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Hatching asynchrony and brood reduction in Tengmalm's owl *Aegolius funereus*: the role of temporal and spatial variation in food abundance

Received: 7 January 2002 / Accepted: 23 July 2002 / Published online: 6 September 2002
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Abstract Hatching asynchrony is the consequence of birds initiating incubation before clutch completion. It has been suggested that variation in hatching asynchrony in owls is extensive, and therefore they should be excellent objects to study the effects of spatio-temporal variation in food abundance on this phenomenon. We examined how abundance and predictability of food affected hatching asynchrony in Tengmalm's owl *Aegolius funereus* (Linnaeus), which mainly feeds on voles which fluctuate in 3- to 4-year cycles in northern Europe. Hatching span averaged 6–7 days (range 0–13 days) and increased with clutch size. Food supply did not directly influence levels of hatching asynchrony but it influenced indirectly via marked among-year changes in clutch size. During the decrease phase of the vole cycle the proportion of hatchlings producing fledglings decreased with asynchrony, suggesting that chick mortality was most common among asynchronous broods when food became scarce. This finding is consistent with Lack's brood reduction hypothesis, i.e. that if food becomes scarce during the nestling period the youngest nestlings would die first without endangering the survival of the whole brood.

Keywords Bird of prey · Egg viability hypothesis · Lack's brood reduction hypothesis · Reproductive success · Three-year vole cycle

Introduction

Many bird species initiate their incubation before clutch completion, which results in asynchronous hatching of the young (Stoleson and Beissinger 1995). A large variety of hypotheses has been proposed to explain this phenomenon, most of them assuming that hatching asyn-

chrony is an adaptive trait (Magrath 1990; Stoleson and Beissinger 1995; but see Stenning 1996).

One of the main adaptive roles of hatching asynchrony is based on the idea of an optimal brood size in altricial species (Dunlop 1913; Lack 1947): laying too many eggs would result in food shortage during the nestling period, and as a consequence, the nestlings will be underweight and have poor survival. Laying too few eggs, on the other hand, would result in a reduced number of offspring. Between these two extremes, there should be an optimal clutch size that is ultimately regulated by the available food conditions (Lack 1947; Magrath 1990). Lack (1954) proposed that asynchronous hatching could be an adaptation to unpredictable changes in food supply; if food declines abruptly during the nestling period the youngest nestlings would die first without endangering the survival of the whole brood. By contrast, synchronous hatching of young would make them equally competitive, which in case of food shortage could result in poor growth of the whole brood (Magrath 1990).

Birds of prey, and owls in particular, are traditionally considered classical examples of species exhibiting extreme hatching asynchrony (Wiebe and Bortolotti 1994; Stoleson and Beissinger 1995; Wiebe et al. 1998; Viñuela 1999, 2000; Wiehn et al. 2000). Yet, paradoxically, there are virtually no detailed studies on hatching asynchrony in owls (but see Wilson et al. 1981). To our knowledge, our paper is one of the few long-term studies to examine hatching asynchrony in a bird of prey species, in which both sexes have important roles in parental care and whose reproductive output is largely determined by multi-year density fluctuations in their main prey. In addition, until now only a few studies have examined levels of phenotypic plasticity for hatching asynchrony or natural variation in it within a population (Stenning 1996).

Tengmalm's owl *Aegolius funereus* L. is a small nocturnal bird of prey, which mainly feeds on voles of the genera *Clethrionomys* and *Microtus*. In northern Europe, vole numbers fluctuate in regular 3- to 4-year cycles,

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during which the difference in density of voles varies 50- to 200-fold between the low and high vole years (Korpimäki and Norrdahl 1991; Klemola et al. 2000). The proportion of these voles in the diet of breeding owls varies from 10% to 90% being highest in good vole years (Korpimäki 1981, 1988a). During poor vole years, the owls can use alternative prey, including shrews (*Sorex* spp.) and small passerine birds, but at such times the over-winter survival of owls is low (Hakkarainen et al. 2002) and only experienced high-quality individuals are able to breed (Korpimäki 1988b). The owls are able to breed as yearlings, although yearling males do not breed during years of food scarcity (Korpimäki 1981, 1988b; Laaksonen et al. 2002). First eggs are usually laid in late March to early April, and the timing of laying depends largely on winter vole densities (Korpimäki and Hakkarainen 1991). Yearly mean clutch size varies from 4.0 to 6.7 and is most closely related to spring vole densities (Korpimäki and Hakkarainen 1991). The female lays eggs at 48-h intervals, and starts to incubate, on average, after laying her second egg (Korpimäki 1981), which results in highly asynchronous hatching of eggs. Incubation of the first egg takes on average 29.2 days and that of the last 26.6 days, but the eggs hatch in the order in which they were laid (Korpimäki 1981).

