

Interactive effects of food and age on breeding in the Montagu's Harrier *Circus pygargus*

BEATRIZ E. ARROYO,^{1,2*} VINCENT BRETAGNOLLE¹ & ALAIN LEROUX³

¹Centre d'Etudes Biologiques de Chizé – CNRS, 79360 Villiers en Bois, France

²Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC-UCLM-JCCM), c/Ronda de Toledo s/n 13005 Ciudad Real, Spain

³Chemin du Chêne –86190 Quincay, France

We evaluated the direct and interactive effects of food and age on reproduction in the Montagu's Harrier *Circus pygargus*, to test whether variation in food supply was likely to affect age-specific breeding probability or success. Younger females were more frequently non-breeders than older females. When breeding, older females laid earlier, produced larger clutches, failed less often and had higher number of fledglings than younger females. Probability of breeding was higher, laying was earlier, and clutch size and number of fledglings per pair increased with increasing food abundance. A significant interaction between food and age was observed in both breeding probability and breeding performance: older females were more likely to breed than younger females when food abundance was low, and younger females performed less well in good food conditions than older females. Overall, differences between age groups were most marked in extreme food conditions, regardless of the quality of the conditions.

In vertebrates, breeding rates are expected to be modulated by the cost of reproduction (Williams 1966) and are dependent on extrinsic as well as intrinsic factors (e.g. Roff 1992, Stearns 1992), food supply and age being the most common (Clutton-Brock 1988, Sæther 1990). Food supply has been shown to affect reproduction through an influence on parental body condition (Meijer *et al.* 1989, Pietiäinen & Kolunen 1993), timing of breeding (Daan *et al.* 1988, Meijer *et al.* 1990) and breeding rates or success (Martin 1987, Sanz & Moreno 1995, Brinkhof & Cavé 1997, Wiehn & Korpimäki 1997). Age also influences the probability of breeding in birds, with young individuals being generally more common than older birds among the non-breeding population (Newton & Rothery 1997, Kenward *et al.* 1999). Moreover, in most birds, reproductive performance increases with age, at least in the early years of life (Newton 1989, Sæther 1990). Age-related differences in breeding performance may appear if there is a lower efficiency in resource gathering (mates, food, nests) in young birds (Forslund &

Pärt 1995). They may also appear through an optimization of reproductive effort (the relative amount of resources allocated to reproduction), which should increase as the residual reproductive value decreases (Schaffer 1974, Newton & Rothery 1997).

Food supply and age may have interactive effects (Boeckelheide & Ainley 1989, Sydeman *et al.* 1991, Ratcliffe *et al.* 1998). For example, if the costs of reproduction increase with decreasing food conditions, and age-related breeding patterns are related to reproductive constraints, we should expect that the probability of whether to breed or not under different conditions changes with age: young females should more frequently be non-breeders in low food conditions. Similarly, if differences in breeding performance arise due to young birds being less skilled, this should be particularly noticeable when resources are scarce and/or more difficult to gather. Regardless, differences between age groups should be more marked in poor food conditions.

Here we evaluate the relationship between food and age on reproduction for the Montagu's Harrier *Circus pygargus*. This species feeds on a large variety of prey (Arroyo 1997), but some populations specialize on voles and are thus exposed to strong annual

*Corresponding author.
Email: beatriz.arroyo@uclm.es

variation in food availability, as vole populations can be cyclical (Salamolard *et al.* 2000). We evaluated whether breeding probability or performance changes with age in a vole-eating population of this species, and whether differences between age groups varied according to vole abundance.

METHODS

Study areas and breeding parameters

Data were collected in three study areas located in western France which cover 200–350 km² each: (1) Marais de Rochefort (45°57'N, 0°55'W), with data available from 1988 to 2000; (2) south of Deux Sèvres (46°11'N, 0°28'W), with data collected from 1994 to 2000; and (3) Baie de l'Aiguillon (46°24'N, 1°24'W), with data collected from 1996 to 2000. These areas were located c. 50–60 km from each other. Suitable breeding habitat for Harriers also occurs in between the study areas, although breeding density is lower than within the study areas (pers. obs.).

