

Variable but predictable prey availability affects predator breeding success: natural versus experimental evidence

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Abstract

Food supply is a major source of variation in breeding success for predators, and to what extent individuals are able to cope with temporal variability in food availability remains an outstanding question in life-history studies. We confronted the natural variation in clutch size and breeding success with results from a food supplementation experiment during egg formation, conducted over several contrasted years of natural food supply in an avian specialist predator, the Montagu's harrier *Circus pygargus*. This raptor mainly preys on common vole *Microtus arvalis* a cyclic microtine under temperate latitudes. Vole abundance together with timing of breeding accounted for most of the variance in clutch size and number of fledglings. Results from empirical and experimental data were overall in agreement. Fed pairs consistently increased clutch size compared with controls in all experimental years, whereas no effect of food supplementation on egg volume was detected. Supplemented pairs, however, did not fledge significantly more chicks than controls. The costs entailed by the increase in clutch size appear nevertheless to be limited compared with previous studies. Food supply seemed therefore to display sufficient predictability throughout a breeding season to afford individuals the opportunity to adjust their breeding effort to an optimal number of offspring, in agreement with Lack's anticipation hypothesis.

Introduction

The importance of food supply in limiting animal populations and shaping life-history strategies has been long debated since Lack's influential synthesis (Lack, 1954; Martin, 1987, 1995; Newton, 1998). Although it is currently largely admitted that diversity in life-history patterns mainly results from differences in specific schedules of mortality (i.e. the balance between juvenile and adult mortality; Ghalambor & Martin, 2001), food supply has been traditionally viewed as the major factor affecting reproductive success at the population level (e.g. Grant *et al.*, 2000; Davis, Nager & Furness, 2005). Food supply may affect reproduction through influencing parental condition (Curio, 1983; Dijkstra *et al.*, 1990; Pietiäinen & Kolunen, 1993), timing of breeding (Meijer, Daan & Hall, 1990; Aparicio & Bonal, 2002), number of breeding events (Grant *et al.*, 2000) or breeding success (Sanz & Moreno, 1995; Brinkhof & Cavé, 1997), among other traits.

Food limitation can affect individual reproductive output at different breeding stages according to their relative costs in terms of energy. Understanding the mechanisms causing variations in breeding success requires an accurate knowledge of the level of food supply available in the environment, as such conditions may vary between years or study sites (Tremblay *et al.*, 2003) and also during the breeding

season. However, direct and accurate estimates of food supply levels are rarely available in studies on breeding success. Vole-eating predators constitute good models in this context to evaluate the relationship between food supply and reproductive output, as vole species often undergo huge variations of density, and thus provide to their predators highly contrasted levels of food supply for reproduction (e.g. Korpimäki, 1990; Wiehn & Korpimäki, 1997; Brommer, Pietiäinen & Kolunen, 2002).

Our study model, the Montagu's harrier *Circus pygargus* is a specialist predator of the common vole *Microtus arvalis* in western France (Salamolard *et al.*, 2000). Prey cyclicality provides a gradient of environmental quality, with vole densities varying by more than 100-fold among years (Lambin, Bretagnolle & Yoccoz, 2006). We explored how clutch size variation is linked to female feeding rate, and then investigated how reproductive performance was affected by vole abundance, assessed twice a year through intensive trapping.

To investigate the causal link between vole abundance and breeding success, we designed an experimental test in which we provided additional food to parents during the prelaying and laying periods. As a consequence of this food supplementation, we expected a general increase in clutch size and/or egg volume. The aim of this food supplementation experiment was to test two different sets of hypotheses.

First, the *threshold hypothesis* states that natural food conditions will affect the subject's response to food supplementation, with a stronger effect expected under unfavourable food conditions (Nager, Rüeger & Van Noordwijk, 1997). Here we tested the *threshold hypothesis* along a quantitative gradient of food conditions, in contrast to most studies so far that usually compare favourable and unfavourable years.

Secondly, we contrasted the *constraint* and *anticipation hypotheses*. The *constraint hypothesis* postulates that food acts as a limit for the reproductive output from the laying period (Perrins, 1970), whereas, alternatively, the *anticipation hypothesis* postulates that parents should adjust their breeding effort according to the maximum number of offspring they will be able to raise (Lack, 1954). This latter hypothesis assumes that chick rearing is more costly than any other breeding stage, and further requires that parents are able to predict early in the breeding season the level of food supply they will experience during the rearing period. The two hypotheses differ on the outcome of the experimentally induced increase in clutch size: whereas the *anticipation hypothesis* predicts reduced breeding success for supplemented pairs, the *constraint hypothesis* predicts that fed pairs would benefit from early food supplementation by improving their breeding performance. We measured the consequences of the food supplementation experiment on the current reproductive output.