In this paper, we examine how food abundance and, in particular, predictability of food supply may affect hatching spans of Tengmalm's owl broods. Our data have been collected under highly fluctuating and relatively predictable food conditions, which enables us to study how food abundance and its expected changes may influence hatching patterns of owls. In addition to temporal variation in prey abundance, we will also investigate the role of spatial variation in food abundance, which in this case will be assessed through variation in territory quality. We have also been able to capture the majority of breeding owls at their nests, and therefore we can take into account parental traits in the analyses.

According to Lack's brood reduction hypothesis, we predict that brood reduction (i.e. chick mortality) should be highest during the low, and especially during the decreasing vole years when prey availability is permanently low or declines abruptly at the time when the owls are breeding. Secondly, the idea of facultative manipulation of hatching asynchrony (see Pijanowski 1992; Wiebe 1995) suggests that the degree of asynchrony should differ with respect to prey availability, and that it should be highest during low or decreasing vole years and higher on poor than good territories (see above).

Materials and methods

The study was conducted in the Kauhava region (ca. 63°N, 23°E), western Finland, during 1984–1997. The study area covered 1,300 km² and contained about 500 nest-boxes and known natural cavities suitable for Tengmalm's owls. Nest-boxes were checked in late March, April and May. Most nests found were visited regularly enough to determine clutch size, hatching date and number of fledglings (Korpimäki 1981, 1987, 1988a, b, c). Laying dates were

back-dated from hatching dates by using 29 days as the length of the incubation period (Korpimäki 1981).

Territory quality was ranked by grading the territories according to the number of breeding attempts on a given territory during a 10-year period between 1977 and 1990: from 1 (one breeding attempt) to 5 (at least five breeding attempts per 10 years) (see Korpimäki 1988c for further details). For the statistical analyses, ranks 1 and 2 were combined to indicate a poor territory, and ranks from 3 to 5 to indicate a good territory (see Hakkarainen et al. 1997). In low vole years, poor (ranks 1–2) and good (ranks 3–5) territories have approx. the same abundance of small mammals, while in increase and peak vole years vole abundance is higher in good territories (Table 1 in Hakkarainen et al. 1997). The number of potential prey birds is also higher in good than in poor territories (Table 2 in Hakkarainen et al. 1997). Good territories are also typically situated in a landscape that is dominated by productive spruce forests and agricultural fields, whereas poor territories are normally situated in sparse pine forests with a high proportion of peatland bogs (Korpimäki 1988a). Furthermore, prey delivery rates and nest defence index of males are significantly higher in good than in poor territories during peak vole years (Hakkarainen et al. 1997).

Males and females were trapped at the nest during the early nestling period (Korpimäki 1992). They were weighed to the nearest gram and their wing and tail lengths were measured to the nearest millimetre. Owls were aged on the basis of the state of the moult in the primary feathers (Lagerström and Korpimäki 1988; Hörnfeldt et al. 1988). Four age classes (1-year-old, 2-year, 3-year and older) were differentiated in the field, but in statistical analyses only two age classes (1-year and older) were used, because breeding success of yearling owls is consistently lower than that of older individuals but there are no obvious differences between 2-year and older individuals (see Laaksonen et al. 2002 for further information).

We used wing length as a measure of body size (see Hakkarainen et al. 1998), and as an index of body condition (BCI) we used the residuals of the regression of body mass on body size after log-transformation. The BCI was not associated with body size in either sex (males: $F_{1,69}=0.001$, $P=0.99$; females: $F_{1,73}=0.002$, $P=0.98$) and therefore the danger of misinterpreting data was eliminated (see Jakob et al. 1996 for details).