Searching effort was intensive, and we are confident that all nests in each area were located. Nests were visited as early as possible 3–5 times after laying, to collect data on clutch size, productivity (number of fledglings per pair) and nest success. Nest visits did not have any apparent effect on nest failure. All birds were monogamous during the study period. Laying date was estimated directly for some nests, which were visited before laying had finished, or by backdating from hatching date. This was known directly from visits at hatching time in some nests, or estimated from body measurements of nestlings in other cases (Brignon 1997). In all cases, an incubation period of 29 days per egg and 2-day periods between laying consecutive eggs were assumed, which is the most common pattern for the species (Cramp & Simmons 1980, Arroyo *et al.* 2004).

Prey abundance estimates

The main prey of Montagu's Harrier in western France is the Common Vole *Microtus arvalis*, which constitutes 60–90% of the diet in biomass (Butet & Leroux 1993, Salamolard *et al.* 2000). Vole abundance varies cyclically across years in western France, with peaks every 3 years (Salamolard *et al.* 2000). An index of vole abundance was estimated annually for each study site using line-trapping (Butet & Leroux 1993, Salamolard *et al.* 2000). Data from Rochefort

and Deux Sèvres were obtained in April (predominantly pre-laying period) and June (predominantly nestling period), but only June data were available for Baie de l'Aiguillon. To allow comparisons, June data from all three areas were used for all analyses. June and April data were highly correlated (Salamolard *et al.* 2000). Between 36 and 96 lines of 51 traps were set in each area in each trapping period. Traps were checked and removed 24 h after setting. Different crop types were sampled (cereal, pasture and fodder crops, oilseed rape and sunflower/corn). We obtained mean vole abundance each year in each study site by correcting for the overall surface of a given crop type in each study area (i.e. by multiplying the average number of voles in each crop type by the percentage area covered by that crop type). Data are expressed as captures/100 night-traps.

Female age and breeding status

Female age was obtained from three sources. First, a wing-tagging programme on nestlings was carried out for between 6 and 12 years duration according to study area (> 500 fledglings wing-tagged). A total of 28 females wing-tagged as nestlings bred at least once in the study areas, producing 38 reproductive events where the exact age of the female was known (between 1 and 9 years). Secondly, Montagu's Harrier females in the year subsequent to hatching (first-years) still hold their juvenile primaries and characteristic uniform secondaries (Arroyo & King 1996). All breeding females could therefore be classified as first-years or adults (i.e. 2 years old or older), providing 60 reproductive events of unmarked first-year females. Finally, adult females were trapped at the nest and wing-tagged. Their exact age was not known, unless they were ringed. However, a minimum age could be estimated, assuming an age at capture of at least 2 years (as they had adult plumage patterns). Estimated ages went up to > 13 years old (i.e. for birds breeding 11 years after capture). Females with estimated ages were not included in the analyses on the effect of age, except if > 7 years old (see below). Annual adult survival for Montagu's Harriers in France is c. 75% (Arroyo *et al.* 2004). Therefore, median life span for this species is about 5 years. Females were thus classed as young (1–3 years old), middle aged (4–6 years old) or old (\geq 7 years old). Birds whose estimated age was 7 years or older were also included in analyses as 'old' birds.

Adults were captured only once in their life. Trapping was carried out throughout the season, and

included both breeders and (assumed) non-breeders. Trapping techniques included mainly pole-traps and bow-nets over the nestlings. Trapping did not have any apparent effect on breeding, with all birds returning to their nest or their normal behaviour as soon as they were released. Breeding success of trapped birds was similar to that of non-trapped birds (unpubl. data).

Each year we recorded every wing-tagged female present in the study areas, its age (when known), and whether it ultimately produced a clutch or not. A 'non-breeder' was subsequently defined as a female observed in the study areas but not producing a clutch. This included females observed in the study area for only short periods of time (i.e. floaters that may have not had a mate or territory). 'Probability of breeding' was therefore defined as the probability of producing a clutch in the study area, if observed there. Given the observation pressure, it is highly unlikely that this included birds that had attempted to breed and failed before nests were found. Observations of females in the year of their capture were not included (given that most captures were for breeding females, thus biasing results). Those females were only included if re-sighted in subsequent years.

