

# EFFECT OF BROOD SIZE MANIPULATIONS ON PARENTS AND OFFSPRING IN THE BARN OWL *TYTO ALBA*

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When the overall food demand of the young increases, parents can either increase their effort to feed the brood, potentially reducing their residual reproductive value, or alternatively maintain their effort, leading to offspring mortality. In long-lived species where fitness is related to the number of breeding attempts, life-history theory suggests that parents should restrict any increase of reproductive effort in a current brood so as not to compromise their survival prospects. We investigated this hypothesis in the Barn Owl *Tyto alba* by performing brood size manipulations. We enlarged or reduced broods by two nestlings to create some broods requiring more parental investment and others requiring less. We monitored the effect on the parents and the offspring. Total body mass gained by all nestmates from the 24th to the 25th day after the first hatching, a measure correlated with parental feeding rate, was not significantly different between enlarged and reduced broods. Body mass and body condition of male and female parents during the manipulation, re-nesting rate and their reproductive success measured the year after the manipulation were not significantly affected by the experiment. Nestling mortality was higher, and body mass of the surviving male and female nestlings was lower in enlarged than reduced broods. In conclusion, we detected an effect of brood size manipulations on nestlings but not on parents. In the Barn Owl, this suggests that when broods require extra parental effort, parents do not jeopardize their future reproductive success, and brood reduction occurs.

Key words: *Tyto alba* - brood size manipulation - nestling survival - future reproductive success

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## INTRODUCTION

In evolutionary terms, fitness of an individual is defined as the number of genome copies passed across generations (Stearns 1992). Fitness therefore increases with the number of high quality offspring produced during a lifetime. To achieve the highest fitness, iteroparous parents have to optimize the allocation of resources between all breeding attempts, and between themselves and the offspring. When a brood requires more investment than parents are initially willing to devote, for instance because the food availability declines, they either invest more energy in foraging to maintain a constant feeding rate, or they maintain foraging effort and deliver less food that

would be required for the entire brood to be raised. Under the first strategy, the future reproductive success of the parents will be reduced because of the trade-off between reproductive investment and parental body maintenance (Williams 1966; Gustafsson & Pärt 1990; Daan *et al.* 1996). Under the second strategy, sibling competition will negatively affect the quality of the offspring because of the trade-off between number and quality of the offspring, and as a consequence brood reduction will occur (Smith *et al.* 1989), a probable outcome in long-lived species for which the value of a current brood is relatively small compared to that of future broods (Sæther 1988; Stearns 1992).

The medium-sized Barn Owl *Tyto alba* is



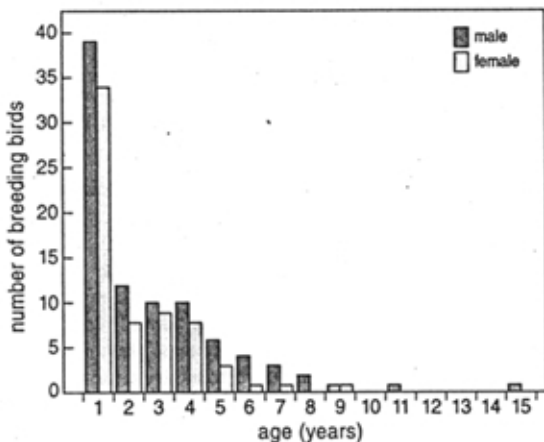


Fig. 1. Frequency distribution of the age of 89 males and 65 females breeding in the study area from 1988 to 1998. All birds have been ringed as nestling. For every individual only age at last capture was considered. Mean age is 2.9 for males and 2.3 for females.

long-lived (Fig. 1) and females are slightly larger than males. Clutch size varies markedly compared with other owls and raptors, and second clutches are frequent and larger than first clutches. The 5 to 6 eggs (range: 2 to 18) hatch at intervals of about 2.5 days resulting in an age hierarchy among the siblings. During the rearing period of two months, unpredictable bad weather conditions often happen, and brood reduction and cannibalism occur during these periods of decreased prey availability (Baudvin 1978). Brood reduction events affecting late-hatched young happen more often in large than small broods, and seem to be the result of starvation rather than siblicide (Cramp & Simmons 1985; Taylor 1994). This suggests that under an increased food demand by the offspring, parents do not increase their foraging effort or at least not to a level that prevents starvation of junior offspring. This outcome would be not surprising because as in other owls (Korpimäki 1992; Marti 1997; Brommer *et al.* 1998) and the Sparrowhawk *Accipiter nisus* (Newton 1989) fitness is more related to the number than to the size of the broods produced during a lifetime.