Difference in wing chord between the largest and the smallest nestling divided by mean wing chord of the brood was used as an index of hatching asynchrony (see Wiebe et al. 1998). Wing lengths of nestlings were measured on average 2–3 days after the hatching of the last egg. Only those broods in which wing chord of every chick was measured before the oldest chick was 16 days old (corresponding with the detected maximum hatching span, 13 days) were included in the analyses. The wing length of the oldest chick was also used as a covariate in analyses because the asynchrony index appeared to be higher in nests that were measured late after hatching. The wings of chicks grow linearly during the nestling period, and are not affected by hatching order or food supply (Carlsson and Hörnfeldt 1994), and so are reliable indicators of the time of hatching. Nestlings were ringed and weighed, and their wing lengths measured again, when the oldest member of the brood was 28 days old, just before fledging (at 29–36 days; Korpimäki 1981, 1988d). As for parent owls, we used the ratio of body mass to wing length as an index of body condition (see above). We calculated a mean body condition index for each brood and used this in subsequent analyses.

Data on hatching asynchrony for 1989 were not available and therefore this year was omitted from the analyses. Nests in which food levels or brood sizes were experimentally manipulated were also omitted from analyses of breeding success (Korpimäki 1988d, 1989; Ilmonen et al. 1999). Clutches of 2 and 8 eggs were omitted from all analyses of hatching asynchrony due to small sample sizes (2 and 3 nests, respectively), but they were included in analyses of variation in clutch size. Similarly, only one randomly selected breeding record for each male and female were included, and thus altogether 79 nests were used in the analyses.

Small mammal abundance in four main habitat types was estimated by snap-trapping twice a year (May and September). Based on these data, local food abundance was classified into the following phases: (1) the increase phase (1985, 1988, 1991, 1994, 1997) when vole abundance increased from a moderate level in spring, (2) the decrease phase (1986, 1992, 1995) when vole numbers crashed from a peak or moderate level early in spring, and (3) the low phase (1984, 1987, 1990, 1993, 1996) when vole abundance was low early in spring and also throughout the breeding season of owls (for more details see Korpimäki and Norrdahl 1989; Fig. 5 in Wiebe et al. 1998). The total number of Tengmalm's owl nests also strongly varied with respect to prevailing phase of the vole cycle; in low vole years approximately 20 nests, in increase years approximately 60 nests and in the decrease vole years approximately 80 nests per year were found. In this study, we have used approximately 20% of the total number of nests recorded during 1984–1997. We believe that our sample is representative of the whole study population, as there were no obvious differences in laying dates or clutch sizes between nests included in or excluded from the analyses (Table 1).

ANOVA/ANCOVA models were first run with first-order interaction terms but if these were not significant, they and also non-significant covariates were subsequently dropped from the model starting from the least significant term to increase power of statistical tests. For analysis of nestling mortality, we used logistic regression in PROC GENMOD of SAS statistical software (SAS Institute, Cary, N.C., USA). Number of dead chicks per brood was entered as the dependent variable and the total number of chicks as binomial denominator. All variables were tested for normality and homogeneity of variances, and if necessary, log-transformed to improve the normality of data. Two-tailed *P*-values are reported throughout.

Results

Variation in breeding parameters

Timing of egg-laying in Tengmalm's owls varied significantly between different phases of the vole cycle (Table 1). The owls started to lay eggs significantly later during low vole years than during increase or decrease vole years (Tukey's test, $P < 0.05$). Clutch size varied from 2 to 8 eggs. It was affected by the phase of the vole cycle, and Tukey post hoc tests indicated that it did not differ significantly between increase and decrease phase of the vole cycle, but was smallest during the low phase (Table 1). The number of hatched young was influenced by the vole cycle, and was also smallest during the low phase (Tukey's test, $P < 0.05$; Table 1). Similarly,

number of fledglings differed with respect to the phase of the vole cycle, and was significantly higher during increase than low or decrease vole years (Tukey's test, $P < 0.05$; Table 1). None of the aforementioned breeding parameters was significantly influenced by age of parents (laying date: male age $F_{1,64} = 0.44$, $P = 0.51$, female age $F_{1,64} = 1.68$, $P = 0.20$; clutch size: male age $F_{1,60} = 0.18$, $P = 0.67$, female age $F_{1,60} = 0.61$, $P = 0.44$; number of hatchlings: male age $F_{1,60} = 0.00$, $P = 0.99$, female age $F_{1,60} = 0.01$, $P = 0.97$; number of fledglings: male age $F_{1,61} = 0.71$, $P = 0.40$, female age $F_{1,61} = 0.05$, $P = 0.83$).