Statistical analyses

All analyses considered age as a three-class categorical variable (as defined above), and food abundance as a continuous variable (although data on food abundance are presented as categorical in tables and figures for simplicity). Food abundance categories for the tables and figures were calculated as follows: high (peak phase of the vole cycle, > 4.5 voles/100 trap nights), medium (increase phase of the vole cycle, 1.5–4.5 voles/trap nights) and low (crash phase of the vole cycle, < 1.5 voles/trap nights).

For analyses of the variation in age structure of the population in relation to food, the CATMOD procedure and a maximum-likelihood approach (SAS 1988) were used, with age as a dependent variable. The CATMOD procedure performs modelling of categorical (but not necessarily binomial) data. In other words, PROC CATMOD fits linear models to functions of response frequencies. The probability of breeding when present was analysed with a binomial response variable, also with the CATMOD procedure and a maximum-likelihood approach.

To assess the patterns of age-specific variation in reproductive parameters, relative laying dates, rela-

tive clutch sizes and relative fledging success were calculated for each female as the difference from the mean value for all females for each year and area. Thus, we accounted for the fact that overall reproductive parameters varied between years and between areas (see Arroyo *et al.* 1998 for clutch sizes) and that age classes were not equally represented in all circumstances (see below). General linear models (GLMs) were fitted to the relative data, with age as an explanatory variable. The relationship between reproductive parameters and food was analysed using data from all nests (whether the age of the female was known or not), and raw values of laying date, clutch size or productivity (number of fledglings) as explanatory variables. The interactive relationships between food, age and breeding performance were analysed in two ways. The first used a GLM with relative productivity (number of fledglings) as the response variable. Residuals of all GLM models were normally distributed. The second used a logistic regression with probability of breeding failure as a response variable, and relative laying date, age, food and their interaction as explanatory variables. Relative laying date was included as it is known to influence breeding success, and it varied among age groups (see Results).

Where wing-tagged females were concerned, most (66%) observations belonged to different females, but 34% of observations included data corresponding to the same female in different years (with 2–5 observations per female). Overall, not enough data existed to look at within-individual variation in breeding performance. To control for potential biases arising from pseudoreplication, we also analysed the data using only one random observation per female. Results were very similar, so we used the whole data set to maximize sample size. Statistical analyses were carried out using SAS 8.00 (SAS 1988).

RESULTS

Age, food and breeding probability

The probability of finding females of different age classes in the breeding population (based on wing-tagged females) changed significantly with food abundance (CATMOD $\chi^2 = 6.66$, $P = 0.03$). The proportion of young females decreased with decreasing food abundance, whereas the opposite was found for old females (Fig. 1). Similar results were obtained when looking at the probability of finding females with first-year plumage in the breeding population,

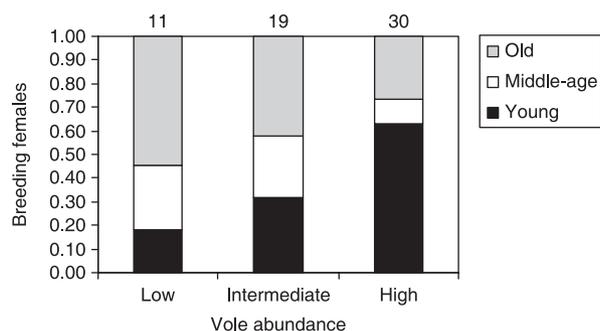


Figure 1. Age structure of the breeding female population (age identified through wing-tags) according to food conditions in western France. n = number of known-aged wing-tagged breeding females. Note that vole abundance is presented as a categorical variable in the figure, but was analysed as a continuous variable (see text).

which increased significantly with increasing food abundance ($\chi^2_1 = 40.2$, $P < 0.001$). Thus, the age structure of the female breeding population significantly changed with food abundance (Fig. 1).