Material and methods

Predator-prey monitoring

Data were collected in two study sites in west-central France (46.1°N/0.7°W), between 1995 and 2002: the *Rochefort* marshes (RO) and the plain of *Niort-Brioux* in *Deux-Sèvres* (DS). Vole abundance varies cyclically among years in this part of France, with a 3-year period (crash, intermediate and peak years successively; Lambin *et al.*, 2006). Vole abundance was measured at the scale of a study site by intensive five-trapping conducted twice a year in April and June, respectively, corresponding to the laying and brooding periods for harriers. Trap-lines consisted of a 100-m transect of 51 traps deposited in main habitat types (20–36 trap-lines in RO, 80–96 in DS). Vole abundance (one value/site/year in spring and one in summer) was then defined as the average of capture/trap-line/24 h between habitats (weighted according to their relative area). In contrast with the pattern observed in northern vole species, vole densities typically increased throughout the harrier-breeding season in this area, thus offering a certain level of predictability to their predators (Millon & Bretagnolle, 2005; Fig. 1).

Montagu's harrier is a medium-sized, semi-colonial raptor inhabiting farmland landscapes of Western Europe, nesting on the ground mainly in cereal crops (Arroyo, Garcia & Bretagnolle, 2004). Mate fidelity is very low, and harriers seem to actively seek for a new mate each year (A. Millon, B. E. Arroyo & V. Bretagnolle, unpubl. data). Nests in both sites were located each year, according to a

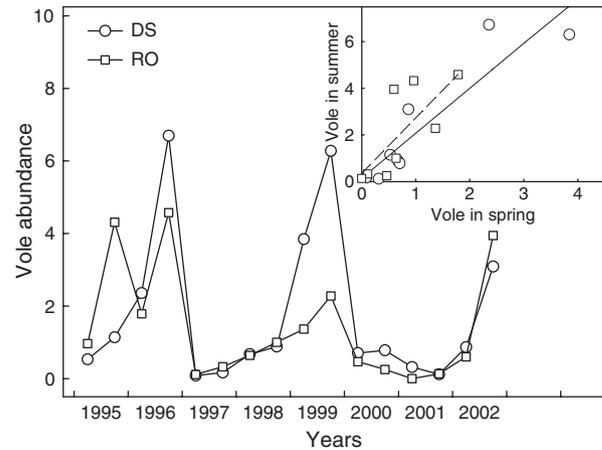


Figure 1 Time-series of vole abundance expressed as the number of capture/trap-line/24 h in RO (open square) and DS (open circle). Vole trapping took place twice a year in spring and summer. The insert panel represents the relationship between spring and summer vole abundance for each study site (dotted line for RO, solid line for DS). RO, *Rochefort* marshes; DS, *Deux-Sèvres*.

standardized effort ($n = 343$ in DS, $n = 231$ in RO), and were visited as early as possible after first-egg laying. One-year-old females (recognizable in flight because of the remaining juvenile feathers) are able to breed only when food is plentiful ($n = 90$), but lay fewer and smaller eggs and breed later than adult females (Arroyo *et al.*, 2004). In the following analyses, only adult (≥ 2 years old) females were therefore considered. There is no reliable criterion to age males. Laying date was estimated according to a standardized method (Arroyo, 2002), and relative laying date (a reflection of the pair's quality) was calculated as the difference with average laying date for that year and area. Egg length (L) and width (W) were measured to the nearest 0.1 mm with a vernier calliper. Egg volume [volume (mL) = $0.51LW^2/1000$; Hoyt, 1979] was averaged over a clutch, provided that all eggs have been measured. Body condition was calculated for chicks of 21–30 days old (i.e. during the last 10 days before fledging) as the difference between observed and theoretical mass from a sex-specific growth curve (Gompertz model; Zach *et al.*, 1984). Females are indeed heavier than males, and chicks can be accurately sexed according to iris colour (Millon & Bretagnolle, 2005). Missing information resulted in varying sample size between different analyses conducted for the different breeding parameters. For instance, nests only visited after hatching ($n = 80$) did not provide reliable data on clutch size. Human-induced nest failures (crop harvesting is the main cause of failure in DS; see Arroyo, Garcia & Bretagnolle, 2002) were also excluded from the analyses concerning breeding success (mainly total failures, $n = 77$). Given the uncertainty about the origin of total failure, hatching success (number of hatchling/clutch size) and fledging success (number of fledgling/number of hatchling) were calculated after having excluded total failure (i.e. no hatchling or no fledgling, respectively).

Behavioural observations were carried out on 34 nests during the prelaying and laying periods over one vole cycle (1996–1998). Prey delivery rate was assessed as the number of food passes between male and female per hour. Sampling duration averaged 10.3 ± 4.9 (SD) hours per nest.

Experimental procedure

Supplementary feeding took place during the harrier prelaying and laying periods ($n = 34$ adult pairs: five in DS and three in RO in 1995, six in DS and eight in RO in 1996, one in 1997, five in 1998, two in 2000, one in 2001 and three in 2002, all of them in DS). Supplementary food consisted of dead common voles or wood mice *Apodemus sylvaticus*. Food was deposited daily on poles placed 20–100 m from the nest, allowing the experiment to be conducted without inducing the female's take-off. Daily supplementary food consisted on average of 47 ± 15 g (SD, $n = 427$). Female feeding rates during the prelaying period averaged 0.506 ± 0.28 (SD) voles h^{-1} (six to seven voles per day or 130 g of food, $n = 225$ observations). Therefore, supplementary feeding approximately represented a third of female daily requirements. Each of the 34 experimental pairs was checked in order to confirm the use of the supplemented food, but the exact quantity of food received by each female was unknown. Food was also provided to pairs for which it could not be actually proven that the food was regularly taken. Moreover, pairs breeding in the same colony as the experimental pairs could have benefited occasionally from extra food. To be conservative, those *uncertain* ($n = 17$) and *close neighbour* pairs ($n = 25$) were excluded from the analysis.