Variation in hatching spans

During the 14-year study period, full records of hatching asynchrony were obtained from 79 nests. Hatching span varied between 0 (synchronous) and 13 (asynchronous) days, but the most common hatching span in the population was 6–7 days (mean \pm SE 6.73 \pm 0.35). Hatching asynchrony increased with clutch size (Fig. 1, Table 2). Broods of yearling females were significantly more synchronous than those of older females (means \pm SE: 5.09 \pm 0.56 vs 6.46 \pm 0.42, Table 2). There was also a positive relationship between hatching asynchrony and female body size (indicated as wing length), which was independent of the phase of the vole cycle, clutch size, female age and territory quality (Table 2). In addition, we found a significant interaction between male age and territory quality (Table 2): broods of yearling males were more asynchronous on poor (means \pm SE: 8.10 \pm 0.59) than on good (5.69 \pm 0.72) territories whereas among adult males the level of asynchrony did not differ with respect to territory quality (6.40 \pm 0.38 vs 6.14 \pm 0.39). Similarly, an interaction between female age and male age indicated that broods cared for by yearling parents were significantly less asynchronous than broods in which at least one of the parents was older (Table 2). Interestingly, phase of the vole cycle did not directly influence levels of hatching asynchrony.

To test whether either among-year variation in laying dates or variable clutch size could account for the absence of relationship between hatching asynchrony and

Table 1 Mean \pm SE laying date, clutch size, number of hatchlings and number of fledglings of Tengmalm's owls *Aegolius funereus* included in the analyses of hatching asynchrony during the three phases (low, increase and decrease) of the vole cycle. In statistical tests, clutch size was corrected for laying date, number of hatch-

lings for clutch size and number of fledglings for number of hatchlings. For comparison, mean laying dates and clutch sizes for the nests not included in the analyses are also shown (the second row). These did not differ significantly from those included (*t*-tests, $P > 0.20$ in all cases). Significant *P* values are shown in bold

	Low	Increase	Decrease	<i>F</i>	<i>P</i>
Laying date*	22.7 \pm 4.5 (26)	5.9 \pm 4.7 (22)	-2.6 \pm 3.9 (21)	10.27	0.0001
	19.7 \pm 2.3 (45)	5.2 \pm 1.6 (145)	-5.1 \pm 1.3 (129)		
Clutch size	4.42 \pm 0.26 (26)	5.69 \pm 0.27 (20)	5.33 \pm 0.22 (20)	9.70	0.0002
	4.55 \pm 0.16 (44)	5.90 \pm 0.08 (139)	6.01 \pm 0.19 (126)		
No. hatchlings	4.53 \pm 0.23 (26)	4.83 \pm 0.25 (22)	4.62 \pm 0.19 (22)	0.55	0.58
No. fledglings	2.92 \pm 0.39 (26)	3.24 \pm 0.41 (21)	2.24 \pm 0.32 (20)	1.87	0.16

* 30 March = -1, 31 March = 0, 1 April = 1, etc.

