.1 g for Diptera.

Prey biomass data were averaged by year or breeding stage (pre-laying, incubation, and chick rearing from nestling through postfledging), determined each year from known laying dates. We used a 30-d incubation period (Cramp and Simmons 1980, Arroyo 1995) starting in the decade when 75% of breeding pairs laid their first egg. First arrivals from wintering areas were always seen in the first 10 days of April (M. Salamolard, A. Butet, A. Leroux, and V. Bretagnolle, *unpublished data*). Diet width (DW) was calculated as $DW = 1/\sum p_i^2$, where p_i is the proportion of prey category i in the diet. To estimate prey consumption per breeding pair for a given year, we calculated the number of prey items (NPI) from the equation of Linden and Wikman (1983), used by Korpimäki and Norrdahl (1991):

$$NPI = ((CA + CY) PPI) / (MMPI \times 10).$$

CA is total food consumption by a pair during the breeding period (twice the daily food requirement of an adult, multiplied by a 130-d breeding period). Mean body mass of adult Montagu's Harriers (males 276.3 g, $n = 12$; females 337.7 g, $n = 17$; M. Salamolard, A. Butet, A. Leroux, and V. Bretagnolle, *unpublished data*) is comparable to that of Short-eared Owls (*Asio flammeus*). Thus, we estimated harrier food requirements as 50 g for adults and 40 g for young birds (Korpimäki and Norrdahl 1991). CY is total food consumption by a young bird during the breeding season (mean brood size per year at fledging, multiplied by a 35-d duration from hatching, arbitrarily set from 25 June to 1 August). PPI is the proportion of the prey type (by biomass) in the harrier diet each year. MMPI is mean mass of the prey type.

TABLE 2. Values and significance levels of Spearman rank correlation coefficients between the abundance (see Table 1 for the method of calculation) of the four different species of small mammals (*Microtus arvalis*, *Apodemus sylvaticus*, *Crocodyrus russula*, and *Sorex coronatus*) trapped in the study area during the period 1986–1997 ($n = 11$ years).

Species	Spring abundance (April)				Summer abundance (July)			
	<i>M. arvalis</i>	<i>A. sylvaticus</i>	<i>C. russula</i>	<i>S. coronatus</i>	<i>M. arvalis</i>	<i>A. sylvaticus</i>	<i>C. russula</i>	<i>S. coronatus</i>
April								
<i>M. arvalis</i>		0.321	0.575	0.787	0.909	0.054	0.757	0.273
<i>A. sylvaticus</i>	0.36		0.345	0.350	0.345	0.050	0.600	0.385
<i>C. russula</i>	0.08	0.33		0.669	0.479	0.450	0.733	0.636
<i>S. coronatus</i>	0.007	0.32	0.03		0.763	0.365	0.800	0.446
July								
<i>M. arvalis</i>	0.0001	0.33	0.16	0.01		0.227	0.709	0.220
<i>A. sylvaticus</i>	0.88	0.90	0.22	0.33	0.5		0.309	0.412
<i>C. russula</i>	0.01	0.08	0.02	0.009	0.01	0.36		0.556
<i>S. coronatus</i>	0.44	0.31	0.07	0.23	0.51	0.21	0.07	

Notes: The sequential Bonferroni correction was applied in order to take into account multiple tests on the same data set; significant coefficients are shown in bold type. Correlation coefficients are shown above the diagonal, and probability levels below the diagonal.

TABLE 3. Percentages of the different prey types (on a biomass basis) in the diet of Montagu's Harriers (*Circus pygargus*) at Rochefort during the period 1986–1997.

Measurement	1986	1988	1989	1990	1991
A) Prey type (%)					
Mammals	57.6	72.4	55.6	82.6	42.4
<i>Crocidura russula</i>	0.6	1.0	0.8	0	1.9
<i>Sorex coronatus</i>	2.5	0	0.8	0	0.4
<i>Apodemus sylvaticus</i>	5.1	0	4.5	0	0
<i>Microtus arvalis</i>	49.2	71.4	49.5	82.6	40.1
Birds	2.4	10.4	5.7	2.1	8.7
Reptiles	0	0	0	0	4.1
Frogs	0	0	0	0	0
Insects	39.8	17.1	38.6	15.3	44.8
Grillotalpidae	0.6	1.5	0.1	0.2	0.9
Gryllidae	10.4	4.6	24.5	13.5	21.3
Odonata	10.5	10.6	6.0	1.2	12.8
Acrididae/Tettigoniidae	17.4	0.3	8.0	0.3	9.4
Other insects	0.7	0.00	0.1	0.0	0.2
B) Diet width†	3.34	1.87	3.12	1.42	4.15
C) Sample size (n)					
No. pellets (total = 1216)	78	83	69	60	196
No. items (total = 8817)	865	443	726	267	2233
No. nests‡	6	10	11	13	7

† Diet width (DW) was calculated as: $DW = 1/\sum p_i^2$, where p_i is the proportion of prey category i in the diet.

‡ The number of nests sampled is minimal because some of the pellets were collected from within colonies.

