Research

Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates

Alexandre Millon and Vincent Bretagnolle

A. Millon (a.millon@abdn.ac.uk) and V. Bretagnolle, Centre d'Études Biologiques de Chizé, CNRS–UPR 1934, Carrefour de la Canauderie, FR–79360 Villiers-en-Bois, France. Present address for AM: Dept of Zoology, Univ. of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, Scotland, UK.

The consequences of cyclic fluctuations in abundance of prey species on predator continue to improve our understanding of the mechanisms behind population regulation. Among predators, vole-eating raptors usually respond to changes in prey abundance with no apparent time-lag and therefore contradict predictions from the predator–prey theory. In such systems, the interplay between demographic traits and population growth rate in relation to prey abundance remains poorly studied, yet it is crucial to characterize the link between ecological processes and population changes. Using a mechanistic approach, we assessed the demographic rates associated to the direct and indirect numerical responses of a specialist raptor (Montagu's harrier) to its cyclic prey (common vole), using long term data from two adjacent study sites in France. First-year survival rates were weakly affected by vole abundance, probably due to the fact that Montagu's harriers are trans-Saharan migrants and thus escape the vole collapse occurring in autumn–winter. Recruitment of yearling as well as breeding propensity of experienced adult females were strongly affected by vole abundance and at least partially shaped the trajectory of the breeding population. We argued that the strong density dependent signal detected in predator time series was mostly the phenomenological consequence of the positive direct numerical response of harriers to vole abundance. Accounting for this, we proposed a method to assess density dependence in predator relying on a cyclic prey. Finally, the variation in Montagu's harrier population growth rates was best explained by overwinter growth rates of the prey population and to a lesser extent by previous residual predator density.

Theoretical investigations of predator–prey interactions have highly contributed to the development of population ecology, since seminal papers pointing out the inherent tendency of predator–prey systems to oscillate (Lotka 1925, Volterra 1926, Nicholson and Bailey 1935). While experiments conducted in laboratory have provided insightful results (Costantino et al. 1997), the integration between theory and data collected in the wild remains largely a challenge for modern ecologists (Bonsall and Hassell 2007). Currently, even if studies succeed in fitting population models to real data, relevant ecological processes were only rarely identified and their relative contributions to population growth rate poorly quantified. There is growing evidence however that complex interactions between endogenous (density-dependent) and exogenous (stochastic) forces are driving dynamics of population from different trophic levels in the wild (Dennis and Otten 2000, Thompson and Ollason 2001, Coulson et al. 2004). The density paradigm is largely prevalent so far in population dynamics studies, although Krebs (2003) preferred to advocate the use of a mechanistic approach, by quantifying the effect of relevant ecological factors on the growth rate of a population (Sibly and Hone 2003).

In the wild, predator dynamics are of course deeply affected by spatio-temporal variation in prey availability (Messier 1994, Redpath and Thirgood 1999, Vucetich and Peterson 2004). This is especially apparent in predators relying upon a cyclic prey, for which particularly strong between-year variations in food supply have been recorded. Predator–prey relationships are classically analysed using functional and numerical responses of the predator to changes in prey density (Redpath and Thirgood 1997, Sinclair and Krebs 2003). In this framework, the direct numerical response simply consists in plotting predator and prey densities in a phase plan (Solomon 1949, Holling 1965), while the indirect numerical response links predator's population growth rates to prey abundance (Caughley et al. 1987), thus implying the role of demography. Indeed, the numerical response of a predator is in fine the result of specific demographic traits, which are potentially subject to complex interactions with density or food supply. However, the interplay between predator abundance, growth rate, and demographic parameters in relation to prey density, has been remarkably rarely studied in cyclic prey–predators systems (but see Brommer et al. 2002, Hone and Sibly 2003). To date, a synthetic analysis of the

mechanisms underpinning the numerical response of vole-eating predators is still lacking, probably because this requires long-term accurate data on prey density and predator demographic rates, and that such data are particularly difficult to collect.

The Montagu's harrier *Circus pygargus* is an opportunistic predator which can be locally specialised on a single prey species (Arroyo et al. 2004). In France in particular, this species appeared to be highly dependent on common vole *Microtus arvalis* abundance, and displayed a type II functional response as well as a numerical response to the cyclic dynamics of its prey (Salamolard et al. 2000). The present study was based on more than 1000 harrier nests monitored in parallel to vole abundance, from two large study sites surveyed over 11 and 20 years respectively. Our main objective was two-fold. First, we analysed the predator population dynamics by contrasting different models of numerical responses. If prey density constitutes an obvious candidate to explain predator dynamics, there is now a body of evidence pointing out the importance of intrinsic predator density dependence (Sinclair and Krebs 2003, Vucetich and Peterson 2004, Hone et al. 2007), although the processes actually involved remain to be thoroughly assessed (Abrams and Ginzburg 2000). Here, we tested these two hypotheses by formulating additive models of numerical response, accounting for the inherent density-dependence in the cyclic prey dynamics. Second, using a mechanistic approach (Krebs 2003), we investigated the direct and indirect influences of prey abundance on predator demographic parameters such as age-specific survival (estimated by capture–mark–resighting analyses), fecundity, recruitment and breeding propensity. Finally, we discussed to which extent this combined approach shed a new light on the understanding of complex prey–predator interactions, such as those involving a cyclic prey.

Material and methods

Study sites

Long-term data concerning harriers and voles were collected from two neighbouring areas of central–western France: the marshes of Rochefort (hereafter RO, 45°57′N, 0°55′W) and the Niort-Brioux cereal farmland in south Deux-Sèvres (hereafter DS, 46°11′N, 0°28′W) separated by 25 km from border to border. RO has been studied since 1986 and consists of 190 km^2 of marshland that have been gradually converted to cereal production over the last 20 years, at the expense of marshland falling from 81% in 1987 to less than 50% in 1994 (Butet and Leroux 2001). DS has been studied since 1995 and covers 340 km^2 of a rather homogenous intensive farmland mainly dedicated to cereal production in which the area of perennial crops (key habitats for voles, mainly alfalfa, ryegrass and meadows) varied annually between 9 and 13.5%.

Predator and prey species

The Montagu's harrier is a small-bodied (mean ± 1 SD: 281 g ± 28 for males, 340 g ± 31 for females), trans-Saharan vagrant and ground-nesting raptor. Its feeding regime has been described as both opportunistic and specialist at the scale of its Palearctic distribution (Arroyo et al. 2004). In central–western France, the common vole accounted on average for two thirds of its dietary biomass (Salamolard et al. 2000). Females are able to reproduce as yearling (i.e. one year old), whereas males do not reproduce before two years old (Arroyo et al. 2004).

Harrier density was calculated as the number of nests per 100 km^2 in each year for each study site. The overall dataset consists of 1019 nests of Montagu's harrier (452 in RO and 567 in DS). With a constant effort, we intensively searched for nests during the pre-laying period, and found most of them during the egg stage (annual averages, RO: 64%, DS: 73%). We then checked nests 3–8 times during the nestling period to assess breeding success. We assume that no nest remained undetected at the end of the breeding season. The Montagu's harrier is semi-colonial (Cornulier and Bretagnolle 2006), with colonies of up to 30 pairs. Territorial defence is restricted to a very small area around the nest, such that home ranges overlap between neighbouring males (unpubl.). Non-breeding individuals do not occupy a territory, and therefore their numbers cannot be directly assessed. As a surrogate, we measured the proportion of wing-tagged birds observed in a given year but for which we did not find a nest. This method includes birds that spend the entire breeding season in the study site as well as birds resighted only once, which may have temporarily emigrated to breed elsewhere.