Supplementary feeding started as soon as possible when harriers selected their nest sites and stopped within 4 days after clutch completion. The proportion of manipulated pairs in DS found within a colony ($n = 17$) or isolated ($n = 6$) [see Cornulier & Bretagnolle, (2006); Montagu's harriers in RO almost exclusively bred among colonies] did not differ from control ($\chi^2_1 = 0.196$, $P = 0.66$). However, pair settlement was detected at different stages before laying; therefore, food supplementation duration varied among experimental pairs (average \pm SD: 11 ± 5 days). Nevertheless, we did not find any relationship between clutch size ($n = 34$) and neither duration of the supplementation ($F_{1,32} = 1.24$, $P = 0.23$) nor number of days of supplementation before laying ($F_{1,32} = 0.29$, $P = 0.77$). Very late breeding pairs (≥ 21 days after mean laying date) were removed from the control group ($n = 14$), as they most probably concerned re-nesting attempts after early failure.

Statistical analyses

Statistical procedures were performed using R (version 2.5.1, R Development Core Team, 2006). We used linear and generalized linear mixed-effects models to investigate variation in five breeding parameters (clutch size, mean egg volume, hatching success, fledging success and number of fledglings) of Montagu's harrier under natural conditions

(raw data on control pairs only). The error distribution of the response variables was identified to conduct appropriate analyses (Gaussian for clutch size, mean egg volume and number of fledglings; binomial for hatching and fledging success). Year was treated as a random effect to take into account between-year variation. All models were initially fitted with vole abundance and relative laying date as covariates, study site as a two-level factor and all second-order interaction terms. Only statistically significant interaction terms ($P < 0.05$) are reported unless otherwise stated (Table 3). A similar approach was used to analyse variation in chick body condition (Gaussian error structure) near fledging, although brood identity was included as a random factor nested within year, as brood mates cannot be considered as fully independent statistical samples. Brood size at fledging and sex were included as explanatory variables in addition to vole abundance, relative laying date and study site, but only second-order interactions involving sex were examined. Model selection was conducted by dropping non-significant explanatory variables sequentially (backward stepwise procedure). Random effects were always retained in the final model but a log-likelihood test was performed to test whether the random effect (i.e. between-year variance) was significantly different from 0 (Faraway, 2006).

To investigate the effect of food supplementation, only years when the experiment was conducted were included in the analysis (i.e. 1995–1998 and 2000–2002 in DS, 1995–1996 in RO). Backward model selection started from an initial model containing all variables selected during the previous analysis, year as a random factor and experimental treatment as a two-level factor (control/supplemented pairs) in interaction with vole abundance only.

Spring vole abundance (\log_{10} -transformed) was used for clutch size, egg volume and hatching success, but summer vole abundance (\log_{10} -transformed) was used for brood size at fledging, fledging success and chick body condition. Descriptive statistics are expressed as mean \pm SD unless otherwise stated. Coefficient of variation (CV) was calculated using yearly averages for each study site.

Results

Natural variation in breeding performance

The number of eggs laid by a female Montagu's harrier was directly related to the frequency of prey deliveries by its male during the prelaying period ($F_{1,31} = 5.9$, $P = 0.021$, controlling for relative laying date: $F_{1,31} = 5.9$, $P = 0.021$; Fig. 2). Clutch size ranged from 2 to 8 eggs, averaged 4.17 ± 0.92 ($n = 277$, CV = 22%), and varied annually in relation to food abundance (annual averages from 3.00 ± 0.76 to 4.89 ± 0.89 ; Fig. 3a). Harriers laid larger clutches in years with high vole abundance. A strong negative seasonal trend in clutch size was detected, whatever the level of food availability (Table 1). Even when taking into account differences in vole abundance, harriers laid slightly larger clutches in DS (4.29 ± 0.92 , $n = 164$) than in RO (3.95 ± 0.89 , $n = 84$; Table 1). Mean egg volume was found

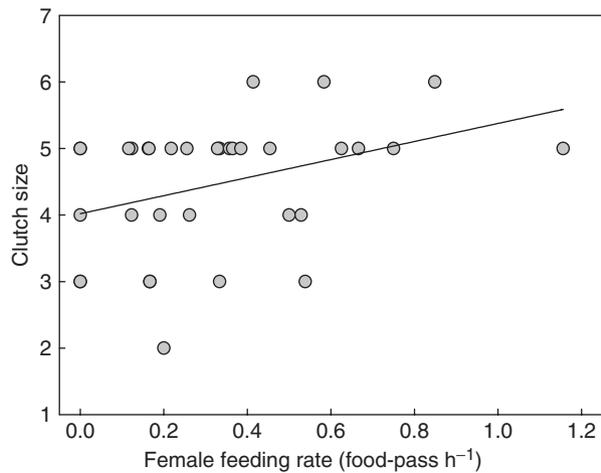


Figure 2 Clutch size according to the female feeding rate by the male (number of prey deliveries per hour) during the prelaying and laying periods ($n=34$ pairs, including control, supplemented, uncertain and neighbour pairs from both RO and DS, see 'Materials and methods'). RO, Rochefort marshes; DS, Deux-Sèvres.