Small-mammal abundance

We used line trapping to estimate species composition and relative abundance of small mammals over this large area. This method is considered particularly appropriate for assessing the amplitude of fluctuations of the harriers' main prey, the common vole (Spitz et al. 1974). Each trapline was 100 m long, consisting of 51 live traps (without bait, type INRA; Aubry 1950), spaced every 2 m, set for 48 h, and checked every 24 h (Butet and Leroux 1993, 1994). The number of traplines varied from 20 to 36 per trapping session. Thus, trapping effort varied from 2040 to 3762 trap-nights per trapping session. One session was in spring (April) and the second in summer (July). A trapping session lasted 4–6 d. Lines were located in three main habitats, cultivated fields, pastures, and fallows, the main habitats used by harriers for hunting (Salamolard et al. 1996). We did not sample woods and marshes. Traplines were placed within the field, perpendicular to the border. The total number of individuals per species caught per trapline was converted either into relative abundance (trapline index = number of individuals/100 trap-nights) averaged per habitat, or into densities (following Spitz et al. 1974). Proportions of the three habitat types changed during the study, so we adjusted the area of each habitat annually to calculate overall vole abundance. Land use over the whole study area was mapped in 1987, 1990, and 1994. We estimated relative proportions of the three habitat types for the other years by interpolation (see Table 1).

Statistical analysis

Statistical analyses were done using SAS 6.03 (SAS 1988). When variables were not normally distributed,

or when sample size was small, we used nonparametric tests. Significance level was set at 0.05, except when multiple tests were done on the same data set, when we applied sequential Bonferroni correction to adjust significance levels. To assess the shape of numerical and functional responses to vole abundance, we compared curve-fitting obtained using linear vs. nonlinear regression models with R^2 as a measure of fit. Nonlinear fit was obtained using PROC NLIN (SAS 1988), with the Holling disc equation ($y = ax/1 + b.x$). This equation was chosen because it best describes functional and numerical responses in simple two-species systems. We used corrected R^2 rather than raw R^2 (the latter being overestimated). All means are expressed ± 1 SD.

RESULTS

The small-mammal community and fluctuations in its abundance

The species diversity of the small-mammal community in our study area was relatively low, with four species accounting for 99.1% of the total numbers trapped. These were common vole, wood mouse *Apodemus sylvaticus*, French shrew *Sorex coronatus*, and white-toothed shrew *Crocidura russula*. Voles alone accounted for most of the total biomass (Fig. 1), 23% to 92% of the small mammals trapped, and 61% to 92% during the peak vole years. No long-term trend was detectable for any of the four species (common vole, $r_s = -0.04$; wood mouse, $r_s = 0.57$; common shrew, $r_s = 0.18$; white-toothed shrew: $r_s = 0.04$; all $P > 0.05$). Standard deviation of log-transformed annual population densities (see Fryxell et al. 1998) ranged from 0.24 to 0.60, and was highest for the common

TABLE 3. Extended.

1992	1993	1994	1995	1996	1997	Mean	CV
78.0	89.7	43.1	84.9	86.6	50.0	67.6	18.2
1.1	0.3	6.2	8.1	0.2	0.5	1.9	2.7
0.5	0	0	0	0	0	0.4	0.8
0	2.8	3.2	0.9	0	0	1.5	2.0
76.3	86.6	33.7	75.9	86.3	49.5	63.8	19.6
3.1	4.0	12.8	4.0	5.1	15.1	6.7	4.4
0	0	0.4	0	0.3	1.1	0.5	1.2
0	0	0.4	0	0	0	0.0	0.1
18.8	6.3	43.3	11.0	8.1	33.8	25.2	15.0
0.2	0.3	0.9	0.7	0.1	0.7	0.6	0.4
8.7	1.4	10.0	1.7	2.6	18.2	10.6	8.0
1.7	1.6	27.1	1.8	1.1	0.2	6.8	8.1
8.1	2.9	5.3	0.5	3.8	14.1	6.4	5.7
0.1	0.0	0.1	6.2	0.4	0.6	0.8	1.8
1.67	1.33	4.52	1.7	1.33	3.12		
105	113	129	110	150	123		
564	318	1437	587	517	860		
9	13	5	11	16	5		