The probability that wing-tagged birds observed in the study areas produced a clutch there increased significantly with female age ($\chi^2_2 = 11.78$, $P = 0.0028$, Table 1). Additionally, annual differences in the age structure of the breeding population arose, at least partly, from a bias according to age in the proportion of birds apparently not engaging in reproduction under different food conditions. The overall proportion of non-breeders increased significantly with decreasing food abundance, but this was less marked for old females (Table 1; $\chi^2_1 = 6.3$, $P = 0.01$ for food abundance, $\chi^2_2 = 6.8$, $P = 0.03$ for the interaction age \times food).

Age, food and breeding performance

For birds that produced clutches, age also had a significant influence on breeding performance. Older

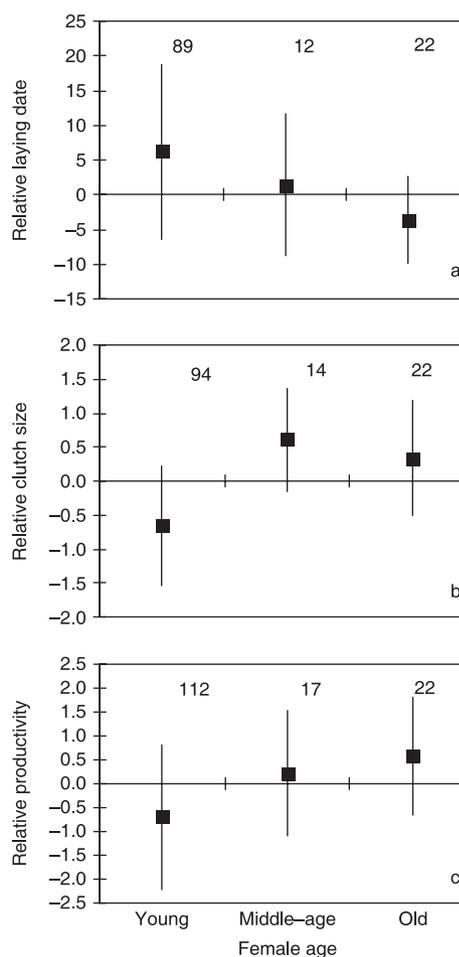


Figure 2. Mean (\pm sd) age-related patterns of variation in (a) relative laying date, (b) relative clutch size and (c) relative productivity (number of young produced). Sample sizes (number of females in each age class) are given above the means.

females laid earlier (GLM $F_{2,88} = 4.75$, $P = 0.01$, Fig. 2a), laid larger clutches ($F_{2,94} = 20.2$, $P < 0.001$, Fig. 2b) and had larger broods ($F_{2,108} = 8.45$, $P < 0.001$, Fig. 2c) than younger females.

Table 1. Proportion of non-breeding wing-tagged females, according to age and food abundance. Sample size (number of observed females) is given in parentheses.

Female age	Food abundance			Total
	High	Intermediate	Low	
Young (1–3 years)	66.7 (12)	60.0 (10)	90.0 (10)	71.9 (32)
Middle age (4–6 years)	50.0 (6)	66.7 (6)	81.8 (11)	69.6 (23)
Old (≥ 7 years)	33.3 (6)	10.0 (10)	44.4 (9)	28.0 (25)
All females*	36.5 (52)	41.9 (74)	64.9 (74)	49.0 (200)

*Values including also wing-tagged birds of unknown age (i.e. wing-tagged as adults).