to be much less variable than clutch size ($CV = 4.6\%$), and was related to vole abundance in RO only (Table 1 and Fig. 3b). Removing the apparent outlier (only two clutches measured in RO in 2001, bottom left corner in Fig. 3b) did not affect the positive relationship between vole abundance and mean egg volume in RO (with RO data only, estimate = 2.06 ± 0.71 , $n = 67$, $F_{1,5} = 8.38$, $P = 0.034$).

Wing-tagged Montagu's harriers involved in several breeding attempts over many years allowed us to calculate repeatability in breeding parameters, following Lessells & Boag (1987). Within-individual repeatability (r_i) in clutch size was not different from zero for both females ($r_i = -0.02$, $F_{35,72} = 0.93$, $P = 0.58$) and males ($r_i = -0.02$, $F_{32,54} = 0.52$, $P = 0.98$). In contrast, repeatability in mean egg volume was very high for females ($r_i = 0.83$, $F_{35,70} = 14.8$, $P < 0.0001$), but not for males ($r_i = -0.01$, $F_{34,59} = 0.97$, $P = 0.53$).

Average hatching success varied between years from 0.823 ± 0.11 and 1 and did not differ between study sites (DS: 0.922 ± 0.14 , $n = 136$; RO: 0.907 ± 0.14 , $n = 65$). The