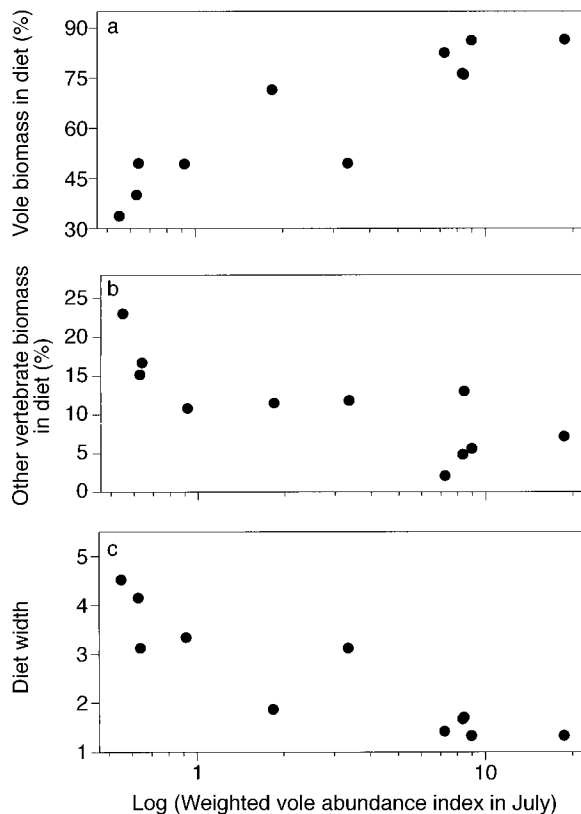


FIG. 2. The relationships between vole abundance (log transformed) and three parameters of the diet of Montagu's Harriers (1986–1997): (a) the percentage of voles in the diet; (b) the percentage of other vertebrates in the diet; and (c) diet width.

vole. A value of 0.60 is high compared to similar values obtained for other small mammals (for a review, see Ostfeld 1988), but within the range for other common vole populations (review in Mackin-Rogalska and Nabaglo 1990). Vole abundance was 50 times higher in April between peak and low vole years, and 45 times higher in July. Vole abundance during the study period (1986–1997) showed four peaks of density, 1987, 1990 (data were not available for April 1990), 1992–1993, and 1995–1996 (Fig. 1, Table 1). The highest vole abundance was obtained in July 1987, with 24.7 individuals/100 trap-nights, which is equivalent to a density of ~ 215 individuals/ha (from calculations in Spitz et al. 1974). The lowest densities were obtained in 1986, 1988, 1991, 1994, and 1997 (Table 1). The common vole possibly showed cyclicity in density in our study area (Fig. 1), as suspected from analysis of longer time series in the region (M. Salamolard, A. Butet, A. Leroux, and V. Bretagnolle, unpublished data). Auto-correlation coefficients were significant only at 3-yr ($r = 0.54$, $n = 18$, $P = 0.03$) and 6-yr lags ($r = 0.87$, $n = 12$, $P = 0.0005$; data from spring and summer trapping sessions). We found no significant correlation of abundance, either in spring or July, between the four species (Table 2). Similarly, spring and summer abundance were correlated for the voles only; no significant relationships were found for the other species (Table 2). No significant correlations were found between abundance in April or July and abundance in July of the previous year for any of the species considered (all $r_s < 0.07$, $P > 0.5$ in all cases).

Diet composition

In biomass terms, the Montagu's Harrier diet consisted mainly of voles, with annual values ranging from

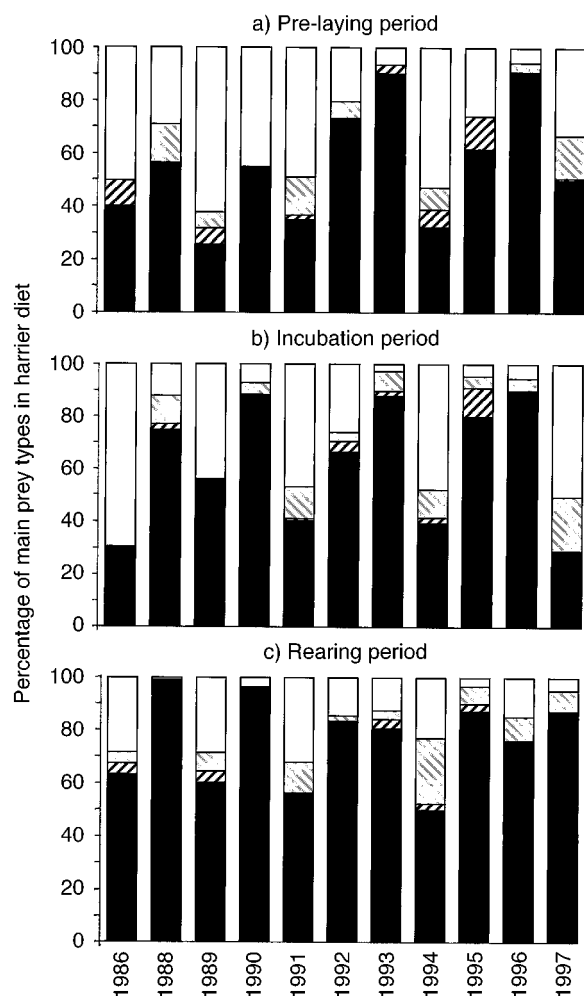


FIG. 3. Percentage of the main prey types (on a biomass basis) in the diet of the Montagu's Harriers during three phases of the breeding cycle: (a) pre-laying, (b) incubation, and (c) rearing period. From bottom to top, the prey are *Microtus arvalis* (black), other mammals (black hatching), other vertebrates (gray hatching), and insects (white).