We calculated the mean number of fledgling per pair (successful or not) and the total harrier productivity as the density of fledgling (per 100 km^2) for each study site (no data for RO in 1986). The proportion of nests located in harvested crops was much higher in DS (99%) than in RO (25%). Despite protection, the annual average of nests destroyed by farming activities reached 15% in DS vs <5% in RO. Nests that failed as a direct consequence of harvesting activities (n = 174) were removed from the dataset when calculating the number of fledgling per pair, as well as those involved in a food supplementation experiment (n = 49 between 1995 and 2002), and in a brood size manipulation (n = 33 in 2004–2005).

Abundance of the common vole was assessed twice a year, in April when harriers settled for breeding and in June towards the middle of the harrier's brood-rearing period, using live trapping without marking (Millon and Bretagnolle 2005). Trap-lines consisted in a 100 m transect of 51 traps (type INRA, without bait, 20–36 trap-lines in RO, 80–96 in DS) deposited for 24 h in randomly selected fields for each session. Vole abundance (one value site^{-1} year^{-1} in spring, and one in summer) was then defined as the average of capture/100 traps/24 h between habitat categories, weighted according to their relative area. Eight different categories of habitat were recognised: winter cereals, maize/sunflower, colza, and 'others' for annual crops; and alfalfa, ryegrass, meadow/pasture and set-aside for permanent crops. The missing data for spring 1990 in RO was estimated from the abundance in summer 1990, using the correlation in vole abundance between spring and summer in all other years (Salamolard et al. 2000). The common vole displays distinctly cyclic dynamics in central–western France, over a three-year period (low L, intermediate I, peak P; Fig. 1). This pattern is consistent with
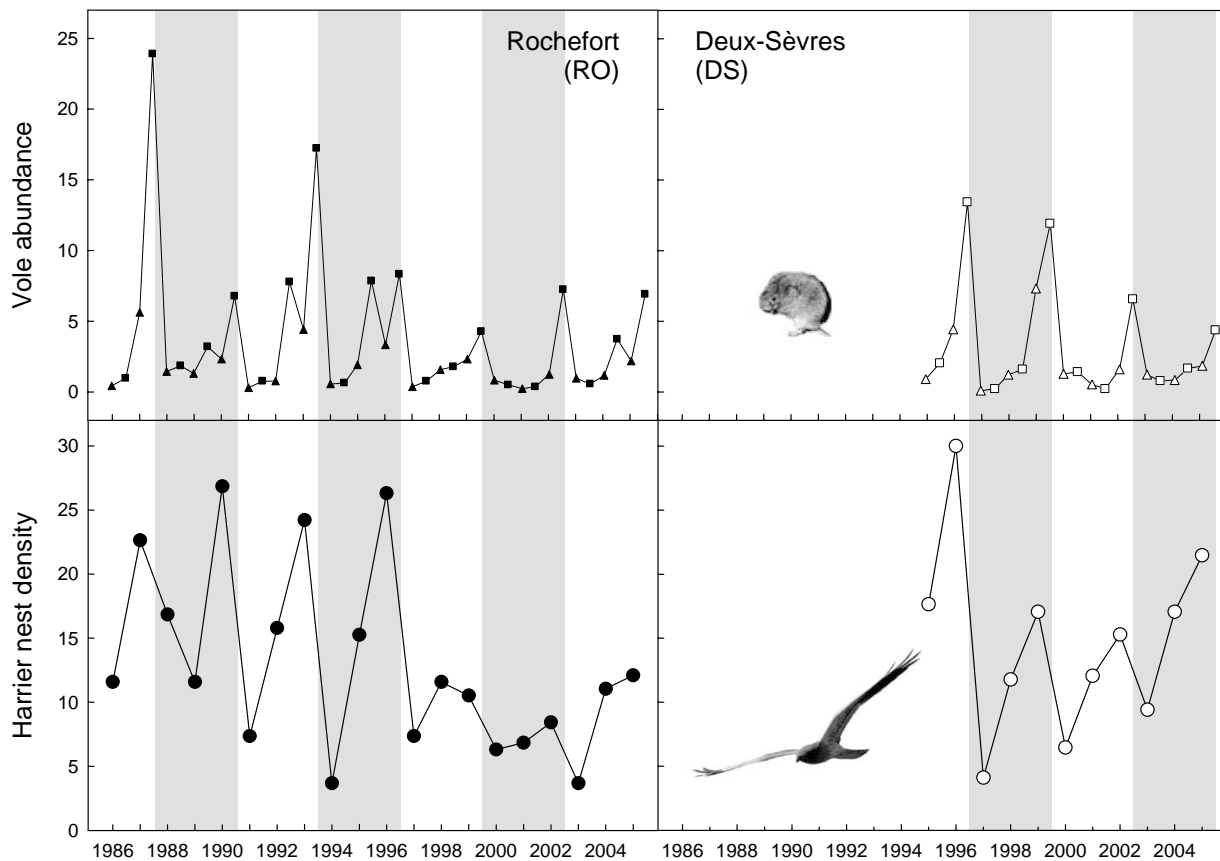
Figure 1. Time-series of vole abundance (voles caught per 100 traps over 24 h, and weighted by habitat type proportion in each study site; triangle in spring, square in summer) and harrier nest density (number of nests per 100 km^2; circle) in Rochefort (RO; left panels and black symbols) and Deux-Sèvres (DS; right panels and open symbols). The alternation of grey and white bars points out a 3-year period corresponding to a vole cycle.

what is observed for northern vole species in Fennoscandia (Lambin et al. 2006). In particular, vole dynamics in our study sites revealed 1) a high amplitude with more than a 100-fold variation between low and peak years, 2) very low densities detected during low years (ranging from 0.8 to 7.9 voles ha^{-1}), and 3) a large-scale geographical synchrony exceeding 100 km and possibly reaching ca 500 km (Lambin et al. 2006).

Modelling predator survival

Age-specific survival rates of harriers were estimated from capture–mark–resighting data in the two study sites. Local apparent survival was estimated for adults from a dataset including birds banded as adults (and mostly trapped on the nest during the chick-rearing period using a clap-net), combining males and females from the two study sites (262 individuals in total; 82 in DS over 1995–2004; 178 in RO over 1988–2004, resighting up to 2005; including birds banded as juveniles only if they subsequently bred in RO, and for which the first breeding event was considered as the first encounter occasion).

A distinct dataset was used for estimating first-year survival rates, and included birds wing-tagged as chicks in RO only, from 12 cohorts between 1988 and 1999 (469 individuals), with a resighting period spanning up to 2003

(>80% of individuals were resighted within the four first years of life). Permanent emigration outside the study area and true mortality are confounded within the capture–mark–recapture framework (CMR), which provides local survival estimates (Lebreton et al. 1992). Therefore, most studies conducted on birds underestimated first-year survival, as dispersal usually take place before the first breeding event and that juvenile dispersal distance often exceeded the size of study sites (van Noordwijk 1995). In our study, 26 of 82 fledglings (31.7%) were resighted outside the study site within the network of sites where harrier nest monitoring occurred for protection purposes. We chose to include them in order to obtain less biased estimates of first-year survival. We acknowledge doing this violated CMR assumptions as the expected lower recapture rate outside the study area could artificially inflate the survival rate. For two reasons however, we believed that such a method indeed provided less biased estimates of first-year survival. First, median age of the first resighting was four year old for both philopatric and dispersing birds, suggesting that resighting probability within areas monitored for protection purpose was similar to our study sites. Second, we did not find any relationship between dispersal distance and vole abundance experienced at birth (unpubl.), allowing us to compare models constrained by vole abundance. Nevertheless, we acknowledged the spatial cover of harrier monitoring (ca 25% of the distribution of the species in

France) did not allow us to grasp all dispersal events and our estimates of first-year survival are therefore to be considered as a minimum figure.