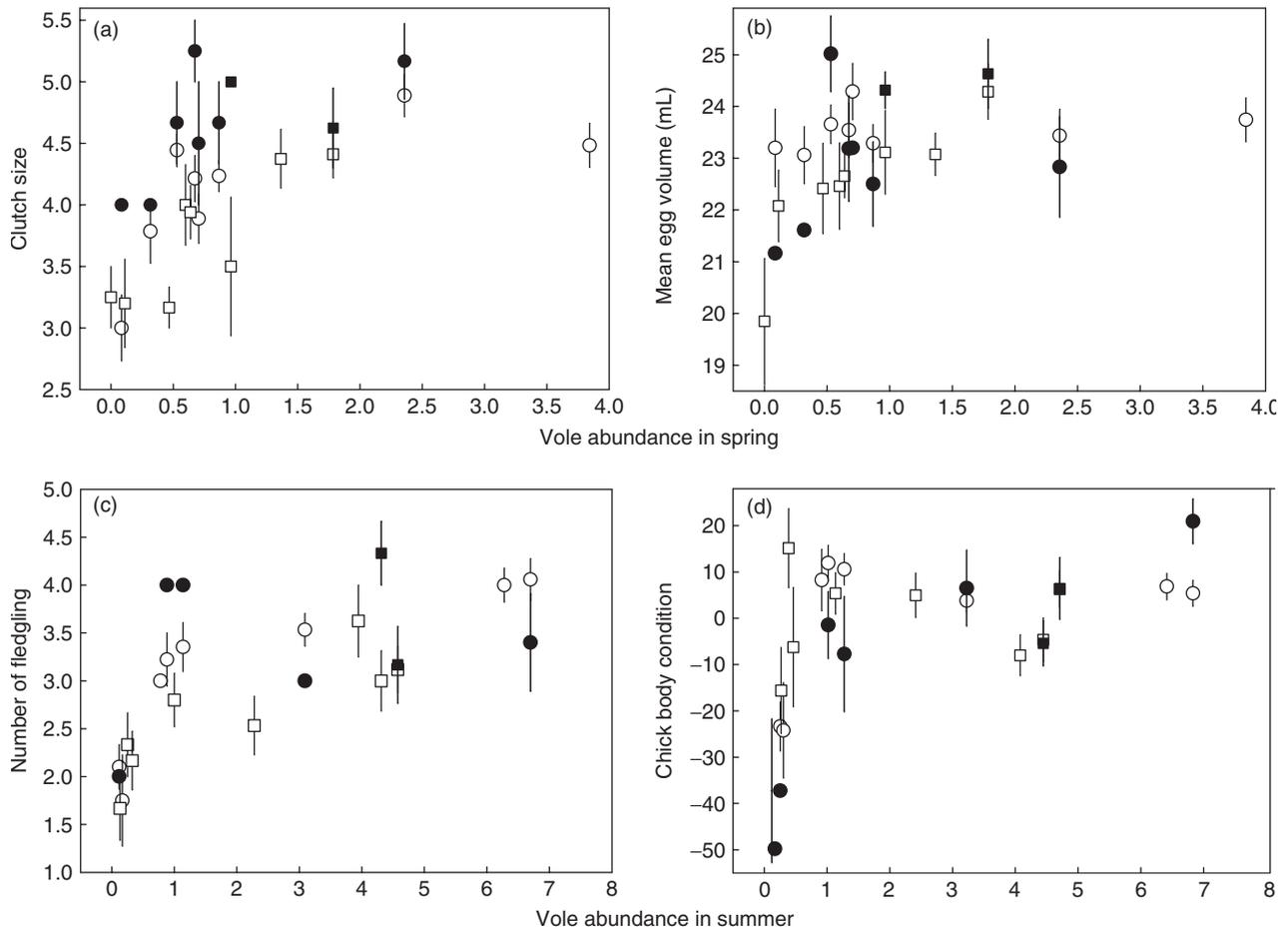


Figure 3 Patterns of variation in average (mean \pm SE) clutch size (a), egg volume (b), number of fledglings per successful nest (c) and chick body condition (males and females combined) at fledging (d) of Montagu's harrier, according to vole abundance. Distinctions were made between the two study sites (open square for RO, open circle for DS), and between control (open symbol) and food supplemented pairs (filled symbol). Vole abundance is expressed as the number of voles/trap-line/24 h. RO, Rochefort marshes; DS, Deux-Sèvres.

Table 1 Generalized linear mixed models of clutch size, mean egg volume and hatching success (number of hatchling/clutch size, for nests with ≥ 1 hatchling) as response variables (with year as random effect)

	d.f.	Estimate	SE	F	P
<i>Clutch size</i>					
Site (RO–DS)	1237	–0.252	0.114	4.8	0.029
Vole (\log_{10} spring)	1237	0.830	0.229	19.8	<0.0001
Relative laying date	1237	–0.035	0.005	54.0	<0.0001
sd random effect ^{NS}		Year: 0.215	Residual: 0.785		
	d.f.	Estimate	SE	F	P
<i>Mean egg volume</i>					
Site (RO–DS)	1197	–0.370	0.289	2.48	0.12
Vole (\log_{10} spring)	1197	0.291	0.449	4.44	0.036
Site \times vole	1197	1.768	0.881	4.02	0.046
sd random effect ^{NS}		Year: 0.018	Residual: 1.920		
	d.f.	Estimate	SE	z	P
<i>Hatching success</i>					
Relative laying date	1190	0.030	0.015	1.96	0.05
Vole (\log_{10} spring)	1190	–0.491	0.375	–1.31	0.19
Relative laying date \times vole	1190	–0.110	0.033	–3.30	0.001
sd random effect ^{***}		Year: 0.00006	Residual: 0.969		

Full models were run with site, vole abundance (in spring, \log_{10} -transformed), relative laying date and all second-order interactions. Numbers of observations are 248, 208 and 201, respectively. sds for the random effect are presented [between-year (*Year*) and within-year (*Residual*)]. The level of significance of the random effect assessed by a log-likelihood test is indicated by a superscript (NS: $P > 0.05$, *** $P < 0.001$).

interaction between relative laying date and vole abundance was significant (Table 1). *Post hoc* comparisons between poor (\log_{10} -transformed values of spring vole abundance ≤ 0) and rich (> 0) food conditions revealed that the relationship between timing of breeding and hatching success was found positive (i.e. late clutches had higher hatching success, estimate = 0.083 ± 0.034 , $F_{1,81} = 2.2$, $P = 0.028$) under poor conditions, but not when voles were plentiful (estimate = -0.004 ± 0.014 , $F_{1,116} = 0.1$, $P = 0.78$).

The number of fledged young per successful pair averaged 3.15 ± 1.12 ($n = 217$, CV = 25.8%) and varied between years and sites from 1.63 ± 0.58 ($n = 8$) to 4.06 ± 0.79 ($n = 23$). Successful pairs produced significantly more fledglings when voles were plentiful (Fig. 3c), and productivity declined with increasing relative laying date (Table 2). The two study sites differed, after controlling for vole abundance and laying date, with more young per successful pair fledging from DS than from RO [3.39 ± 1.06 ($n = 133$) vs. 2.76 ± 1.12 ($n = 84$)]. Fledging success was lower in RO (0.807 ± 0.21) than in DS (0.891 ± 0.18), varied strongly according to vole abundance in summer (Table 2) but was not affected by the timing of breeding.

Chick body condition just before fledging was particularly poor during crash vole years (Fig. 3d). Brood size did not impact body condition and was not kept in the model. The condition of females, but not males, deteriorated over the course of the breeding season (Table 2). Females were in poorer condition in RO (-0.9 ± 28 , $n = 80$) compared with DS (6.2 ± 30 , $n = 224$) whereas males from the two sites fledged with very similar conditions (RO: 1.7 ± 27 , $n = 109$; DS: 0.8 ± 25.2 , $n = 202$; Fig. 4).

Effect of food supplementation

Control and supplemented pairs did not differ in breeding timing (relative laying date \pm SD, fed pairs: -4.4 ± 4.9 ; control pairs: -2.6 ± 6.6 ; one-way ANOVA, $F_{1,171} = 2.24$, $P = 0.14$). The effect of the experiment was kept into final models for clutch size only, the mean clutch size of supplemented pairs being higher than control pairs (respectively 4.79 ± 0.73 vs. 4.35 ± 0.85 , Table 3). Analyses based on the restricted dataset were consistent (Table 3) with previous analyses (Tables 1 and 2), except for mean egg volume and chick body condition, probably as a consequence of reduced contrasts between years. Providing additional food indeed significantly increased clutch size in all years in which the experimental treatment was performed (Fig. 3a). In accordance with the analysis of repeatability, mean egg volume was not affected by the experiment, whatever the food conditions (Fig. 3b). Hatching success was not found to be affected either (Table 3).