33.7% to 86.6% (Table 3). In low years, voles accounted for 40–50% of total biomass, whereas in peak years they represented up to 80–90% of biomass (Table 3). Among mammals, voles showed the highest between-year coefficient of variation of biomass in pellets (20%; Table 3). Vole biomass in pellets was related to vole abundance (Fig. 2a; $r_s = 0.945$, $n = 10$, $P < 0.0001$). This relationship varied with season, being significant only for vole spring values during pre-laying ($r_s = 0.64$, $P = 0.04$) and incubation ($r_s = 0.90$, $P = 0.0003$), and was not significant for summer vole abundance during the rearing period ($r_s = 0.35$, $P = 0.28$). We investigated whether pellet composition varied according to breeding stage and year, using the percentage of pellets containing small mammals: the year effect on pellet composition was highly significant (one-way

ANOVA; $F = 5.82$; $df = 10, 33$; $P = 0.0001$), but breeding stage had no significant effect ($F = 0.65$; $df = 2, 33$; $P = 0.51$). Nonetheless, percentages of voles in the harrier diet increased seasonally (Fig. 3), being, on average, $52.8 \pm 24.5\%$ at pre-laying, $61.4 \pm 24.4\%$ at incubation, and $75.7 \pm 17.6\%$ at fledging. In peak vole years (such as 1993 and 1996), however, the percentage of voles in harrier diet did not increase, as it was high early in the breeding season (Fig. 3). No significant relationships were found between the abundance of other species and their relative percentages in the diet.

The second most important prey biomass after voles was insects. Total biomass ranged from 6.3% to 44.8%, with crickets (1.4–24.5%) and Odonatae (up to 27.1%) making up the bulk (Table 3). Other prey were vertebrates, with total biomass ranging from 2.1% to 23.0%, which consisted mostly of birds (8.7–15.1%). Birds were particularly prominent in pellets in poor vole years (e.g., 1991, 1997; Table 3, Fig. 3). Because of the close relationship between vole abundance and the percentage of voles in the harrier diet, opposing trends occurred between vole abundance and the percentage of other vertebrates (Fig. 2b, $r_s = -0.691$, $N = 11$, $P = 0.018$) and insects ($r_s = -0.909$, $P = 0.0001$). Diet width decreased with increasing vole abundance (Fig. 2c), and was negatively correlated with spring and summer vole abundance ($r_s = -0.817$, $P = 0.0039$, and $r_s = -0.931$, $P = 0.0001$, respectively).

Harrier density and breeding parameters

The number of pairs that settled in the study area varied from 20 to 54 (Table 4). The breeding density ranged from 0.41 to 3.0 pairs/10 km², a sevenfold variation (Table 4). The number of pairs producing fledglings (range 7–50) showed a similar sevenfold variation. The difference between numbers of settled and breeding pairs was especially high during poor vole years (up to 11 pairs), and was lower during peak vole years (0–2 pairs; see Table 4 for densities), although the tendency was not significant ($r_s = -0.49$, $n = 7$, $P = 0.26$). The highest variation in breeding parameters was found in the number of fledglings per brood ($cv = 72.7$; Table 4), these varied from 0.57 fledgling per pair in poor vole years to 2.64 fledglings in peak vole years. We investigated further the relationships between harrier breeding parameters and vole abundance (Fig. 4, Table 5). Some of the breeding parameters were correlated with each other (especially breeding density with breeding phenology, $r_s = -0.93$, $n = 9$, $P = 0.0002$; and clutch size, $r_s = 0.75$, $n = 12$, $P = 0.004$). As expected, breeding density was strongly correlated with spring vole abundance, whereas mean brood size at fledging was correlated positively with summer vole abundance (see Table 5 for statistical tests). The median date of laying onset varied among years by 20 days, and was also negatively correlated with spring vole abundance (Table 5). No such correlation was found

TABLE 4. Breeding parameters of Montagu's Harriers (*Circus pygargus*) at Rochefort during the period 1986–1997, with the number of nests sampled (*n*) in parentheses.

Year	Density† (no. nests/ 10 km ²)	No. pairs‡	Median period of laying onset (d)§		Clutch size		Brood size at fledging		Reproductive success	
			Median	<i>n</i>	Mean ± 1 SD	<i>n</i>	Mean ± 1 SD	<i>n</i>	Mean ± 1 SD	<i>n</i>
1986	1.30	22	2.50 ± 0.58	(4)	2.09 ± 0.83	(11)	0.71 ± 0.21	(4)
1987	2.50	42	3.72 ± 1.02	(18)	2.48 ± 1.58	(33)	0.71 ± 0.36	(18)
1988	1.80	31	3.50 ± 0.92	(18)	1.62 ± 1.24	(29)	0.43 ± 0.33	(18)
1989	2.20	37	7	(21)	3.24 ± 1.20	(17)	2.26 ± 1.28	(19)	0.52 ± 0.40	(16)
1990	3.00 [3.00]	51 [51]	7	(18)	3.80 ± 1.04	(25)	1.85 ± 1.52	(26)	0.42 ± 0.38	(25)
1991	0.60 [1.18]	10 [20]	9	(9)	2.38 ± 1.61	(13)	0.57 ± 1.16	(14)	0.21 ± 0.30	(11)
1992	1.80 [1.86]	31 [32]	8	(25)	4.06 ± 0.80	(18)	2.64 ± 1.44	(25)	0.67 ± 0.35	(18)
1993	2.70 [3.18]	46 [54]	7	(38)	4.03 ± 1.48	(36)	2.33 ± 1.62	(45)	0.58 ± 0.35	(33)
1994	0.41 [1.71]	7 [29]	9	(7)	2.80 ± 0.84	(5)	0.57 ± 0.79	(7)	0.10 ± 0.22	(5)
1995	1.41 [2.06]	24 [35]	8	(23)	3.67 ± 1.20	(21)	2.33 ± 1.57	(27)	0.66 ± 0.32	(21)
1996	2.88 [3.00]	49 [51]	7	(46)	4.00 ± 1.25	(51)	2.14 ± 1.63	(50)	0.49 ± 0.35	(49)
1997	0.77 [1.47]	13 [25]	9	(11)	2.69 ± 1.37	(13)	1.08 ± 1.32	(13)	0.35 ± 0.38	(12)
Mean	1.78	30.2 [37.1]	7.89		2.79 ± 1.38		1.83 ± 1.33		0.49 ± 0.33	
CV (%)	50.5	50.5 [35.4]	11.8		49.5		72.7		67.7	