To test experimentally whether parents increase their investment when the food requirement of the brood is larger than the hatched brood, we enlarged and reduced broods. We predicted that an enlargement would not elicit an increase in hunting effort, and therefore that the total body mass gained by all nestmates in a night, a measure assumed to be correlated to parental feeding rate (Sæther *et al.* 1995), should not be statistically different between the two brood size treatments. Thus, offspring mortality should be higher, and the mean body condition of the surviving nestlings lower in enlarged than reduced broods. Furthermore, body mass, re-nesting rate and future reproductive success should be similar for parents producing an enlarged or a reduced brood. Because a large number of enlarged broods was required for reliable statistical testing, we did not create a control group where some nestlings are exchanged between nests without altering brood size. Our design is conservative because if parents adjust reproductive effort to brood size manipulations, parents of enlarged broods should invest more effort than those of control broods which in turn should invest more than those of reduced broods. Therefore, if we find no difference between enlarged and reduced broods we should have found no difference between enlarged and control broods.

## METHODS

We carried out the study in 1996 and 1997 in a study area of 190 km<sup>2</sup> located in western Switzerland (46°49'N, 06°56'E). Since 1987 we mounted 110 nestboxes on the wall of barns, and we regularly checked them to record laying date, clutch size, hatching success, age of each nestling using wing-length (Schönfeld & Girbig 1975), and number of fledglings (55-day-old nestlings). Nestlings are able to handle and eat prey items without the help of the mother after they are two weeks old (Cramp & Simmons 1985), and prey stores are often partly or entirely consumed during daytime (pers. observ.). When the older nestling was 24 or

25 days old we weighed and determined these prey remains (species, entire or decapitated). Barn Owl parents were captured at the nest and their age was determined by reading rings, or by checking their moult pattern. Primaries and secondaries of yearlings are not abraded, and second-year individuals renew the 6th primary only (Taylor 1994). We distinguished female from male adults by the presence of a brood patch (Cramp & Simmons 1985). We performed analyses with the Systat statistical package (Wilkinson 1989). All statistical procedures are two-tailed with a significance level of 0.05. Means are followed by  $\pm 1$  SD.

### Brood size manipulations

In 1996, we conducted an experiment with combined partial cross-fostering and brood size manipulation. We enlarged 28 broods and reduced 28 others with two nestlings. We exchanged three randomly chosen 0- to 5-day-old nestlings of a reduced nest for one same-aged randomly chosen nestling of an enlarged nest (e.g. Roulin *et al.* 1998 for more details). In many cases, this exchange was performed before all nestlings hatched in a nest. A few days after the brood size manipulation, parents abandoned four enlarged and two reduced broods for unknown reasons. Sample sizes were therefore 24 enlarged and 26 reduced broods. We recognized the origin of the nestlings by painting some feathers with non-toxic drawing ink before ringing them.

### Feeding rate

In 1996, we did not measure feeding rates. To obtain an approximation of the feeding rates of parents rearing enlarged and reduced broods, we calculated a 'brood mass gain index' given by the difference in brood mass between two successive days (sum of the masses of all nestmates + 0.78 x mass of surplus prey items; 0.78 is 'the digestive efficiency' to convert vole to owl flesh, Barton & Houston 1993). We weighed all nestlings and surplus prey items when the senior nestling was 24 and 25 days old (see Sæther *et al.* 1995 for a similar method). To evaluate if the 'brood mass gain