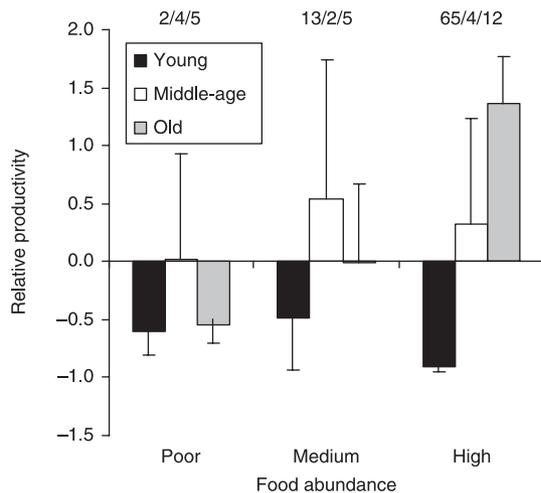


Figure 3. Mean (\pm se) relative productivity in relation to food abundance for young (1–3 years), middle age (4–6 years) and old (≥ 7 years, thick line) females. Sample size (number of reproductive events) is given above the bars.

Food abundance was significantly associated with all breeding parameters considered: breeding was earlier (linear regression $F_{1,383} = 10.3$, $P = 0.001$), clutch size larger ($F_{1,534} = 41.6$, $P < 0.001$) and productivity was higher ($F_{1,632} = 12.9$, $P < 0.001$) with increasing food abundance. There was, additionally, a significant interaction between food and age in explaining breeding performance, expressed either as relative productivity (GLM $F_{3,83} = 5.02$, $P < 0.01$) or as probability of breeding failure (logistic regression $\chi^2_2 = 13.48$, $P = 0.001$), even when controlling for differences in relative laying date. The interaction arose because no positive effect of increasing food abundance was found in young females, some of which still had low productivity in good food conditions. By contrast, the relationship was marked for old females, which only performed poorly when food abundance was very low (Fig. 3).

DISCUSSION

Our results showed that food and age influenced both breeding probability and breeding performance. Furthermore, and as predicted, we observed significant interactive effects between food and age in both breeding probability and breeding performance: older females were more likely to breed than younger females when food abundance was low, and younger females performed less well than older females in good food conditions. We discuss these results below.

Both age and food abundance had a direct influence on breeding probability and breeding performance in the Montagu's Harrier, as observed in many other raptor species (Simmons *et al.* 1986, Pietiäinen 1989, Newton & Rothery 1997, Brommer *et al.* 1998, Kenward *et al.* 1999). The percentage of non-laying females increased in poor food conditions and for younger birds. As in many other bird species (Forslund & Pärt 1995, Martin 1987), laying date became earlier and clutch size increased with increasing age and food conditions.

Birds that were observed in the study area for only short periods of time were defined as non-breeders, but some of these could have been passing migrants and have bred elsewhere. However, environmental conditions (i.e. the phase of the vole cycle) were similar over a relatively large area (Lambin *et al.* 2006), so our assumption is that a large proportion of birds disappearing from the study area will remain non-breeders. Regardless, our results indicate that those same migrants could have stayed to breed in the study area if vole abundance was greater, so the likelihood of staying in the area depends on age and food conditions.

Physiological condition may influence whether and how successfully Montagu's Harriers breed. A nutritional threshold must be achieved for the females to breed (Newton 1979, Weimerskirch 1992). Additionally, laying date, body condition and clutch size are traits that are intimately linked in many bird species, especially raptors: pairs of better quality (whether defined by age, condition or territory quality) usually breed earlier and lay more eggs than others (Newton & Marquiss 1984, Pietiäinen & Kolunen 1993).

In raptors with courtship feeding, female condition before laying and in the incubation period is usually dependent on male food supply. Food provision to females is poorer in bad food years (Korpimäki 1990, Pietiäinen & Kolunen 1993), so this alone may explain the higher probability of non-laying and the lower performance in these circumstances. Food provision to females may also be lower for younger birds, if they are mated to poorer males (Drent & Daan 1980), although the latter was apparently not the case in the closely related Northern Harriers *Circus cyaneus hudsonius*, where the proportion of young females in the breeding population was similar in high and low vole years (Simmons *et al.* 1986). According to the few existing data, mating in the Montagu's Harrier is apparently not assortative in relation to age (our unpubl. data). However, male

quality might not be best explained by age alone. Therefore, the later breeding by younger females may also be partly due to them being fed less adequately. In migratory species, better quality birds also arrive earlier from migration and are thus capable of earlier laying (Sergio & Newton 2003), so the observed differences in laying date may have also been related to differences in arrival dates, as younger birds arrive later (Arroyo 1995). Regardless, no direct or indirect benefits of later breeding may be inferred, whereas the benefits of early breeding are plentiful. For example, later breeding has a strong negative influence on the length of the post-fledging dependency period in this species (Amar *et al.* 2000, Arroyo *et al.* 2002), which in turn is likely to have an influence on fledging survival.