Notes: The study area is 17 000 ha and did not vary between years. See *Methods* for exact definitions of these parameters. Note that sample sizes may vary within years because not all nests were discovered at the egg-laying stage.

† The density of settled pairs is given in brackets for 1990–1997. The first number is the density of breeding pairs (with nests).

‡ The first number is for breeding pairs; the number in brackets is for settled pairs.

§ The median 10-d period when >50% of the first eggs have been laid.

|| Reproductive success is calculated for each nest as brood size/clutch size and is then averaged for the year.

for breeding success, nor were any of the breeding parameters correlated with vole densities in the previous year (Table 5). The shapes of relationships between various breeding parameters and vole abundance were more curvilinear than linear (Fig. 4). For instance, breeding density and weighted vole abundance in April showed higher fit to a nonlinear model (corrected $R^2 = 0.74$) than to a linear model ($R^2 = 0.53$; Fig. 4). Similar results were found for the other breeding parameters. This suggested that the response of the harriers to increasing vole densities was stronger at low vole densities, and satiated rapidly. All parameters related to breeding performance were correlated positively with vole abundance, but were not significantly correlated with vole abundance during the preceding summer after Bonferroni correction (Table 5). None of these correlation was significant for other small-mammal species.

We tested whether percentages of the main prey types (from pellet analysis) and breeding parameters of Montagu's Harriers were correlated. We found significant values (applying the Bonferroni correction) only for the percentage of mammals in the diet and clutch size ($r_s = 0.836$, $n = 11$, $P = 0.001$). The percentage of voles in the diet was correlated strongly with breeding phenology ($r_s = -0.83$, $n = 9$, $P = 0.005$) and with clutch size ($r_s = 0.89$, $n = 11$, $P = 0.0002$). The strength of this relation varied across the breeding season. Vole biomass in the diet in the pre-laying period was correlated with clutch size ($r_s = 0.78$, $n = 11$, $P = 0.0045$), whereas vole biomass in the diet in the incubation period was correlated with breeding phenology ($r_s = -0.83$, $n = 9$, $P = 0.0058$). No other

significant correlations were found, suggesting that the number of voles eaten was a good predictor of the initial reproductive investment in this species, but not reproductive success.

We used the data obtained from pellets, phenology, and breeding performance of Montagu's Harriers to evaluate the "kill rate" of a breeding pair (following Korpimäki and Norrdahl 1991). Voles were the main prey (in terms of number of individuals taken, Table 6), contributing 10 times more, on average, than the second most important prey (birds). The calculated number of voles taken by a pair of Montagu's Harriers during the season increased rapidly with spring (corrected $R^2 = 0.69$) or summer vole abundance (corrected $R^2 = 0.87$). The best nonlinear fit was obtained with mean vole abundance between April and July (corrected $R^2 = 0.88$), and was much higher than linear fit ($R^2 = 0.61$), suggesting that harriers were satiated at the highest common vole densities (Fig. 5).

DISCUSSION

We will compare our results with those obtained farther north on predator–prey systems, emphasizing three points: the predator category (generalist or specialist) of Montagu's Harrier, the response type (functional or numerical) of Montagu's Harrier, and the nature of the prey–predator relationship at this temperate latitude.

Is Montagu's Harrier a specialist predator?