GOF tests were performed with U-Care ver. 2.02 (Choquet et al. 2003) and model selection, following a step-down approach from the most global model fitting adequately the data (Lebreton et al. 1992), was performed in M-Surge ver. 1.8.1 (Choquet et al. 2004). We used the Akaike information criterion (AIC) to select the most parsimonious model (Burnham and Anderson 2002). Constraints were applied on both recapture (P) and survival (S), using biological hypotheses-oriented approach (Lebreton et al. 1992). Reduced-parameters models were built by constraining annual survival to be either constant over the study period, year-specific, or a function of vole abundance. The effect of vole abundance on survival and recapture rates was investigated by 1) comparing annual survival estimates between the different phases of the vole cycle (investigating three different combinations: L/I/P [3 parameters], LI/P [2] and L/IP [2]; so-called model 'phase' [low L, intermediate I and peak P]), and 2) using a linear-logistic function ($\text{logit}[S] = \log[S/[1-S]] = \alpha + \beta[\text{vole abundance}]$; so-called model 'vole'). For the analysis considering adult birds from the two study sites, we averaged vole abundance measured in RO and DS for the common period (1995–2005), those values being highly correlated between sites (spring: $r_s = 0.76$, $p = 0.009$; summer: $r_s = 0.88$, $p = 0.0005$; Fig. 1).

Statistical analyses

The inter-annual population growth rate was calculated as $r = \ln(N_t) - \ln(N_{t-1})$, where N was the density of nests for harriers or the measure of abundance for voles. Direct and indirect numerical responses and harrier demographic parameters were investigated using generalized linear models and the glm function in R ver. 2.4.1. Model selection was made within the information-theoretic framework using the Akaike information criterion (AICc) corrected for small sample size, and Akaike weights (w_i) were interpreted as strength of evidence (Burnham and Anderson 2002). Competing models with $\Delta\text{AIC} > 4$ are considered to have considerably less support than models with $\Delta\text{AIC} < 2$ (Burnham and Anderson 2002). A Gaussian distribution of error with an identity link was used, except for the proportion of yearling females in the breeding population for which we chose a binomial distribution of error with a logit link. Time-series analyses (PRCF: partial rate correlation function based on growth rates, and CCF: cross-correlation function based on densities) were conducted on the longest dataset only (RO), after having detrended the data (Turchin 2003).

Results

Harrier nest density was highly variable in the two study sites, ranging from 3.7 to 30 pairs per 100 km² (RO: CV = 55%, n = 20 years; DS: CV = 49%, n = 11; Fig. 1). The between-year variation of vole abundance was higher than

for harriers and also very similar between the two study sites (RO: CV = 112%, n = 20; DS: CV = 108%, n = 11; Fig. 1). As described elsewhere in Europe (Hörnfeldt et al. 2005), the amplitude of the vole cycle seemed to fade out, and this was especially obvious in the longer time-series, RO. A time-series analysis (PRCF) conducted on data from RO showed significant negative coefficients between growth rates at lags 1 and 2 (Fig. 2a–b). Estimates for direct and indirect density dependence indicated a cyclic pattern with a dominant period of three years for both prey and predator dynamics (Royama 1992, Turchin 2003). The cross-correlation analysis (CCF) further revealed the perfect synchrony between voles and harriers (Fig. 2c).

Direct and indirect numerical responses

We first investigated the direct numerical response of predators (Solomon 1949, Holling 1965), by plotting harrier density and vole abundance recorded the same year in a phase-plan. We considered four models including vole abundance in spring or summer, ln-transformed or not. The best fit was achieved with ln-transformed vole abundance in summer ($R^2 = 56.6$, all $\Delta\text{AICc} > 6$). This model emphasized the positive relationship between prey and predator abundance within the same year, but also pointed out a ceiling in harrier density for highest vole abundance (Fig. 3a). Based on this model, we tested for an additive or interactive effect of site, and the model accounting for an additive site effect performed equally well ($\Delta\text{AICc} = 0.11$), revealing a slightly higher harrier density in DS compared to RO under similar vole abundance ($R^2 = 59.5$).

The indirect numerical response (Caughley et al. 1987, Sibly and Hone 2003), involving harrier population growth rate between year $t-1$ and year t, was then considered as a function of vole abundance in spring (spV) or summer (suV), with or without a one-year time lag (denoted respectively V_{t-1} and V), harrier density with a one-year time lag (H_{t-1}), and vole growth rate (rV) between summer ($t-1$) and the following spring (t) (or overwinter growth rate, Table 1). Harrier population growth rates were asymmetrically distributed around 0 with more positive than negative values, and ranged between -1.986 and 1.421. The influence of vole abundance experienced the previous year ($t-1$) on predator growth rates was negative and slightly non-linear (compare models 2–3 and 5–6 in Table 1, Fig. 3b). A model based on the ratio between summer vole abundance and harrier density in year $t-1$ (Vucetich and Peterson 2004) explained a similar amount of variance in harrier growth rates (model 7). Considering harrier density in the previous year ($t-1$) improved the fit sharply, and the apparent direct density dependence in predator appeared to be linear (compare models 8 and 9, Fig. 3c), this model explaining 55.4% of the variance in harrier population growth rate and performed the best among the above one-parameter models.