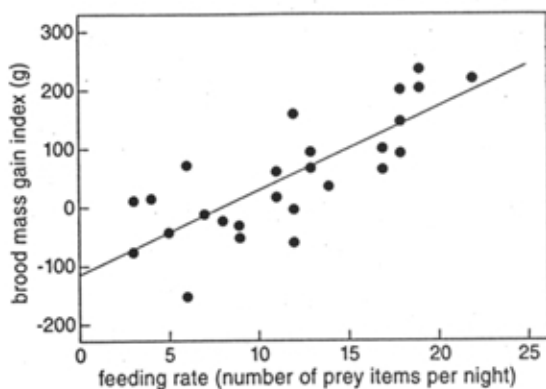


Fig. 2. Relationship between brood mass gain index (y) and feeding rate (x). Linear regression,  $y = -118 + 14.3x$ ,  $F_{1,25} = 39.3$ ,  $P < 0.001$ ,  $R^2 = 0.61$ . Feeding rate was measured when the oldest nestling was on average 35-day-old.

index' is representative for most part of the rearing period, in each brood we determined it several times when the senior nestling was 14-39 days. By randomly choosing one 'brood mass gain index' per brood we show that it does not significantly vary along this period (brood size treatment as a factor and age as a covariate in ANCOVA-analysis; age:  $F_{1,47} = 0.90$ ,  $P = 0.35$ ). With an infra-red sensitive video camera, we filmed parental feeding trips in 27 nests in 1997. This demonstrated that the 'brood mass gain index' was related to the combined number of prey items brought by both parents to the nest in one night (Fig. 2).

### Effects of brood size manipulations on parents

To test potential short-term effects of brood size manipulations on parents, we measured the wing length of 35 randomly chosen females (15 in enlarged and 20 in reduced nests) and weighed them at the 20th day of incubation and on average  $18 \pm 4$  days after the manipulation of brood size, and of 26 randomly chosen males (13 in enlarged and 13 in reduced nests) on average  $24 \pm 8$  days after the manipulation of brood size. A condition-index was calculated as the ratio body mass/wing length. No difference in laying date and clutch

size was found between adults captured and not captured for the analyses of body mass and body condition (Mann-Whitney *U*-test, all *P*-values > 0.31).

To test for potential long-term effects, we compared the proportion of adults from the two experimental groups that produced a second clutch in 1996, and that bred in 1997. For the re-nesting adults, we recorded laying date, clutch size, and brood size at fledging in 1997. Because most birds changed mate (82%), we considered male and female parents of the same manipulated brood separately. To assess potential effects of brood size manipulations on the parental feeding rates in 1997, we filmed a random sample of the re-nesting adults (7 males and 7 females from enlarged broods, and 10 males and 6 females from reduced broods) during two successive nights when the oldest nestling of the brood was on average  $35 \pm 6$  days of age. Feeding rate was recorded as the average number of feeding trips per night.

### Effects of brood size manipulations on offspring

Nestling Barn Owls lose body mass prior fledging, and thus brood size manipulations may independently affect different components of the body mass growth curve. A recent study conducted on captive Barn Owls showed that chicks raised under restricted food conditions grew at smaller rate, and achieved a lower maximal body mass but fledged with the same body mass as chicks raised under *ad libitum* food conditions (Durant & Handrich 1998). Therefore, it seems that body mass at fledging is not appropriate to measure phenotypic quality. Since, however, the effect of brood size manipulations on body mass growth is as yet unknown, we individually weighed all nestlings during the period of maximal growth rate (25 days) and at fledging (55 days) (e.g. in a brood of three nestlings, we visited the nest approximatively six times during daytime). Enlarged broods were visited more often than reduced broods, but since parents were most often not in nestboxes adults from the two treatments

were probably equally disturbed. We checked if dead nestlings were partially cannibalized by the nestmates or the parents, and in the 1996 autumn we sampled pellets in nestboxes to search for bones of Barn Owls. Bones were determined by the comparison with bones found in a pellet containing the ring of a nestling Barn Owl.