Optimal foraging theory predicts that diet composition should depend on the density and relative value of the preferred prey, independently of the abundance of alternative prey (Pulliam 1974, Charnov 1976, Pyke

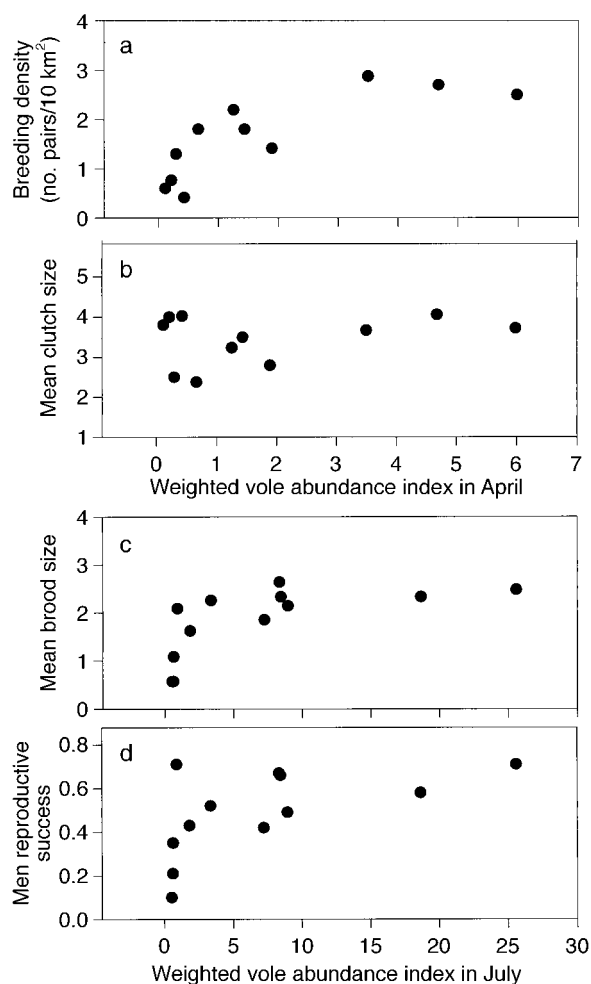


FIG. 4. Relationships between breeding parameters of Montagu's Harrier and vole abundance (see Table 1): (a) breeder densities; (b) mean clutch sizes; (c) mean brood sizes; and (d) mean reproductive success.

TABLE 6. The "kill rate" (see Korpimäki and Norrdahl 1991), i.e., the number of the most important vertebrates preyed upon by a breeding pair of Montagu's Harriers during the breeding season at Rochefort, 1986–1997.

Year	<i>Crocivura</i>	<i>Sorex</i>	<i>Apodemus</i>	<i>Microtus</i>	Birds	Reptiles
1986	12	48	38	368	19	0
1987	5	5	9	663	69	5
1988	19	0	0	510	75	0
1989	15	15	34	376	43	0
1990	0	0	0	603	15	0
1991	30	7	0	256	56	35
1992	22	11	0	599	25	0
1993	7	0	21	661	31	0
1994	99	0	20	216	82	3
1995	154	0	7	580	31	0
1996	5	0	0	647	38	3
1997	9	0	0	334	102	10
Mean	31	7	11	484	49	5
SD	47	14	14	165	28	10

et al. 1977). From our study, the response of Montagu's Harrier is in accordance with these predictions, with a positive relationship between vole abundance and the percentage of voles in the harrier's diet. No correlations were found with the other small-mammal prey. Similar results have been found in other raptors (e.g., Korpimäki 1985a,b, 1986a, 1988, Steenhof and Kochert 1988, Korpimäki and Norrdahl 1991, Redpath 1991, 1992). Moreover, optimal diet theory predicts that diet width should increase when abundance of the preferred prey decreases (Schoener 1971, Ellis et al. 1976, Pyke et al. 1977). This was also found in our study, which confirmed common voles as the preferred prey upon which harriers specialize. Similar specialization on common voles has been found in other studies (Paris 1996), and Montagu's Harrier is thus a specialist predator in parts of France. Incidentally, the breeding range of Montagu's Harrier in France overlaps the distribution of cyclic populations of the common vole (Butet and Leroux 1989; see the map in Delattre et al. 1992).

TABLE 5. Spearman rank correlation between breeding parameters (density of breeding pairs, median decade of laying onset, mean clutch size, mean number of chicks at fledging, and reproductive success) of Montagu's Harrier (*Circus pygargus*) and the abundance of voles (from Table 1) at Rochefort during the period 1986–1997, in spring, summer, and in summer of the previous year.

Season of vole abundance	Density of breeding pairs	Median 10-d period of laying onset	Mean clutch size	Mean brood size at fledging	Mean reproductive success
Spring					
r_s	0.838†	−0.882†	0.772	0.680	0.465
P	0.0013	0.0038	0.0053	0.0212	0.1498
n	11	8	11	11	11
Summer					
r_s	0.788†	−0.751	0.804†	0.853†	0.665
P	0.0023	0.0282	0.0016	0.0004	0.0182
n	12	9	12	12	12
Previous summer					
r_s	−0.196	0.312	−0.364	−0.731	−0.709
P	0.5637	0.4140	0.2716	0.0107	0.0146
n	11	9	11	11	11

† Values are significant with sequential Bonferroni correction.