As a consequence of the experimentally induced increase in clutch size, we expected either an increased number of fledglings or, conversely, higher brood reduction because of increased within-brood competition in supplemented nests. Twenty-four experimental pairs out of 31 raised at least one fledgling (77.4%, human-induced partial failure included), a proportion that did not differ from control pairs [120/141 (83.3%), $\chi^2_1 = 0.095$, $P = 0.92$]. Among successful pairs, those that were fed tended to fledge more chicks than control pairs (Fig. 3c), but this difference was not significant, and fledging success was found to be similar between treatments ($n = 23$ fed pairs, human-induced partial and total failure excluded, Table 3).

Table 2 Generalized linear mixed models of number of fledglings and fledging success (number of fledgling/number of hatchling) in successful broods as response variables (with year as random effect)

	d.f.	Estimate	SE	F	P
<i>Number of fledglings</i>					
Site (RO–DS)	1206	–0.498	0.127	15.4	0.0001
Vole (log ₁₀ summer)	1206	0.912	0.129	64.6	<0.0001
Relative laying date	1206	–0.037	0.008	25.7	<0.0001
SD random effect ^{NS}		Year: 0.112	Residual: 0.894		
	d.f.	Estimate	SE	z	P
<i>Fledging success</i>					
Site (RO–DS)	1206	–0.555	0.221	–2.54	0.012
Vole (log ₁₀ summer)	1206	1.423	0.283	5.03	<0.0001
Vole × site	1206	–0.889	0.384	–2.32	0.02
SD random effect ^{NS}		Year: 0.285	Residual: 0.975		
	d.f.	Estimate	SE	F	P
<i>Chick body condition</i>					
Site (RO–DS)	1202	–7.855	3.910	0.64	0.42
Vole (log ₁₀ summer)	1202	7.963	4.395	3.80	0.053
Relative laying date	1202	–0.464	0.212	0.83	0.42
Sex (M–F)	1399	–5.843	2.276	5.42	0.02
Relative laying date × sex	1399	0.563	0.212	6.44	0.012
Site × sex	1399	10.716	4.079	6.90	0.009
SD random effects ^{***}		Year: 6.03	Residual: 20.30		
Brood nested in year: 17.90					

Full models were run with site, vole abundance, relative laying date and all second-order interactions. Number of observations is 217. Generalized linear mixed models of number of chick body condition as the response variable (brood nested in year as random effects). The full model was run with sex and brood size at fledging in addition to the previous variables as well the interactions between sex and all variables ($n=615$ nestlings from 213 broods). sds for the random effect are presented [between-year (*Year*) and within-year (*Residual*)]. The level of significance of the random effect assessed by a log-likelihood test is indicated by a superscript (NS: $P>0.05$, *** $P<0.001$).

Table 3 Generalized linear mixed models investigating the response of clutch size, five breeding parameters (year as random effect) and chick body condition at fledging (brood nested in year as random effects)

	Clutch size (34, 139)			Mean egg volume (32, 124)			Hatching success (26, 125)		
	Estimate	F	P	Estimate	F	P	Estimate	z	P
Exp × vole	–0.45 ± 0.48	0.86	0.35	–0.03 ± 1.39	0.001	0.98	0.20 ± 1.37	0.144	0.89
Exp (S–C)	0.27 ± 0.13	4.33	0.039	–0.01 ± 0.39	0.01	0.98	–0.04 ± 0.36	–0.01	0.92
	Number of fledglings (23, 133)			Fledging success (23, 133)			Chick body condition		
	~Site + vole + Relative laying date			~Site + vole			~Sex + vole × exp		
	Estimate	F	P	Estimate	z	P	Estimate	F	P
Exp × vole	–0.40 ± 0.46	0.74	0.39	–0.48 ± 0.69	–0.70	0.48	21.8 ± 10.6	4.27	0.04
Exp (S–C)	0.16 ± 0.21	0.58	0.44	–0.07 ± 0.33	–0.07	0.94	–10.3 ± 6.5	0.08	0.78

Initial models are those selected when analysing natural variation (see Tables 1 and 2 and ‘Materials and methods’), but using a dataset restricted to years and sites in which the experiment was conducted, and adding the experimental treatment (a two-level factor) in interaction with vole abundance only. Final models selected from the restricted dataset are shown below as well as estimate (\pm se), statistic (z or F) and P-value for the effect of food supplementation (exp) and its interaction with vole abundance (exp × vole), even if not kept in the final model (in this case, estimates were taken from the last model including the variable during model selection). Sample sizes, respectively, of supplemented (S) and control (C) pairs are given in brackets (see ‘Results’ for chick body condition). Significant P-values in bold.