We extended the analysis to test the hypothesis that predator dynamics were not only related to prey density, but also to predator density (Vucetich and Peterson 2004, Hone et al. 2007), by adding harrier density the previous year ($t-1$) in a model accounting for the prevalent (year t)
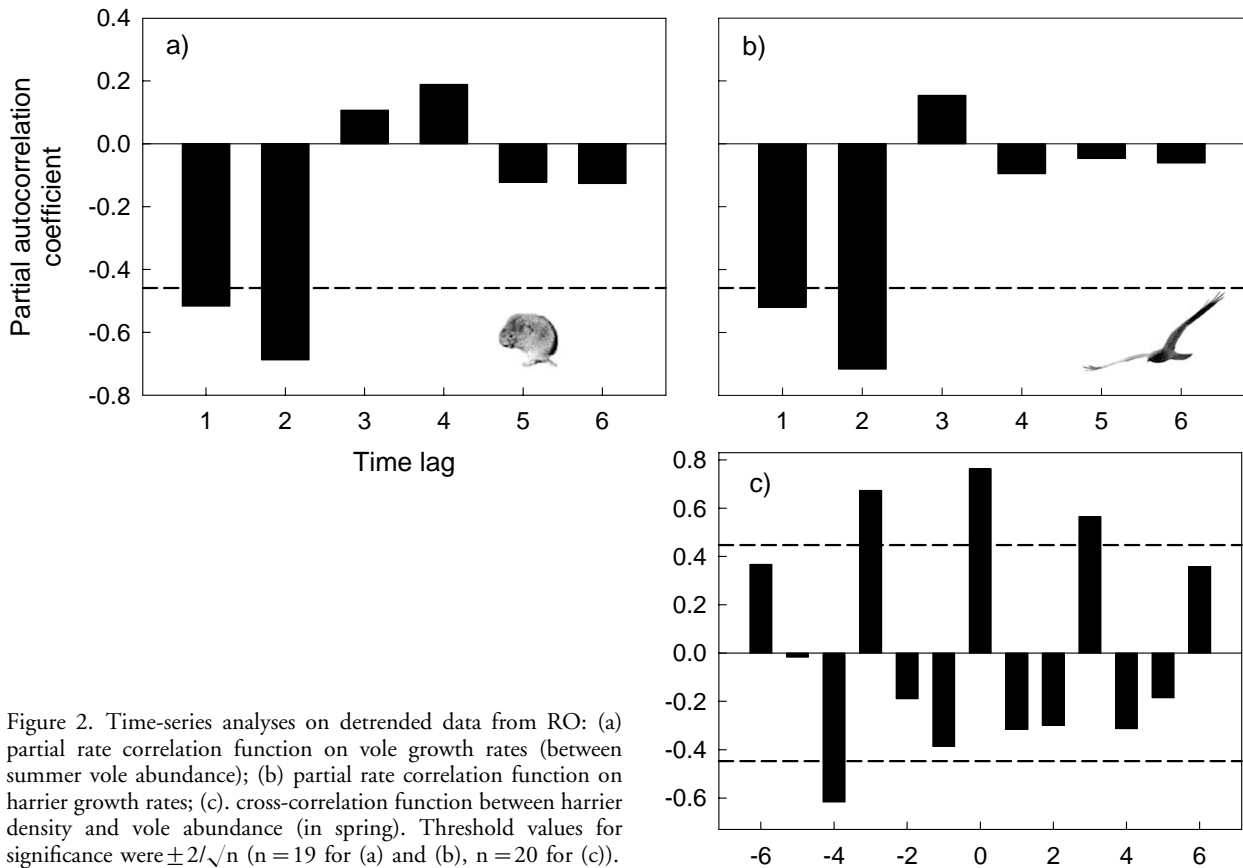
Figure 2. Time-series analyses on detrended data from RO: (a) partial rate correlation function on vole growth rates (between summer vole abundance); (b) partial rate correlation function on harrier growth rates; (c). cross-correlation function between harrier density and vole abundance (in spring). Threshold values for significance were $\pm 2/\sqrt{n}$ (n = 19 for (a) and (b), n = 20 for (c)).

vole abundance (in summer). In accordance with results found in barn owl (Hone and Sibly 2003, based on data from Taylor 1994), this model explained an important proportion of the variance (75.5% vs 82% for the barn owl analysis, model 10). The fitted regression (± 1 SE) was:

$$r = 0.928\ (0.202) + 0.052\ (0.014)\ suV$$
$$- 0.089\ (0.012)\ H_{t-1} \quad (1)$$

In such a model, 53.4% of the variance in harrier population growth rate was explained by previous harrier density, and only 22.1% by vole abundance. Nevertheless, this relationship was likely to result at least partially from the phenomenological interaction between the vole cyclic dynamics (determining the succession of growth rate values) and the direct numerical response of harriers (Fig. 1, 3a). The density dependence occurring in vole dynamics then potentially inflated the estimate of predator density (Fig. 2a–b). To deal with this problem, we first used overwinter vole growth rate instead of vole abundance, and then extracted the residuals from a linear regression between summer vole abundance and harrier density (ln-transformed values, accounting for site). The residuals of this regression (harrier residual density, denoted $resH_{t-1}$) were not associated with vole abundance ($F_{1,27} < 0.001$, p = 0.98). Model 11 with overwinter vole growth rate alone explained 71.5% of the variance. Considering residual harrier density with a one-year time lag further improved the fit (model 12; $R^2 = 78.4\%$), and provided the most parsimonious model (Table 1). The estimates from this model were as follows:

$$r = 0.272\ (0.083) + 0.384\ (0.042)\ rV$$
$$- 0.649\ (0.225)\ resH_{t-1} \quad (2)$$

Removing the temporal autocorrelation in estimates imposed by prey cyclicity strikingly reduced the explanatory power of predator density (Fig. 4): overwinter vole growth rate explained then 71.5% of total variance in harrier growth rate vs only 6.9% explained by residual harrier density. Finally, accounting for a site effect did not improve the fit of the indirect numerical response (model 13).

Age-specific survival estimates

The umbrella model to estimate first-year survival started with age-specific estimates ($S_{a1-2 \times t}$, $P_{a1-2 \times t}$), accounting for a transient effect expected in a dataset including the juvenile phase (Choquet et al. 2003), and fitted the data adequately (GOF test, $\chi^2 = 28.95$, DF = 37, p = 0.51). The most parsimonious model (S_{a1-2}, P_{a1-2}) retained age-specific survival and recapture (Fig. 5a). First-year survival rate averaged = 0.310 ± 0.06 (model S_{a1} in Table 2a). The two models constrained by vole abundance performed less well though the AIC values differed by less than 2. Chicks fledged during peak vole years ($S_{a1} = 0.325 \pm 0.07$) survived only slightly better than those raised under lower vole abundance ($S_{a1} = 0.298 \pm 0.06$).

GOF test revealed that the full model ($S_{sex \times t}$, $P_{sex \times t}$) fitted the adult dataset well ($\chi^2 = 82.26$, DF = 83, p = 0.50). Recapture was constrained by sex and ln-transformed values of spring vole abundance ($P_{sex + vole}$; see below for
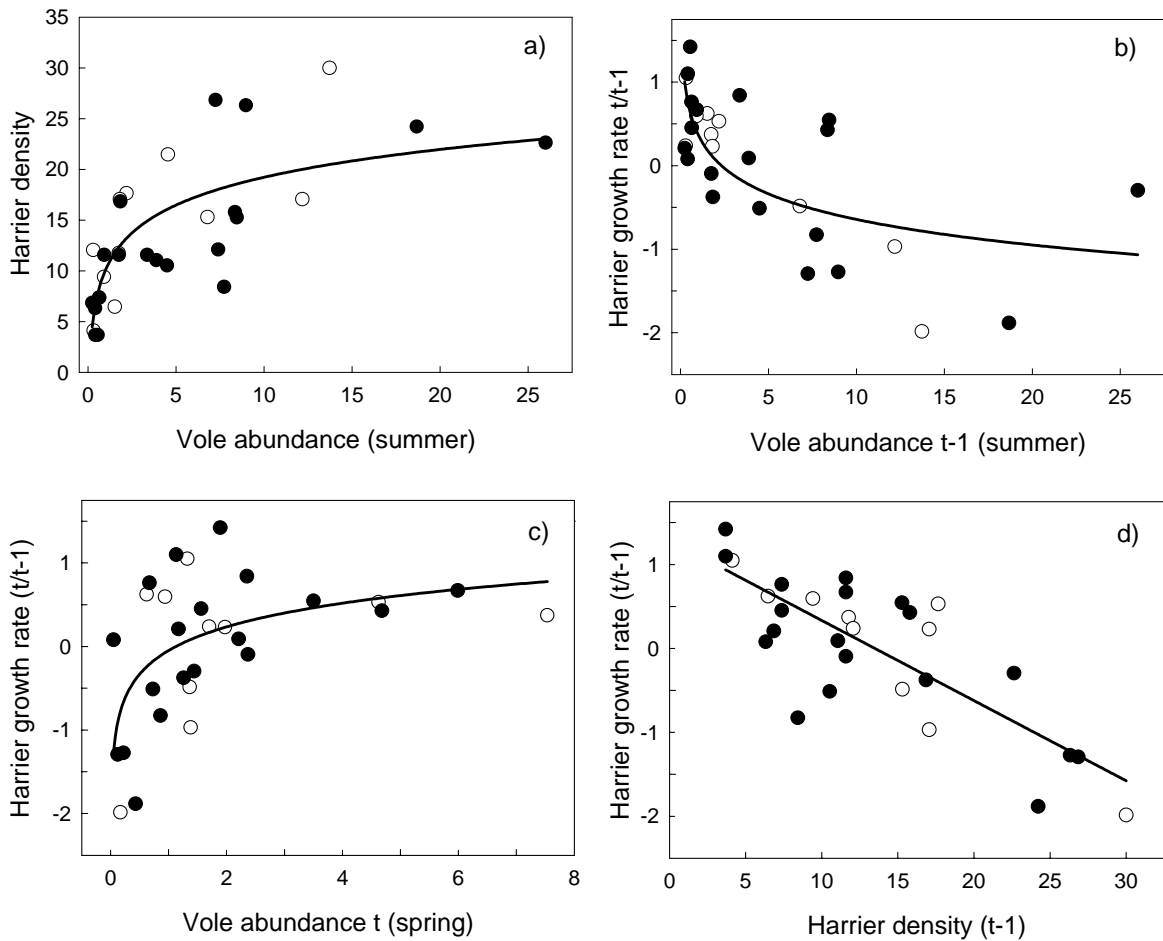
Figure 3. (a) Direct numerical response (predator density) to variation in vole abundance, and indirect numerical response (predator growth rate) to: (b) vole abundance (summer) in year $t-1$; (c) vole abundance (spring) in year t; and d) harrier density (number of nest per 100 km^2) in year t. Open circles for DS and black circles for RO.