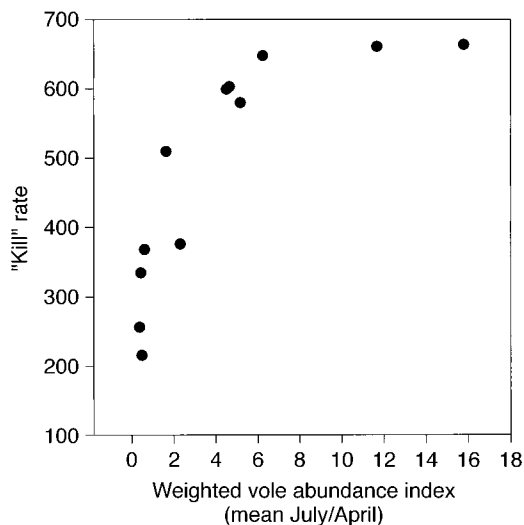


FIG. 5. Relationship between the "kill rate" (the number of common voles preyed upon by a breeding pair of Montagu's Harriers over the breeding season; data from Table 6), and the vole abundance (averaged over the year, i.e., including spring and summer trapping sessions) at Rochefort during the period 1986–1997.

However, Montagu's Harrier is not a vole specialist everywhere in its breeding range. The main prey is hares in central Spain (Arroyo 1997), birds in England and northern France (Underhill-Day 1993, Farcy 1994), birds and reptiles in Hungary, the Ural steppes, and the Netherlands (Schipper 1973; review in Arroyo 1997), birds and insects in Italy (Martelli and Parodi 1992), and insects in southern Spain (Corbacho et al. 1995). The Montagu's Harrier diet is therefore adaptable and only consists largely of voles where these are abundant. During the low phase of vole cycles, or in areas where voles are absent (or scarce compared to other potential prey), their diet can include a large percentage of other mammalian species, birds, and insects (Schipper 1973, Farcy 1994; C. Riols, *unpublished data*).

In conclusion, some Montagu's Harrier populations show a dietary response typical of a specialist (as in our study). Incidentally, these harrier populations fluctuate, whereas populations in other areas do not (Arroyo 1995), which suggests that fluctuations and vole specialization are connected. However, there is a wide spectrum of prey in different geographical areas, with a decrease of diet diversity with latitude (Arroyo 1997). Montagu's Harriers therefore seem able to cope with temporal and/or spatial variability in food availability, qualifying as specialist predators in some areas and generalists in others, which makes categorization difficult; overall, Montagu's Harrier could be defined as an "opportunistic-specialist" predator (see also Arroyo 1997).

Numerical and functional response by Montagu's Harrier

Specialist predators often show stronger numerical responses (in either density or breeding parameters) to

variations in prey abundance than do generalist predators (review in Newton 1979). Our results show that the breeding ecology of Montagu's Harrier in our study area depends ultimately on vole abundance. Its numerical response showed a strong relationship with the prey, with at least some birds tracking vole abundance without a time lag. No correlation was found between breeding density (or breeding parameters) and the abundance of small mammals in the previous summer. The numerical changes of specialist predators are supposed to be due to changes in emigration and immigration rates (e.g., Korpimäki et al. 1987, Korpimäki and Norrdahl 1991). Although Montagu's Harrier is a strictly migratory species that is nonterritorial (Salamolard 1997), breeding adults are relatively faithful to their breeding site (few wing-tagged breeders were found far from their past breeding sites), even in poor vole years (M. Salamolard, A. Butet, A. Leroux, and V. Bretagnolle, *unpublished data*). In such years, the birds form pairs, even though they may not breed, and seem to stay in the region. The relatively low mobility of adult Montagu's Harriers between and within years cannot explain the rapid increase of breeding density during high vole years. Those harriers that can move rapidly to the best food areas are the nonbreeders and juveniles. Floaters are apparently an important component of some raptor populations (see Rohner 1996). Juvenile dispersal of wing-tagged Montagu's Harriers is relatively high (Amar et al. 2000), and we found that yearling females could vary from 0% to 30% of the breeding population. Interestingly, breeding yearling females accounted for 1.7–6% in years of increasing vole numbers, but reached 19–30% in peak vole years, and fell to 0% when vole abundance was lowest (M. Salamolard, A. Butet, A. Leroux, and V. Bretagnolle, *unpublished data*). A similar situation has been described in Northern Harriers (*Circus c. hudsonius*), in which the percentage of subadults nesting was higher when vole numbers increased (Hamerstrom et al. 1985). We therefore suggest that adult nomadism is probably not the way in which Montagu's Harrier populations track high vole densities, and that recruitment from the floating population, especially the first-time-breeders (1-yr-old females) can explain the numerical response in this species. This has been defined as "juvenile nomadism" (Andersson 1980).

Clutches of Montagu's Harrier were larger in peak vole years (see also Arroyo et al. 1998). Clutch sizes in this species are especially variable (Arroyo et al. 1998). This fits the model developed by Andersson (1980), which predicts that large clutch sizes should also favor nomadism, as noted in other raptors (Korpimäki and Hakkarainen 1991, Korpimäki and Norrdahl 1991; but see Potapov 1997 for a contradictory result). Raptor species can also adjust their egg sizes to vole availability, laying larger eggs in good vole years than in poor ones (Pietiäinen et al. 1986, Korpimäki and Sulkava 1987, Hakkarainen and Korpimäki

1994, Wiebe and Bortolotti 1995). This has also been found in Montagu's Harrier (V. Bretagnolle and B. Arroyo, *unpublished data*). Other studies have found a relationship between clutch size or brood size and the abundance of voles (Jedrzejewski et al. 1994). However, brood size in some species is maximal during the increasing phase, and not during the peak, of small-mammal abundance (Korpimäki and Hakkarainen 1991).