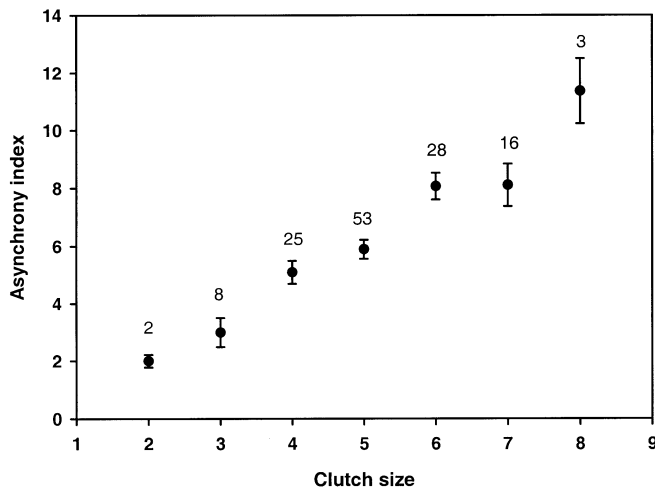


Fig. 1 Relationship between the hatching asynchrony index (see Methods) and clutch size in broods of Tengmalm's owls *Aegolius funereus*. Means are shown with sample sizes above the standard error bars. Data from all years are combined

Table 2 ANCOVA table for the effects of parental traits, phase of the vole cycle (increase, decrease, low), territory quality (poor, good) and clutch size on hatching asynchrony of Tengmalm's owl. Wing length of the oldest chick was included in the model to control for the effect of varying dates of wing length measurement. Note that non-significant interactions, covariates (condition of parents, male size and laying date) and factors (phase of the vole cycle and male age) were gradually removed from the model. Significant *P* values are shown in bold

Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>
Female age	1	15.63	4.76	0.033
Territory quality	1	9.23	2.81	0.099
Clutch size	4	14.63	4.46	0.003
Female age × male age	1	26.07	7.94	0.007
Male age × territory	1	13.77	4.20	0.045
Female size	1	16.24	4.95	0.03
Chick wing	1	112.15	34.16	0.0001
Error	55			

laying date we included a year effect in the model and tested it by using only the most common clutch size (5 eggs). In this analysis, neither year ($F_{8,14}=0.71$, $P=0.68$) nor laying date ($F_{1,14}=1.16$, $P=0.30$) was significantly associated with levels of asynchrony.

Hatching asynchrony and reproductive success

On average, 93% of eggs hatched (hatching failures being most common during low vole years, Table 1) and 58% of these hatchlings survived until fledging (55% in the low phase, 62% in the increase phase and 52% in the decrease phase). Chick mortality was mainly due to starvation (see Korpimäki 1981, p. 30), whereas complete brood losses (8 cases, 12%) were probably due to death

Table 3 ANCOVA tabulations for the effects of phase of the vole cycle (increase, decrease, low), clutch size and hatching asynchrony (covariate) on (A) number of fledglings and (C) mean body condition of the brood at fledging in Tengmalm's owl. Chick mortality (B; number of dead chicks per brood as the nominator and total number of chicks as the denominator) was analysed using logistic regression in SAS PROC GENMOD. Significant *P*-values are shown in bold

A. Number of fledglings				
Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>
Cycle	2	0.20	0.09	0.91
Clutch size	4	11.89	5.46	0.0008
Asynchrony	1	0.67	0.31	0.58
Cycle × asynchrony	2	1.67	0.77	0.47
Error	60			

B. Chick mortality				
Source of variation	<i>df</i>	log-likelihood	χ^2	<i>P</i>
Cycle	2, 60	2.39		0.30
Clutch size	4, 60	12.36		0.015
Asynchrony	1, 60	0.02		0.89
Cycle × asynchrony	2, 60	7.04		0.030

C. Mean body condition of the brood at fledging				
Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>
Cycle	2	0.05	2.33	0.12
Clutch size	4	0.05	2.28	0.09
Asynchrony	1	0.0001	0.03	0.86
Cycle × asynchrony	2	0.06	2.98	0.07
Error	23			

of either parent or nest desertion. We found that brood size at fledging was affected by clutch size but not by the phase of the vole cycle or degree of hatching asynchrony or their interaction (Table 3 a). Proportion of dead chicks in the brood (chick mortality) was affected by clutch size and also by the interaction between the phase of the vole cycle and asynchrony (Table 3 b). This interaction revealed that (1) during the low phase of the vole cycle the brood mortality appeared to decrease with asynchrony, (2) during the increase phase there was no obvious relationship between the two variables, and (3) during the decrease phase of the vole cycle the mortality among broods increased with asynchrony indicating that brood reduction was most common among asynchronous broods when food became scarce during the breeding season of owls (Fig. 2). The mean body condition of the fledglings of the brood was not affected by the phase of the vole cycle (mean ± SE; low: 1.15±0.04; increase: 1.20±0.06; decrease: 1.15±0.08), clutch size or the level of hatching asynchrony, but it was marginally influenced by the interaction between asynchrony and the phase of the vole cycle (Table 3 c). These results remained the same when the effects of cycle phase and hatching asynchrony were tested separately for the body condition of the oldest and youngest chick in the brood (all tests $P>0.10$).