Table 1. Relative performance of models investigating harrier indirect numerical response as a function of vole abundance in spring (spV) or summer (suV), with or without time lag (respectively V_{t-1} and V), harrier density with a one-year time lag (H_{t-1}), vole growth rate (rV) between summer $(t-1)$ and the following spring (t), and residual harrier density (resH$_{t-1}$; Methods). R-square (R^2), difference in Akaike information criterion corrected for small sample size with the best model (ΔAICc), and AICc weights (w_{AICc}) are presented. Site as a two-level factor (RO/DS). The best model written in bold face.

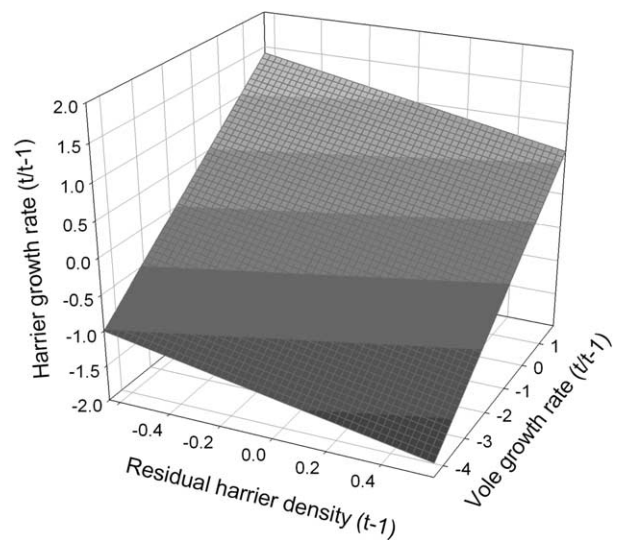| Harrier population growth rate, $r = \ln(N_t) - \ln(N_{t-1})$			
Model	R^2 (%)	ΔAICc	w_{AICc}
(1) $b_0 + b_1$spV	16.3	36.91	0
(2) $b_0 + b_1$spV$_{t-1}$	48.3	22.94	0
(3) $b_0 + b_1$suV$_{t-1}$	42.6	26.00	0
(4) $b_0 + b_1\ln($spV$)$	29.3	32.03	0
(5) $b_0 + b_1\ln($spV$_{t-1})$	41.9	26.32	0
(6) $b_0 + b_1\ln($suV$_{t-1})$	48.8	22.64	0
(7) $b_0 + b_1(\ln[$suV$_{t-1}]/\ln[$H$_{t-1}])$	42.5	26.03	0
(8) $b_0 + b_1$H$_{t-1}$	62.5	13.62	0
(9) $b_0 + b_1\ln($H$_{t-1})$	55.4	18.67	0
(10) $b_0 + b_1$suV$+ b_2$H$_{t-1}$	75.5	3.58	0.088
(11) $b_0 + b_1$rV	71.5	5.69	0.030
(12) $b_0 + b_1$rV$+ b_2$resH$_{t-1}$	**78.4**	**0**	**0.524**
(13) $b_0 + b_1$rV$+ b_2$resH$_{t-1}+ b_3$site	79.7	0.77	0.357

Figure 4. Harrier population growth rate (indirect numerical response between year $t-1$ and t) as a function of harrier residual density $(t-1)$ and overwinter vole growth rates (between summer $t-1$ and spring t).
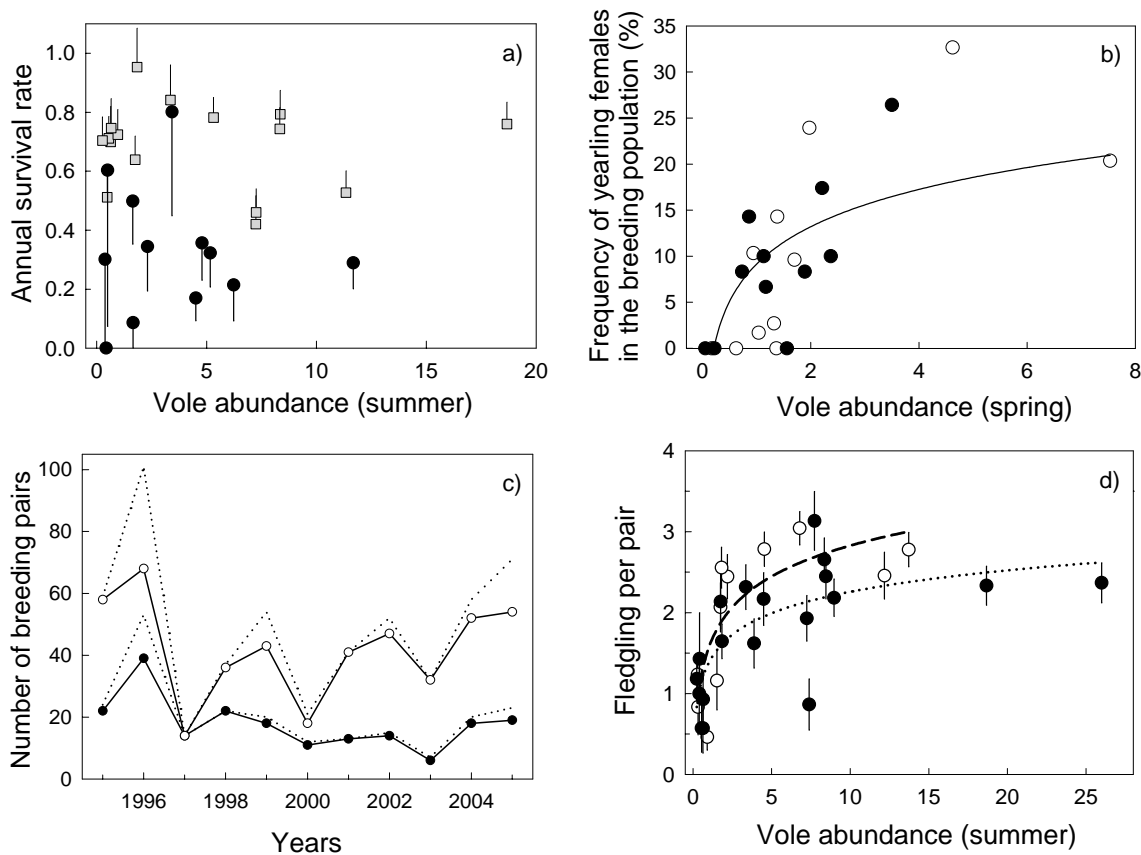
Figure 5. (a) Age-specific annual survival rates for adults (grey squares) and juveniles (first-year survival; black circles) according to mean vole abundance. Juvenile survival (mean −1 SE, cohorts 1988–1999) was estimated for RO only, according to the model S a1 ×t,a2 P a1,2 (model 4 in Table 2a). Adult survival (mean+1 SE, 1988–2004) was estimated from the model S t P sex+vole, combining harriers from RO and DS (model 1 in Table 2b). (b) Variation in the proportion of yearling females in the breeding population (data were not available for RO before 1995). (c) Compared time-series of nest numbers in RO and DS including all females (adult ≥2 year-old+ yearling, dashed lines), or adult females only (solid lines and dots). (d) Fledglings per pair (mean±1 SE); failures caused by wheat harvesting activities were removed (Methods). Open circles for DS, and black circles for RO.