We found a slightly significant interaction between the experiment and vole abundance on chick body condition (Table 3, Fig. 3d). A *post hoc* analysis (model: ~Sex + exp) contrasting low and high vole abundance in summer (> or

<2 voles line⁻¹/24 h, see Fig. 3d) further revealed that chicks tended to suffer more from the consequences of the experiment when raised under a poor environment [186 chicks (20 from supplemented pairs) from 70 broods;

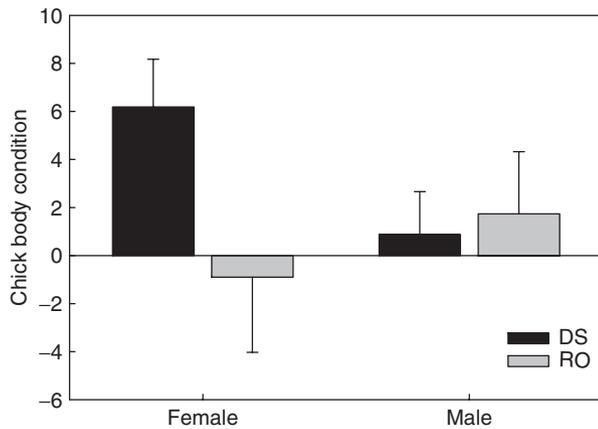


Figure 4 Chick body condition before fledging (average \pm SE of residual mass according to sex-specific growth curves) according to sex and site.

estimate: -17.0 ± 9.1 , $F_{1,64} = 3.49$, $P = 0.067$], while there was no detectable effect when voles were abundant [305 chicks (57 from supplemented pairs) from 95 broods; estimate: 7.0 ± 5.5 , $F_{1,91} = 1.25$, $P = 0.21$].

Discussion

By combining multiple sources of evidence – behavioural observations, empirical and experimental data on breeding parameters – we were able to finely assess the underlying causes of variation in Montagu's harrier reproductive success. Clutch size, which is directly linked to female feeding rates during prelaying, and number of chicks fledged were the most sensitive breeding parameters in response to vole abundance, a typical result for a specialist predator preying on cyclic prey species (Korpimäki, 1990; Korpimäki & Wiehn, 1998). Strong between-year variation in breeding success related to vole abundance showed that adjustment in clutch size was not sufficient to prevent brood reduction and breeding failure under poor food conditions. Finally, higher vole abundance allowed harrier chicks to fledge in better condition.

We found a consistent difference between the two study sites regarding most of the breeding rates. Harriers in RO (mixed cereal and natural habitats) laid smaller clutches, experienced lower fledging success and ultimately raised fewer fledglings compared with harriers breeding in DS (cereal habitat only). These differences were not attributable to lower vole abundance in RO solely, as our analyses have accounted for variation in prey abundance between the two study sites. In addition, female chicks fledged in the worst condition in RO compared with DS, while no difference was detected concerning males. Interestingly, this result supports a previous finding that the secondary sex ratio, although subject to variation according to vole abundance, was biased towards males in RO but not in DS (Millon & Bretagnolle, 2005). Variation in environmental conditions affects not only Montagu's harriers breeding rates but also sex ratio and offspring quality. What triggers, in addition to

prey abundance, the between-sites difference remains, however, unknown.

Empirical and experimental results agreed in showing that clutch size was a more plastic trait than egg size with regard to food abundance. Pairs receiving supplementary food during the laying period laid on average 0.44 more eggs than control pairs. To test the robustness of this result, we repeated the analysis by deleting years with less than three fed pairs and found a similar effect of the food supplementation. Fed females may have suffered from repeated approaches to their nest during the feeding experiment compared with control females. This effect was probably negligible as they were not forced to leave the nest, and food supplementation indeed triggered a positive effect on clutch size. Such an effect was slightly lower than the variation observed between intermediate and peak phases of a vole cycle. Experiments conducted on birds usually resulted in an advance of laying date only, and many tests provided negative results with regard to an additive effect on clutch size (11 out of 21 in Newton, 1998). While timing of breeding and vole abundance accounted for most of the variation in clutch size in Montagu's harrier, it is noteworthy that the effect of food supplementation was independent of laying date in our study.

Measures of repeatability (an estimate of the upper limit of heritability) revealed the consistency in egg size within females over successive breeding seasons, corroborating general findings in birds that egg size is primarily driven by female characteristics rather than by environmental variables (Christians, 2002). In contrast, repeatability for clutch size was very close to zero for both females and males, a result only found in the Tengmalm's owl *Aegolius funereus* so far (Korpimäki, 1990), and this might reveal an adaptation of vole specialist predators to highly variable food conditions. This also suggests that not controlling for individual identity between years may raise some level of pseudo-replication in egg volume but not in clutch size analyses.