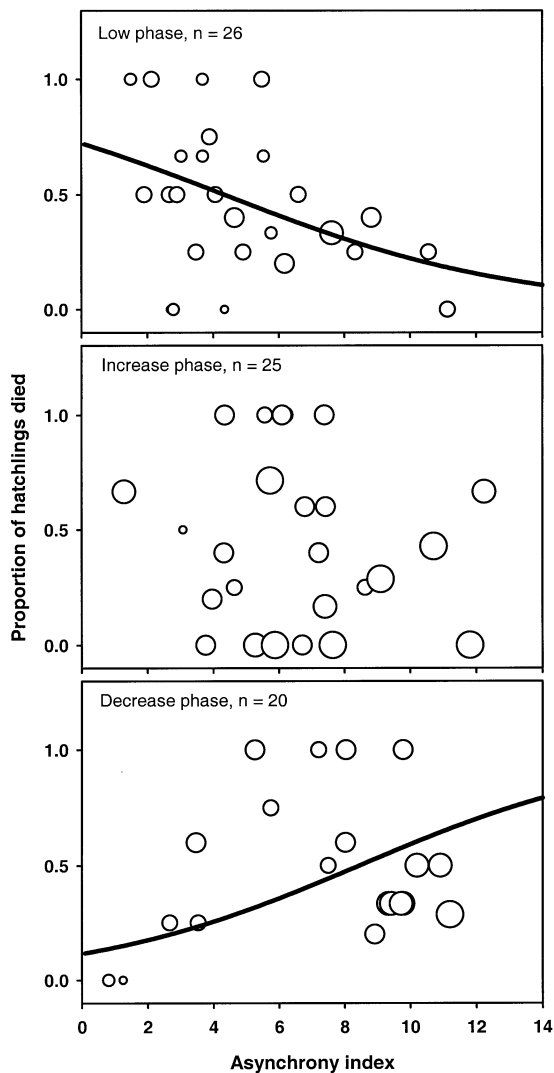


Fig. 2 Relationship between the chick mortality (no. of dead chicks / no. of hatchlings) and the level of hatching asynchrony during low, increase and decrease phase of the vole cycle. Significance levels between mortality and asynchrony were as follows: low phase: log-likelihood $\chi^2=7.11$, $P=0.008$; increase phase: log-likelihood $\chi^2=1.35$, $P=0.25$; decrease phase: log-likelihood $\chi^2=5.70$, $P=0.017$

Discussion

We found that hatching spans of Tengmalm's owl chicks were longest in nests with largest clutch sizes (Fig. 1). This was quite expected as Tengmalm's owl females usually start to incubate after laying the second egg (Korpimäki 1981), and therefore large clutches inevitably result in long hatching spans. Food abundance (i.e. the phase of the vole cycle) did not directly influence hatching patterns (Table 2), but it strongly correlated with clutch size (Table 1). Thus it seems that food abundance determines clutch size, which in turn is the major factor in determining the degree of hatching asynchrony (but see below for other contributing factors).

Broods of yearling Tengmalm's owl females were more synchronous than those by older females and hatching was also most synchronous in broods in which both parents were yearlings. This may indicate that young and inexperienced individuals started incubation of the clutch later relative to laying of the first egg, and / or that their laying intervals were shorter than those of experienced females. Females can disperse widely (up to >500 km) between successive breeding attempts while males are usually resident after their first breeding attempt (Korpimäki et al. 1987; Korpimäki 1988c). As a result, males may be adapted to local fluctuations in prey abundance, and may even be able to anticipate future changes in it (Hakkarainen and Korpimäki 1994a, b). The mean breeding lifespan of males is 3.5 years (maximum recorded 11 years; Korpimäki 1992; Hakkarainen et al. 2002), and thus their knowledge of the local environment may be enhanced by longevity. In contrast, the non-resident females may not have reliable cues about the phase and direction of local vole fluctuations, because the duration and amplitude of these cycles vary regionally (Hansson and Henttonen 1985).