model selection on recapture). Average local survival rate from the constant model (model 5 in Table 2b; S = 0.670±0.02) was very close from adult survival estimated with the juvenile dataset ($S_{a2}=0.650±0.04$). Models with time-varying survival or survival varying according to the phases of the vole cycle (LI, P) performed equally well (ΔAIC =0.82, Fig. 5a). This suggests that if vole abundance partially affected local survival of adult Montagu's harrier, another important source of variation in survival over time remained unknown. There was further evidence that females were more affected by vole abundance than males (model 3; ΔAIC =1.48). From model 3, male adult survival was assumed constant (0.660±0.03), while female survival rates greatly varied following low or intermediate years of the vole cycle (0.806±0.07), or following a peak year (0.599±0.04). This discrepancy might reflect sex-specific costs of reproduction, but also possibly permanent emigration achieved by females in response to vole cyclicity. In addition, the fact that sex-specific local survival rates were very closed (from model 7; female: 0.672±0.03, male: 0.668±0.03) actually suggested that actual adult survival rates were probably higher for females than for males, as permanent emigration (that entails a reduction in local

Table 2. (a) Model selection for first-year survival (Sa1) based on birds banded as chicks. Adult survival (Sa2) was kept constant through time while recapture was modeled as age-specific (Pa1,a2) for each of the four models presented. (b) Model selection for local adult survival rates (S) based on birds banded as adults (Methods). Recapture was modeled as sex-specific and vole dependent ($P_{sex+vole}$) for each of the seven models presented. The effect on survival of vole abundance categorized according to phase of the vole cycle (low L, intermediate I and peak P) was modeled using three different combinations but only the best model is presented hereafter (Methods). Deviance, number of parameters (np), AIC value, and AIC difference with the best model (ΔAIC) are presented.

Model	Deviance	np	AIC	ΔAIC
(a) First-year survival				
(1) S a1	724.53	4	732.53	0
(2) S a1 ×vole	723.96	5	733.96	1.43
(3) S a1 ×(phase LI/P)	724.40	5	734.40	1.87
(4) S a1 ×t	711.03	15	741.03	19.50
(b) Adult survival				
(1) S t	1134.95	21	1176.95	0
(2) S phase LI/P	1163.77	7	1177.77	0.82
(3) S fem ×(phase LI/P)	1162.43	8	1178.43	1.48
(4) S sex ×(phase LI/P)	1161.01	9	1179.01	2.06
(5) S constant	1173.06	5	1183.06	6.11
(6) S vole (ln summer)	1172.97	6	1184.97	8.02
(7) S sex	1173.67	6	1185.04	8.09

survival estimates) was recorded for females but never for males.

Breeding propensity and pattern of recruitment

Recapture rates can be considered as a proxy to assess the variation of breeding propensity of Montagu's harrier through time, as the resighting effort was kept constant during the study period. The best model revealed a positive effect of ln-transformed vole abundance in spring on recapture rates, with a higher intercept for males than for females ($P_{sex + ln[spV]}$). Models constrained by vole abundance in spring or overwinter vole growth rates performed equally well ($\Delta AIC < 1$; results not shown). Estimates of recapture from this model ranged from 0.762 ± 0.06 to 0.860 ± 0.04 for males, and from 0.630 ± 0.08 to 0.765 ± 0.05 for females, over the gradient of vole abundance. The impact of vole abundance on harrier breeding propensity was probably even stronger than suggested by estimates of recapture rates. Indeed, an analysis based on a sub-sample of wing-tagged adult individuals subsequently resighted at least once, indicated that the proportion of harriers present in the study sites and effectively breeding (i.e. having a nest) increased from 62% during a low vole year (n = 29), to 79% in an intermediate year (n = 29), and up to 94% during a peak vole year (n = 47).

The proportional contribution of yearling females to the breeding population was positively related to vole abundance in spring (Fig. 5b). The model incorporating ln-transformed values of vole abundance performed better than a model with non-transformed values ($\Delta AICc = 14.9$). Models accounting for a site effect did not find any support ($\Delta AICc > 2$ in both cases). Yearling females accounted for up to 33% (n = 101) of the female breeding population in a peak vole year (DS 1996) and thus substantially contributed to harrier population growth rate (up to a 50% increase). Most of the increase between intermediate and peak phases of the vole cycle was actually attributable to recruitment of yearling females (Fig. 5c).

Fecundity

Montagu's harriers fledged on average 2.12 ± 1.68 offspring (n = 863 broods; both sites combined, wheat harvesting-induced failure excluded). Fledged brood size increased with vole abundance, with a consistent difference between the two study sites in favour of DS (Table 3, Fig. 5d). Accounting for the seasonal growth of the vole population between spring and summer did not improve the fit of the model (compare model 1 and 3). Maximum mean brood size at fledging was reached for intermediate prey densities and might reveal the maximal fecundity for the species. However, the over-representation of yearling females in the breeding population during peak vole years lowered breeding parameters mean values, as first-year females laid smaller clutches than older and/or experienced one (Arroyo et al. 2004). Overall, peak vole years contributed dispro-portionately to harrier productivity: 62% of all fledglings produced over 11 years were produced during the four peak years in DS, and 55% in RO (7 peak years out of 19 years).

Discussion

Individual behaviour and life-history traits interact with population density and stochastic events to determine the growth rate of a population. Combining individual- and population-level analyses might provide fruitful insights for understanding the ecological processes underpinning population dynamics (Krüger 2007). Using this approach, that has only seldom been used so far to tackle predator dynamics subject to cyclic prey variations, we tried to identify the mechanisms driving the trajectories of two Montagu's harrier populations preying on a cyclic vole species.

Unsurprisingly, the numerical responses (both direct and indirect) and the average fecundity of Montagu's harriers were strongly affected by vole abundance. Less expected was the weak influence of vole abundance on age-specific survival estimates. Considering the growing evidence supporting that conditions experienced early in life impact individual future life history (Reid et al. 2003), we expected a strong cohort effect in first-year survival. The influence of vole abundance at birth on first-year survival was however weak (Table 2). Such a result could appear at first glance as contradicting results obtained in resident owl species under northern latitudes, for which first-year survival was dependent on the density of prey during the following the winter (Petty 1992, Brommer et al. 2002). Montagu's harriers spend however only 4–5 months per year on their breeding grounds, and juveniles leave their natal ground and start their migration about two to five weeks after fledging. Consequently, they escape the collapse in vole numbers occurring during the following autumn–winter, which has been identified as the key period determining survival of tawny and Ural owls (Petty 1992, Brommer et al. 2002). Wintering conditions in the Sahel area, especially the abundance of locusts that constitute the bulk of harrier diet in winter (Arroyo et al. 1995), is likely to be the most important factor accounting for the variation of first-year survival in Montagu's harriers (Fig. 5a).