Multiple constraints and the threshold hypothesis in clutch size

Martin (1987) advanced that the limited number of years in which food supplementation experiments were conducted, reduced the probability of finding a positive effect on clutch size. The effect of such experiments on clutch size is indeed expected to be stronger under poor environmental conditions, and this has been confirmed in many bird taxa (the *threshold hypothesis*; review in Nager *et al.*, 1997). Our aim here was thus to replicate food supplementation over several years in which accurate natural food supply was simultaneously measured. Only in a handful of studies involving food supplementation was natural food supply accurately assessed (Korpimäki, 1987; Wiebe & Bortolotti, 1994; Korpimäki & Wiehn, 1998; Dawson & Bortolotti, 2002; though using different experimental designs). In our study, supplemented females were able to lay larger clutches even during peak vole years, suggesting that Montagu's harrier females

did not reach their physiological limits in laying capabilities during peak vole years. Our results therefore did not support the *threshold hypothesis stricto sensu*. Previous studies conducted on raptors feeding on cyclic microtines also provided little support for this hypothesis (Tengmalm's owl: Korpimäki, 1988; Eurasian kestrel *Falco tinnunculus*: Wiehn & Korpimäki, 1997). Wiehn & Korpimäki (1997) suggested this could result from the unpredictable within-year dynamics of microtine in northern latitudes, preventing predators from estimating the food abundance they would experience later in the season. The predictable nature of the vole dynamics between spring and summer in our study system, however, in contrast to the general pattern of vole dynamics under northern latitudes (Norrdahl, 1995), turns this proposition down (Fig. 1). The reason why clutch size was also limited by food availability even in years of high food abundance could originate from higher competition with other vole-eating predators but also from the way in which Montagu's harrier males trade their time budget between mate guarding and foraging during the fertile period of females. Food-supplemented males brought more food to females without increasing foraging effort, thus without unattending their mates. Males of Montagu's harrier adjust their mate guarding and copulation behaviour in relation to the risk of extra-pair copulation (EPC; Arroyo, 1999; Mougeot, Arroyo & Bretagnolle, 2001). The EPC risk for this semi-colonial species is expected to be higher when voles are abundant and, therefore, when harrier local density is high. This additive constraint, positively related to vole abundance, may therefore underpin the constant effect of food supplementation observed along the gradient of food abundance.

Constraint versus anticipation hypotheses: a matter of predictability?

The traditional opposition between Perrins' (1970) *constraint hypothesis* (clutch size proximately constrained by energy availability during laying) and Lack's (1954) *anticipation hypothesis* (clutch size supposed to match the maximum number of offspring parents would be able to fledge, given food conditions that will prevail during brood rearing) has been recently refined based on growing evidence that female decisions concerning clutch size arise from the integration of different factors throughout all breeding stages (review in Monaghan & Nager, 1997). Several authors emphasized that egg formation or incubation (Heaney & Monaghan, 1996; Monaghan, Nager & Houston, 1998) could incur costs that may be as high as those generated during the offspring-rearing period. We found that food-supplemented Montagu's harriers increased their clutch size independently of laying date and irrespectively of natural food supply, but they did not fledge more chicks, suggesting increased egg or nestling losses, a result consistent with the *anticipation hypothesis*.

Lowered breeding performance for pairs laying an extra egg may be due to a negative correlation between egg number and quality (Monaghan, Bolton & Houston, 1995),

an alteration of incubation efficiency decreasing hatching probability (Siikamäki, 1995) or a higher incubation effort affecting parent ability to cope with brood rearing (Heaney & Monaghan, 1996). In addition, experimental pairs may be unable to provide sufficient food to satisfy the energy requirements of their brood, as it has been described following either a manipulation in parental investment (Monaghan *et al.*, 1998) or a brood enlargement (Dijkstra *et al.*, 1990). In our study, the additive costs of reproduction in terms of reproductive success following enlarged clutch size were remarkably weak, as experimental and control pairs did not significantly differ in hatching or fledging success or in the overall proportion of successful pairs. The only detected cost concerned chick body condition. Chicks raised by supplemented pairs during low vole years had indeed slightly less favourable body condition than controls, while there was no difference during good vole years. This result is interesting because it would support an extended *threshold hypothesis*, as costs entailed by an experimental manipulation (here an 'experimentally increased' clutch size following food supplementation during prelaying and laying periods) were differentially expressed according to food availability. Nevertheless, additional costs may have been expressed in terms of adult residual reproductive value (under the hypothesis that supplemented pairs increased their current reproductive investment, Dijkstra *et al.*, 1990), for which we have no data available.

In contrast, a prelaying supplementary food experiment in the American kestrel *Falco sparverius*, Wiebe & Bortolotti (1994) found a strong reduction in reproductive output through a higher rate of brood reduction in fed pairs. They argued that fed pairs manipulated hatching span according to a biased estimation of natural conditions and hence experienced higher chick mortality. Brood manipulation experiments conducted in Tengmalm's owls during both increase and decrease phases of the vole cycle (Korpimäki, 1988) incurred lower reproductive success, but only during the decrease phase, whereas owls were able to raise additional chicks during the increase phase. In our study, if extra food might have biased harrier information about environmental quality (i.e. mostly vole abundance), supplemented pairs fledged the same number of chicks as control pairs.

In conclusion, the cyclic dynamics of voles strongly affected breeding parameters of a specialist predator such as the Montagu's harrier. Nevertheless, the consistent seasonal increase in vole abundance within the predator breeding season might allow birds at least partly to cope with this strong environmental variation and to adjust their breeding effort according to prey availability.

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