Overall, breeding performance (evaluated as number of fledglings per female) increased significantly with food abundance and with female age. This was partly related to the later breeding and the smaller clutch size in younger females and in poor food conditions. However, younger females also had higher frequency of breeding failure in good food conditions, even when controlling for differences in laying date. The most common factors influencing nest failure in this species are predation and abandonment as a result of starvation (Arroyo 1995, Arroyo & García 2006), which may also be related to the nutritional levels of the females. Thus, differences between younger and older females could imply that older females are more competent at tasks such as nest defence, and as stated above possibly also mated to better providers. If low-quality individuals live a shorter time, the observed increase in reproductive performance with increasing age may also be caused by differences in average quality of individuals between age groups. The interaction between age and food in relation to breeding performance, which showed that older females were better able to profit from good food conditions than younger females, also suggests that the former have a higher reproductive ability or that the average quality of young females is lower than in older age groups.

Finally, we also found interactive effects between age and food abundance in relation to breeding probability, which suggest also differences in the relative investment for different age groups. On the one hand, old females were more likely to breed than younger females when food conditions were very low. Poor food abundance is likely to increase costs of reproduction (Hamer *et al.* 1991, Hakkarainen & Korpimäki 1995). It could pay birds not to breed if

the costs of reproduction were disproportionately large, impairing the capacity for self-maintenance, and thus survival (Curio 1983). Thus, most age groups probably benefited from not breeding in conditions when breeding output was likely to be very low, i.e. when cost of reproduction was not compensated for in terms of fitness. In contrast, females beyond the average lifespan of the species (and thus with low residual reproductive value) should invest proportionally more in current reproduction (Newton & Rothery 1997) and were accordingly those with the highest probability of breeding even in extremely poor food conditions. In very good food conditions, young females had a higher probability of not breeding compared with older birds. This pattern could result from constraints, if young females find it more difficult to breed (i.e. to obtain a mate or sufficient body condition to allow egg production) even in good food conditions. Nevertheless, females might also benefit from starting to breed at older ages, if delayed breeding increases survival as found for Merlins *Falco columbarius* that delayed first breeding (Espie *et al.* 2000).

Overall, we predicted that variation in food supply was likely to affect age-specific breeding probability or success, and that differences between age groups would be more marked in very poor food conditions. However, there were greater differences between age groups in reproductive performance in good food than in poor food conditions, where, nevertheless, the number of young females breeding was very small, and thus perhaps only high-quality individuals bred. Overall, differences between groups were not only noticeable in very poor food conditions, as predicted, but also in very good food conditions. In other words, differences between age groups were most marked in extreme food conditions. If that is the case, it should be expected that interactive effects should not be noticeable in areas where food abundance is sufficient but does not change as dramatically as in western France, or in populations where the diet is more generalist.

Many people helped with fieldwork over many years. Particular thanks are due to C. Attié, R. Bernard, E. Cléré, L. Courmont, T. De Cornulier, T. Dieuleveut, O. Duriez, E. Fojt, M.-H. Froger, A. Millon, C. Nicolai, C. Pacteau, F. Pervanchon, D. Pinaud and M. Salamolard. We thank the Service de protection des Végétaux (La Rochelle and Poitiers) for lending us the vole traps. This research benefited from funds made available to P. Duncan and V. Bretagnolle by the Région Poitou Charente and the CNRS (Contrat de Plan Etat-Région 1994–98), and from

DIREN Poitou-Charentes & Ministère de l'Environnement in 1998, 1999 and 2000. Henri Weimerskirch, Steve Redpath, Mick Marquiss, Hannu Pietiäinen, Rob Simmons, Fabrizio Sergio and Mike Madders commented upon and improved this or previous versions of the manuscript.