A noteworthy result of the survival analysis arose from the apparent link between the three different phases of the vole cycle (low, intermediate and peak) and local survival of adult breeders. A substantial amount of the temporal variation in adult survival seemed to be explained by the succession of the different phases of the vole cycle rather than by vole abundance per se (compare models 2 and 6 in Table 2b). This effect was likely to be more pronounced for

Table 3. Relative performance of models investigating the variation in number of fledgling per nest (annual average). sgrV was the seasonal growth rate of vole (ln[suV] −ln[spV]). See Table 1 for definition of other acronyms. The best model written in bold face.

Model	Fledgling per nest		
	R^2 (%)	$\Delta AICc$	w_{AICc}
(1) $b_0 + b_1 suV$	27.6	13.1	0.001
(2) $b_0 + b_1 sgrV$	18.7	16.59	0.000
(3) $b_0 + b_1 sgrV + b_2 suV$	32	13.54	0.000
(4) $b_0 + b_1 ln(suV)$	52.7	0.34	0.354
(5) $b_0 + b_1 ln(suV) \times b_2 site$	58.5	1.25	0.225
(6) $b_0 + b_1 ln(suV) + b_2 site$	**56.7**	**0**	**0.420**

females, with considerably reduced local survival following a peak vole year (ca 20%), while male survival rate was mostly independent of vole abundance. This difference is unlikely to be explained by actual mortality but could rather reflect higher dispersal propensity for females after having bred in a peak vole year. Predators facing cyclic fluctuations of prey density might have integrated the succession of the three different phases of the vole cycle (characterised by positive temporal autocorrelation for transition L-I and I-P, but also by a negative autocorrelation for the transition P-L), and developed particular adaptations to cope with time-varying but predictable selection pressures (Hakkarainen and Korpimäki 1994, Appleby et al. 1997). A phase-dependent dispersal strategy could be such an adaptation, allowing females to escape the low vole phase expected after having experienced a peak vole year, and to seek for more profitable areas for breeding. Dispersal distances exceeding 300 km of adult females (breeding dispersal) from our study sites have been indeed recorded (unpubl.).

The two populations of Montagu's harrier monitored here tracked changes in prey density with no time lag, as reported for other vole-eating raptors under northern latitudes (Fig. 1,2; Korpimäki and Norrdahl 1991, Korpimäki 1994, Brommer et al. 2002, Hörnfeldt et al. 2005), in contrast to predictions from predator-prey models (Elton 1924, Lotka 1925, Volterra 1926). Processes underpinning synchronous prey–predator dynamics such as nomadism (large-scale adult and/or juvenile dispersal to track prey availability, Andersson 1980, Saurola and Francis 2004), or breeding skipping (Brommer et al. 1998), have been suggested although their relative importance have not been assessed so far. We detected a positive influence of vole abundance on recapture rates that can be used as a proxy for breeding propensity of adult birds, but may also reveal temporary emigration. The occurrence of a breeding skipping strategy was further suggested by the proportion of wing-tagged birds effectively involved in reproduction. Virtually all birds present during peak vole years had a nest, while this proportion fell to less than 65% during low vole years.

At this stage it is worth mentioning that a drawback inherent to most studies on bird population dynamics, is that population size usually refers to the breeding fraction of the population, and largely ignores the more elusive fraction of non-breeders. In our study system, the size of the total population of Montagu's harrier (breeders+floaters) was much likely at its highest during the spring following peak vole year. The year following this peak however, predators experienced a drought in prey availability, and only few birds were indeed able to breed (Fig. 1). This result further emphasised the importance of recruitment of unexperienced birds as well as breeding propensity of experienced individuals in the observed dynamics of Montagu's harrier. The age of first breeding for females indeed was likely to be cohort dependent (i.e. dependent on the vole phase at birth): from Fig. 5c, we can infer that females born in peak vole years were mostly recruited two years later during the subsequent intermediate year, while females born in this year were recruited as yearling and contributed actually to most of the breeding population growth between intermediate and peak vole years. However our data did not allow us to quantify the relative contribution of these demographic processes (phase-specific recruitment and breeding propensity) to the variation of harrier population growth rates. More empirical works are needed to quantify these demographic processes moreover in a spatial context, as less than 25% of the breeding females only were actually born in our study sites (estimates from a ringing survey, unpubl.).

The results of this study provides additional support to the view that predator dynamics are not solely related to prey abundance, but also sensitive to predator density (Akçakaya 1992, Hone and Sibly 2003, Krebs 2003, Vucetich and Peterson 2004, Hone et al. 2007). Models assessing the indirect numerical response with both prey- and predator-related explanatory variables explained more than 75% of the variance in harrier population growth rates. We wish to outline here however that investigating density dependence in predators subject to cyclic prey variation is a perilous exercise. Indeed a prey population cycle with a three-year dominant period as displayed by common voles in western France (Fig. 1; Lambin et al. 2006), entails direct (lag = 1 year) and indirect (lag = 2 year) density-dependent processes (Fig. 2a–b; Royama 1992, Turchin 2003). Therefore, the direct numerical response of Montagu's harrier to vole abundance (Fig. 3a) transferred the density-dependent signature of the prey dynamics in the dynamics of the predator. The density dependence estimated from model 10 (Table 1, Eq. 1) following Hone and Sibly (2003) was hence at least partially the phenomenological consequence of the direct numerical response of harriers to the cyclic variation in vole abundance. We proposed here that using prey growth rates (rather than prey density) and residual predator density (rather than predator density) accounted for prey cyclicity, and provided better estimates of density dependence in predator. Though explaining a very similar proportion of variance, these two models (10 and 12, Table 1) strikingly differed about the importance granted to density dependence (partial R^2 of respectively 53% and 7%). We concluded therefore that Montagu's harrier dynamics primarily explained by vole dynamics, and to a lesser extent by intrinsic density dependence (Fig. 4).

What are the processes resulting in density dependence in Montagu's harrier? Processes such as spacing behaviour, mutual interference, or effects of pathogens have been proposed among others to regulate animal populations (reviewed by Murdoch 1994, Sutherland 1996). The Montagu's harrier is a semi-colonial species which can tolerate a high level of nest clumping (Arroyo et al. 2001), and the degree of coloniality seemed to be independent from the vole cycle in our study sites (Cornulier et al. pers. comm). Furthermore a recent study provided support for an Allee effect (i.e. positive density dependence) on reproductive traits in an expanding population of Montagu's harrier (Soutullo et al. 2006). We rather suggest that a buffer effect may be at the origin of the negative density dependence pattern observed in this system. Under this hypothesis, we assume that high prey density allows the totality of the population to breed, while in years with low prey density, only high-quality individuals were able to maintain a sufficient condition for breeding. The breeding population of Montagu's harrier was therefore not a random sample of available individuals, but was biased in terms of individual

quality according to the prevalent vole abundance. Then, if survival and/or breeding propensity were linked to individual quality, we can expect a higher proportion of previous breeders to remain in the population from a low to an intermediate than from a peak to a low vole year, thus generating a density dependent pattern. The vole dependent recruitment of yearling females provided indirect support for the existence of the above-mentioned link.