We also detected an interaction between male age and territory quality in hatching asynchrony, which indicated that broods of yearling males were more asynchronous on poor than on good territories, but among adult males the level of asynchrony did not differ with respect to territory quality. In Tengmalm's owl, male age may be important because males provision females prior to and during incubation and during first 3 weeks of the chick-rearing period. Adult males breeding on poor territories may have a better knowledge of their territories as a result of potential earlier breeding attempts on the same area and thus have a higher hunting success. By contrast, yearling males are probably less experienced hunters and may thus not be able to provision their mates adequately. Moreover, they may not be able to anticipate changes in prey abundance in the course of the breeding season. Yearling males are also only able to breed during increase and decrease vole years, but not during low food years (Korpimäki 1981, 1988b; Laaksonen et al. 2002). In addition, food availability is probably lower in poor territories (see Hakkarainen et al. 1997), which could contribute to asynchronous hatching of young through e.g. potentially longer laying intervals. Females in poor territories may also start incubation earlier, thereby adjusting hatching asynchrony to territory and male quality.

The degree of hatching asynchrony increased with female body size. So far, we are unable to satisfactorily explain this phenomenon, which appeared to be independent of clutch size, laying date, female age, territory quality and the phase of the vole cycle. It may, however, be due to the fact that large females predominantly start to breed early in spring. Indeed, our long-term data from 1980–1997 suggests that this is the case, as there is a negative correlation between female wing length and laying date ($r=-0.14$, $P=0.008$, $n=374$). In March, the night temperatures in the study area can fall below -20°C (Korpimäki 1981). The cold weather may force

the female to start the incubation immediately after having laid the first (and probably also the most important) egg to prevent it from cooling (see also Moreno et al. 1994). Normally the effective incubation does not start until the second egg has been laid (Korpimäki 1981). This seems to support the egg-viability hypothesis (Arnold et al. 1987), which has so far mainly been tested in temperate or subtropical areas (Veiga and Viñuela 1993; Stoleson and Beissinger 1999; Viñuela 2000). A clear prediction of this hypothesis is that hatching asynchrony should decrease as the season advances, which was not the case in this study as no direct effect of laying date was found. However, this could be due to the fact that laying dates varied markedly between years and, on the other hand, the obvious effect of clutch size may have masked the effect of laying date. Nevertheless, we found no evidence to support this idea when clutch size was kept constant.

Hatching asynchrony and the brood reduction hypothesis

We found that during decrease vole years brood reduction (chick mortality) was more common in asynchronous nests than in synchronous ones (Table 3 b, Fig. 2; see also Viñuela 2000). This result is in accordance with Lack's (1954) brood reduction hypothesis, which suggests that the chicks might benefit from asynchronous hatching especially during poor and/or unpredictable food conditions such that in asynchronous broods the youngest nestling would easily die without jeopardising the survival of the entire brood if food becomes scarce (Wiebe et al. 1998; Wiehn et al. 2000). Especially during the decrease vole years the vole abundance declined throughout the breeding season of owls (Fig. 5 in Wiebe et al. 1998), and consequently the survival prospects of young owls were likely to be poor (Korpimäki and Lagerström 1988; Hakkarainen et al. 1996). On the other hand, food abundance was much better during increase than decrease or low vole years, and vole populations did not decrease during the breeding season but rather increased from spring to autumn (Fig. 5 in Wiebe et al. 1998), which might have increased the survival prospects of young owlets (Hakkarainen and Korpimäki 1994a, b). Interestingly, during the low vole years the chick mortality seemed to be highest among synchronous broods. It is possible that during extremely poor food conditions parent owls had difficulties in finding enough food for chicks that had similar energetic demands at the same time.