REFERENCES

- Amar, A., Arroyo, B.E. & Bretagnolle, V.** 2000. Post-fledging dependency and dispersal in hacked and wild Montagu's Harriers *Circus pygargus*. *Ibis* **142**: 21–28.
- Arroyo, B.E.** 1995. *Breeding Ecology and Nest Dispersion of Montagu's Harrier Circus pygargus in Central Spain*. DPhil thesis, University of Oxford.
- Arroyo, B.E.** 1997. Diet of Montagu's Harrier *Circus pygargus* in central Spain: analysis of temporal and geographical variation. *Ibis* **139**: 664–672.
- Arroyo, B.E., De Cornulier, T. & Bretagnolle, V.** 2002. Parental investment and parent-offspring conflicts during the post-fledging period in the Montagu's Harrier. *Anim. Behav.* **63**: 235–244.
- Arroyo, B.E. & García, J.T.** 2006. Diet composition influences annual breeding success of Montagu's Harriers *Circus pygargus* feeding on diverse prey. *Bird Study* **53**: 73–78.
- Arroyo, B.E., García, J.T. & Bretagnolle, V.** 2004. Montagu's Harrier. *BWP Update (The Journal of the Birds of the Western Palearctic)* **6**: 41–55.
- Arroyo, B.E. & King, J.R.** 1996. Age and sex differences in molt of the Montagu's Harrier *Circus pygargus*. *J. Raptor Res.* **30**: 161–184.
- Arroyo, B.E., Leroux, A.B.A. & Bretagnolle, V.** 1998. Patterns of egg and clutch size variation in Montagu's Harriers. *J. Raptor Res.* **32**: 136–142.
- Boeckelheide, R.J. & Ainley, D.G.** 1989. Age, resource availability and breeding effort in the Brandt's Cormorant. *Auk* **106**: 389–401.
- Brignon, A.-L.** 1997. *Croissance et métabolisme chez des poussins de Busard Cendré (Circus pygargus) élevés en captivité*. PhD thesis, Ecole Nationale Vétérinaire de Nantes.
- Brinkhof, M.W. & Cavé, A.J.** 1997. Food supply and seasonal variation in breeding success: an experiment in the European coot. *Proc. R. Soc. Lond. B* **264**: 291–296.
- Brommer, J.E., Pietiäinen, H. & Kolunen, H.** 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.
- Butet, A. & Leroux, A.B.A.** 1993. Effect of prey on a predator's breeding success. A 7-year study on Common Vole (*Microtus arvalis*) and Montagu's Harrier (*Circus pygargus*) in a west of France Marsh. *Acta Oecol.* **14**: 857–865.
- Clutton-Brock, T.H. (ed.)** 1988. *Reproductive Success*. Chicago: University Chicago Press.
- Cramp, S. & Simmons, K.E.L. (eds)** 1980. *The Birds of the Western Palearctic*, Vol. 2. Oxford: Oxford University Press.
- Curio, E.** 1983. Why do young birds reproduce less well? *Ibis* **125**: 400–404.
- Daan, S., Dijkstra, C., Drent, R. & Meijer, T.** 1988. Food supply and the annual timing of avian reproduction. *Proc. Int. Ornithol. Congr.* **19**: 392–407.
- Drent, R.H. & Daan, S.** 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**: 2325–2252.
- Espie, R.H.M., Oliphant, L.W., James, P.C., Warkentin, I.G. & Lieske, D.J.** 2000. Age-dependent breeding performance in Merlins (*Falco columbarius*). *Ecology* **81**: 3404–3415.
- Forslund, P. & Pärt, T.** 1995. Age and reproduction in birds – hypotheses and tests. *Trends Ecol. Evol.* **10**: 374–378.
- Hakkarainen, H. & Korpimäki, E.** 1995. Contrasting phenotypic correlations in food provision of male Tengmalm's owls (*Aegolius funereus*) in a temporally heterogeneous environment. *Evol. Ecol.* **9**: 30–37.
- Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P. & Burns, M.D.** 1991. The influence of food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. *Ibis* **135**: 255–263.