Finally, combining investigations on population growth rates, demographic parameters and evolved breeding strategies (e.g. breeding skipping) of predators in direct relation to prey dynamics, can be particularly helpful to develop a mechanistic understanding of complex predator dynamics such as those involving a cyclic prey. The integration of metapopulation data (i.e. numerical response in space) would further benefit population ecologists for clarifying the consequences of predator prey interactions on population dynamics (Bonsall and Hassell 2007).

References

Abrams, P. A. and Ginzburg, L. R. 2000. The nature of predation: prey dependent, ratio dependent or neither? – Trends Ecol. Evol. 15: 337–341.

Akçakaya, H. R. 1992. Population cycles of mammals: evidence for a ratio-dependent predatio hypothesis. – Ecol. Monogr. 62: 119–142.

Andersson, M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. – J. Anim. Ecol. 49: 175–184.

Appleby, B. M. et al. 1997. Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)? – Proc. R. Soc. Lond. B 264: 1111–1116.

Arroyo, B. E. et al. 1995. Observations on the ecology of Montagu's and marsh harriers wintering in northwest Senegal. – Ostrich 66: 37–40.

Arroyo, B. E. et al. 2001. Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). – Behav. Ecol. Sociobiol. 50: 109–115.

Arroyo, B. E. et al. 2004. Montagu's harrier. – Birds Western Palearct. Update 7: 1–33.

Bonsall, M. B. and Hassell, M. P. 2007. Predator–prey interactions. – In: May, R. and McLean, A. (eds), Theoretical ecology (3rd ed.). Oxford Univ. Press.

Brommer, J. E. et al. 1998. The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. – J. Anim. Ecol. 67: 359–369.

Brommer, J. E. et al. 2002. Reproduction and survival in a variable environment: Ural owls (*Strix uralensis*) and the three-year vole cycle. – Auk 119: 544–550.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference (2nd ed.). – Springer.

Butet, A. and Leroux, A. B. A. 2001. Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. – Biol. Conserv. 100: 289–295.

Caughley, G. et al. 1987. Kangaroos: their ecology and management in the sheep rangelands of Australia. – Cambridge Univ. Press.

Choquet, R. et al. 2003. User's manual for U-CARE. – CEFE/CNRS, < ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/ >.

Choquet, R. et al. 2004. M-SURGE: new software specifically designed for multistate capture-recapture models. – Anim. Biodiv. Conserv. 27: 207–215.

Cornulier, T. and Bretagnolle, V. 2006. Assessing the influence of environmental heterogeneity on patterns of nest-spacing: a case study with two raptors. – Ecography 29: 240–250.

Costantino, R. F. et al. 1997. Chaotic dynamics in an insect population. – Science 275: 389–391.

Coulson, T. et al. 2004. Skeletons, noise and population growth: the end of an old debate? – Trends Ecol. Evol. 19: 359–364.

Dennis, B. and Otten, M. R. M. 2000. Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. – J. Wildlife Manage. 64: 388–400.

Elton, C. S. 1924. Fluctuations in the numbers of animals: their cause and effects. – Brit. J. Exp. Biol. 2: 119–163.

Hakkarainen, H. and Korpimäki, E. 1994. Does feeding effort of Tengmalm's owls *Aegolius funereus* reflect offspring survival prospects in cyclic food conditions? – Oecologia 97: 209–214.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. – Mem. Entomol. Soc. Can. 45: 1–60.

Hone, J. and Sibly, R. M. 2003. Demographic, mechanistic and density-dependent determinants of population growth rate: a case study in an avian predator. – In: Sibly, R. M. et al. (eds), Wildlife population growth rates. R. Soc,. Cambridge Univ. Press, pp. 41–54.

Hone, J. et al. 2007. Evaluation of predator numerical responses. – Wildlife Res. 34: 335–341.

Hörnfeldt, B. et al. 2005. Fading out of vole and predator cycles? – Proc. R. Soc. Lond. B 272: 2045–2049.

Korpimäki, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? – J. Anim. Ecol. 63: 619–628.

Korpimäki, E. and Norrdahl, K. 1991. Numerical and functional responses of kestrels, short-eared owls and long-eared owls to vole densities. – Ecology 72: 814–826.

Krebs, C. J. 2003. Two complementary paradigms for analyzing population dynamics. – In: Sibly, R. M. et al. (eds), Wildlife population growth rates. R. Soc,. Cambridge Univ. Press, pp. 110–126.

Krüger, O. 2007. Long-term demographic analysis in goshawk *Accipiter gentilis*: the role of density dependence and stochasticity. – Oecologia 152: 459–471.

Lambin, X. et al. 2006. Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? – J. Anim. Ecol. 75: 340–349.

Lebreton, J.-D. et al. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67–118.

Lotka, A. 1925. Elements of physical biology. – Williams and Wilkins Co.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. – Ecology 75: 478–488.

Millon, A. and Bretagnolle, V. 2005. Population specific variation of offspring sex ratio according to prey abundance. – Oikos 108: 535–543.

Murdoch, W. W. 1994. Population regulation in theory and practice. – Ecology 75: 271–287.

Nicholson, A. J. and Bailey, V. A. 1935. The balance of animal populations. – Proc. Zool. Soc. Lond. 3: 551–598.

Petty, S. J. 1992. The ecology of the tawny owl *Strix aluco* in the spruce forests of Northumberland and Argyll. – Open Univ.

Redpath, S. M. and Thirgood, S. J. 1997. Birds of prey and red grouse. – Stationery Office.

Redpath, S. M. and Thirgood, S. J. 1999. Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. – J. Anim. Ecol. 68: 879–892.

Reid, J. M. et al. 2003. Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. – J. Anim. Ecol. 72: 36–46.

Royama, T. 1992. Analytical population dynamics. – Chapman and Hall.

Salamolard, M. et al. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. – Ecology 81: 2428–2441.

Saurola, P. and Francis, C. M. 2004. Estimating population parameters of owls from nationally coordinated ring data in Finland. – Anim. Biodiv. Conserv. 27: 403–415.

Sibly, R. M. and Hone, J. 2003. Population growth rate and its determinants: an overview. – In: Sibly, R. M. et al. (eds), Wildlife population growth rates. R. Soc. Cambridge Univ. Press, pp. 11–40.

Sinclair, A. R. E. and Krebs, C. J. 2003. Complex numerical responses to top–down and bottom–up processes in vertebrate populations. – In: Sibly, R. M. et al. (eds), Wildlife population growth rates. R. Soc. Cambridge Univ. Press, pp. 127–147.

Solomon, M. E. 1949. The natural control of animal populations. – J. Anim. Ecol. 18: 1–35.

Soutullo, A. et al. 2006. Density-dependent regulation of population size in colonial breeders: Allee and buffer effects in the migratory Montagu's harrier. – Oecologia 149: 543–552.

Sutherland, W. J. 1996. From individual behaviour to population ecology. – Oxford Univ. Press.

Taylor, I. 1994. Barn owls. – Cambridge Univ. Press.

Thompson, P. M. and Ollason, J. C. 2001. Lagged effects of ocean climate change on fulmar population dynamics. – Nature 413: 417–420.

Turchin, P. 2003. Complex population dynamics. A theoretical/empirical synthesis. – Princeton Univ. Press.

van Noordwijk, A. J. 1995. On bias due to observer distribution in the analysis of data on natal dispersal in birds. – J. Appl. Stat. 22: 683–694.

Volterra, V. 1926. Variations and fluctuations of the number of individuals in animal species living together. – Mem. Acad. Lincei 2: 31–113.

Vucetich, J. A. and Peterson, R. O. 2004. The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. – Oikos 107: 309–320.