The shape of the functional response curve depends on the percentage of the preferred prey species in the diet (Linden and Wikman 1983). In our study, the number of voles taken by a breeding pair of Montagu's Harrier increased rapidly and was saturated when vole densities were over a certain threshold (vole abundance index of 7–8, Fig. 5), resulting in a type II functional response. However, satiation actually may have occurred at higher vole abundance, because food consumption rates may be higher in good vole years than in poor vole years. The fact that fledglings were in better body condition in 1996 than in 1997 (M. Salamolard, A. Butet, A. Leroux, and V. Bretagnolle, *unpublished data*) may support this possibility. Contrary to the functional response, the numerical response increased very quickly, with Montagu's Harrier reaching high breeding density at low vole abundance (abundance index < 5, i.e., 30 voles/ha; Fig. 4). We suggest that the absence of defended feeding territories in Montagu's Harrier may enhance the rapidity of the numerical response, even at low vole densities, by allowing harrier density to match closely with vole abundance. The fact that the numerical response satiated rapidly may be due to the limitations in number of yearling females, i.e., the part of the population that responds mainly to vole increases. Thus, we conclude that the response of Montagu's Harrier is essentially numerical, with juvenile nomadism and differential recruitment to the breeding population varying with food supply. This response was also associated with a modification in spatial distribution: the percentage of isolated pairs decreased from 35% to 18% when the vole density increased.

Vole cycles, predators, and latitude

One discovery about small-mammal population dynamics is the existence of a latitudinal gradient in Fennoscandia: small-mammal cycles (3–4 years) are typically found in the north, whereas cycles are absent in the south (Henttonen 1985, Henttonen et al. 1985; but see Hanski and Henttonen 1996). The generalist–specialist predation hypothesis has been proposed to explain this gradient (Hansson and Henttonen 1985, Hanski et al. 1991, 1993, Turchin and Hanski 1997). Vole-eating raptor assemblages at low latitudes have mainly a functional response, but essentially a numerical response at the higher latitudes (e.g., Korpimäki 1986b), where densities of generalist raptors are usually lower (Hanski et al. 1991). Indeed, no regular multiannual

small-mammal cycles are found in central and western Europe (Hanski et al. 1991, Korpimäki and Norrdahl 1991), except for that of the common vole in extensive agricultural areas (Ryszkowski et al. 1973, Mackin-Rogalska and Nabaglo 1990). In our study, voles were found to cycle (or at least to vary strongly) even though the latitude was temperate (45° N), confirming previous results based on longer time series in France (Delattre et al. 1992, Butet and Leroux 1993, 1994, Giraudoux et al. 1994). We also found that the predator showed a numerical response. These two results therefore contradict the generalist–specialist predation hypothesis. Another system studied at a similar latitude (Canada, 44° N), although on an island, also shared many similarities with systems of higher latitudes, with a predominance of the numerical response (Phelan and Robertson 1978). There, the functional response was weak because there were no alternative prey. In our study site, too, the prey community is restricted to a few species, with a single dominant prey. Strong numerical responses at high latitudes may result from the simplicity and instability of the system at such latitudes (Lutich et al. 1971, Newton 1976). The low species richness of small-mammal communities at high latitudes has also been proposed to explain cyclic predator–prey systems (Hansson and Henttonen 1985), a factor that may also operate in some areas at temperate latitudes, such as in mountains (e.g., *Arvicola terrestris*: Saucy and Gabriel 1996), but not in mild Atlantic climates. We suggest that the apparent reduced diversity of small mammals in our study area compared to other areas (Paillat and Butet 1997, Burel et al. 1998) may be due to strong physical and biological constraints imposed by intensive agricultural practices and/or flooding in winter. Thus, the gradient proposed for Fennoscandian systems may not be applicable to more southerly localities, such as those in temperate ecosystems, except when the small-mammal community is reduced. In such cases, predator–prey relationships can show convergence with those existing in high-arctic systems.

ACKNOWLEDGMENTS

Numerous persons have helped during data collecting, for nest searching and mammal trapping (G. Paillat, O. Gaborit, and L. Courmont). Thanks also to V. Adamandidis for pellet analysis. We thank B. Arroyo, H. Fritz, P. Duncan, and S. J. G. Hall for their critical reviews of previous drafts, P. Duncan and S. J. G. Hall for correcting the English version, H. Fritz for help with data analysis, and S. K. Robinson, E. Korpimäki, and an anonymous referee for greatly improving a previous version. Part of this study has been funded by the Région Poitou-Charentes and CNRS (Contrat de plan Etat-Région) as a grant to P. Duncan, and M. Salamolard benefited from a doctoral dissertation grant from the Région Poitou-Charentes.

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