- Kenward, R.E., Marcström, V. & Karlbom, M.** 1999. Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. *J. Anim. Ecol.* **68**: 1020–1033.
- Korpimäki, E.** 1990. Body mass of breeding Tengmalm's Owls *Aegolius funereus*: seasonal, between-year, site and age-related variation. *Ornis Scand.* **21**: 169–178.
- Lambin, X., Bretagnolle, V. & Yoccoz, N.G.** 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.
- Martin, T.E.** 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* **18**: 453–487.
- Meijer, T., Daan, S. & Hall, M.** 1990. Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. *Behaviour* **114**: 117–136.
- Meijer, T., Masman, D. & Daan, S.** 1989. Energetics of reproduction in female Kestrels. *Auk* **106**: 549–559.
- Newton, I.** 1979. *Population Ecology of Raptors*. Berkhamstead: T. & A.D. Poyser.
- Newton, I.** 1989. *Lifetime Reproduction in Birds*. London: Academic Press.
- Newton, I. & Marquiss, M.** 1984. Seasonal trend in the breeding performance of sparrowhawks. *J. Anim. Ecol.* **53**: 809–830.
- Newton, I. & Rothery, P.** 1997. Senescence and reproductive value in Sparrowhawks. *Ecology* **78**: 1000–1008.
- Pietiäinen, H.** 1989. Seasonal and individual variation in the production of offspring in the Ural owl *Strix uralensis*. *J. Anim. Ecol.* **58**: 905–920.
- Pietiäinen, H. & Kolunen, H.** 1993. Female body condition and breeding of the Ural owl *Strix uralensis*. *Funct. Ecol.* **7**: 726–735.
- Ratcliffe, N., Furness, R.W. & Hamer, K.C.** 1998. The interactive effects of age and food supply on the breeding ecology of great skuas. *J. Anim. Ecol.* **67**: 853–862.
- Roff, D.A.** 1992. *The Evolution of Life Histories: Theory and Analysis*. London: Chapman & Hall.
- Sæther, B.E.** 1990. Age-specific variation in reproductive performance of birds. *Current Ornithol.* **7**: 252–293.
- Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V.** 2000. Responses of an avian predator to cycles in prey density at a temperate latitude. *Ecology* **81**: 2428–2441.
- Sanz, J.J. & Moreno, J.** 1995. Experimentally induced clutch size enlargements affect reproductive success in the Pied Flycatcher. *Oecologia* **103**: 358–364.
- SAS Institute.** 1988. *SAS/STAT User's Guide, Release 6.03 Edition*. Cary, NC: SAS Institute Inc.
- Schaffer, W.M.** 1974. Selection for optimal life histories: the effects of age structure. *Ecology* **55**: 291–303.

- Sergio, F. & Newton, I.** 2003. Occupancy as a measure of territory quality. *J. Anim. Ecol.* **72**: 857–865.
- Simmons, R., Barnard, P., MacWhirter, B. & Hansen, G.L.** 1986. The influence of microtines on polygyny, productivity, age and provisioning of breeding Northern Harriers: a 5 year study. *Can. J. Zool.* **64**: 2447–2456.
- Stearns, S.C.** 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Sydeman, W.J., Penniman, J.F., Penniman, T.F., Pyle, P. & Ainley, D.G.** 1991. Breeding performance in the Western gull, effect of parental age, timing of breeding and year in relation to food supply. *J. Anim. Ecol.* **60**: 135–149.
- Weimerskirch, H.** 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* **63**: 464–473.
- Wiehn, J. & Korpimäki, E.** 1997. Food limitation on brood size: experimental evidence in the Eurasian Kestrel. *Ecology* **78**: 2043–2050.
- Williams, G.C.** 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690.

Received 12 April 2006; revision accepted 22 March 2007.