On the other hand, one could argue that the system we are studying is actually far from the one described by Lack, because in this case food supply may be predictable (and not unpredictable). Due to their longevity and site-tenacity male Tengmalm's owls in fact can anticipate future changes in food abundance, and their mates may be able to adjust their clutch sizes accordingly (Korpimäki and Hakkarainen 1991; Hakkarainen and Korpimäki 1994a, b). Therefore, it may be that the role

of hatching asynchrony should be negligible in this species. However, it seems that during decrease vole years the owls are not fully able to adjust their laying dates and clutch sizes to environmental conditions, and it is in this particular situation when hatching asynchrony is likely to be of bigger importance than just a fine-tuning mechanism.

The result that body condition of fledging owlets was not associated with the phase of the vole cycle or the extent of asynchrony was somewhat unexpected. This result may, however, be confounded by the unknown sex ratio of the brood (see Hörnfeldt et al. 2000) because female chicks may be larger than male chicks at fledging. However, Hipkiss (cited on p. 190 in Hörnfeldt et al. 2000) did not find obvious mass differences between male and female Tengmalm's owl chicks just before fledging. One could also argue that large variation in fledgling condition is perhaps not even expected, providing that the owls can adjust their clutch size to prevailing food levels. In fact, the clearest evidence for the association between hatching asynchrony and chick condition has been found among species living under unpredictable food levels (see Viñuela 2000).

Evaluation of hypotheses to explain hatching asynchrony in Tengmalm's owls

Some hypotheses proposed to explain asynchronous hatching were clearly not supported in this study. Hussell (1972) has proposed that one reason to enhance hatching of young via asynchrony is avoidance of nest predation (see also Clark and Wilson 1981; Magrath 1990). However, only a small percentage (5%) of Tengmalm's owl nests in our study area was lost to predators (Korpimäki 1987; but see Sonerud 1985 for other areas), and therefore the nest predation hypothesis seems unlikely to explain different hatching patterns in good and poor territories.

A possible advantage of asynchronous hatching is that it could reduce the number of nestlings that required a scarce food type at one time (Magrath 1990). However, this does not apply to Tengmalm's owls whose diet consists of similar prey items (small mammals and birds) throughout the entire breeding season. In general, as stated by Magrath (1990) it is possible that no single hypothesis can provide the explanation of hatching asynchrony within or across species, as the hypotheses are not mutually exclusive and different species will be subjected to different selective pressures (Viñuela and Carrascal 1999; Viñuela 2000).

Conclusions

It appeared that in Tengmalm's owl, the temporal variation in prey abundance determined the clutch size, which in turn largely determined the extent of hatching asynchrony. The owls seemed to fine-tune their reproductive

effort in relation to spatial variation (through territory quality) by starting the incubation of their eggs relatively earlier in poor than in good territories and thereby increasing the level of hatching asynchrony in their broods. An important finding was that the association between asynchrony and brood reduction was most intense during decrease vole years when the vole abundance declined throughout the breeding season of owls, and consequently the survival prospects of young owls were likely to be poor. This finding was consistent with Lack's brood reduction hypothesis, which suggests that if food becomes scarce during the nestling period the youngest nestlings would die first without endangering the survival of the whole brood. A proper test of Lack's hypothesis would require (1) simultaneous manipulation of food abundance and hatching patterns (see e.g. Wiehn et al. 2000), and (2) following juvenile survival after fledging (Magrath 1990). However, it has earlier been shown that in Tengmalm's owl there is a strong correlation between fledging success and recruitment rate of offspring (Korpimäki 1992). It is possible that the degree of facultative manipulation of hatching asynchrony may depend on clutch size of the species. For example, American Kestrels, which have relatively small and fixed clutch sizes (4–5 eggs), can probably fine-tune their investment by manipulating hatching spans (Wiebe and Bortolotti 1994) whereas Tengmalm's owls which have large and widely varying clutch sizes (1–10 eggs; Korpimäki 1981) seem to manipulate clutch size instead.

Acknowledgements We thank Vesa Koivunen, Petteri Ilmonen, Mikko Hast, Timo Hyrsky and Mikko Hänninen for great help in the field work, and Dave Currie, Karen Wiebe, Javier Viñuela and an anonymous referee for constructive comments on the draft manuscript. This study was financially supported by the Academy of Finland (to E.K. and H.H.).

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