### Determination of the sex of the offspring

Blood samples were taken from all nestlings which survived until 55 days in order to determine their sex. Blood samples (50  $\mu$ l) were taken from the brachial vein and placed in 100  $\mu$ l storage EDTA-buffer, and then stored at  $-20^{\circ}\text{C}$ . About 50  $\mu$ l blood solution was digested with 0.8 ml TES: 0.03M Tris-HCL pH 7.4, 5mM EDTA pH 8.0, 0.1 M NaCl, 0.5% SDS, and incubated with 50  $\mu$ l proteinase K at  $55^{\circ}\text{C}$  for 15 hours. Genomic DNA was extracted with phenol/chloroform and recovered by ethanol precipitation. After drying, DNA was stored in 200  $\mu$ l MTE at  $5^{\circ}\text{C}$ . The sex of the nestlings was determined by employing PCR amplification of homologous sections of the CHD-W and CHD-Z genes (Griffiths et al. 1996; Griffiths & Korn 1997), using the primers P2 and P8 (Griffiths et al. 1998). PCR amplification was carried out in a total volume of 10  $\mu$ l. The reaction conditions were as follows: 50mM KCL; 10mM Tris-HCL pH 9; 1.5 mM  $\text{MgCl}_2$ ; 0.1% Triton X-100; 200  $\mu$ M of each dNTP; 100 ng of each primer and 0.15 units of TAQ polymerase (Pharmacia). Between 50 and 250 ng of genomic DNA was used as a template. The PCR program was as follows: initial denaturing at  $95^{\circ}\text{C}$  for 2 min, followed by 40 cycles of  $43^{\circ}\text{C}$  for 15 s,  $72^{\circ}\text{C}$  for 30 s and  $94^{\circ}\text{C}$  for 30 s. The program was completed by a final run of  $43^{\circ}\text{C}$  for 1 min and  $72^{\circ}\text{C}$  for 5 min. The PCR products were separated by gel electrophoresis for 2 hours at  $4\text{V cm}^{-1}$  in a 2% agarose gel stained with ethidium bromide. Males (ZZ) produced one band at 330 bp (CHD-Z). Females produced the same band (CHD-Z) and in addition a second band at 350 bp (CHD-W). We checked the accurateness of the test by determining the sex of 74 nestlings by endoscopy or by inspection of the gonads of ten

birds later found dead. All were correctly sexed by the DNA test. In addition, 46 breeding individuals, sexed by breeding behaviour, revealed the same sex by the DNA test.

For each nest, we calculated the mean body mass of all male nestlings and all female nestlings that successfully fledged. The mean rank number (rank number 1 is assigned to senior nestlings) in the age hierarchy of male and female nestlings was not statistically different in enlarged broods ( $U_{23,21} = 251$ ,  $P = 0.83$ ) and reduced broods ( $U_{22,19} = 215$ ,  $P = 0.87$ ).

## RESULTS

### Brood size manipulations

To study how parents and offspring are affected by brood size manipulations, four conditions have to be verified: 1) breeding pairs should be randomly assigned among brood size treatments. There were no significant differences between the two experimental groups in laying date ( $U_{26,24} = 309$ ,  $P = 0.95$ ), clutch size ( $U_{26,24} = 372$ ,  $P = 0.23$ ), number of hatchlings (Table 1), or age of the breeding males ( $U_{26,24} = 295$ ,  $P = 0.87$ ) and females ( $U_{26,24} = 333$ ,  $P = 0.67$ ); 2) just after manipulation, the median brood size of reduced and enlarged broods significantly differed (Table 1); 3) the size of the created broods should lay within the natural range. Brood sizes ranged from 2 to 9 nestlings; 4) parents should not discriminate between own and foster nestlings. Mortality was lower for cross-fostered nestlings (11 out of 99

cross-fostered nestlings died, 11%) than for non-cross-fostered ones (49 out of 165, 30%; Chi-square test:  $\chi^2_1 = 12.1$ ,  $P < 0.001$ ). This may be related to their lower mean rank number in the age hierarchy just after the manipulation (cross-fostered nestlings:  $2.6 \pm 1.3$ ; non-cross-fostered nestlings:  $3.1 \pm 1.5$ ; paired  $t$ -test:  $t_{49} = 2.3$ ,  $P = 0.023$ ). Indeed, the youngest nestlings of broods usually suffer higher mortality rates (Taylor 1994). Body mass of the surviving cross-fostered and non-cross-fostered nestlings was not significantly different (mean body mass at 25 and 55 days of age as repeated measures ANOVA: cross-fostered versus non-cross-fostered nestlings as a factor:  $F_{1,88} = 0.25$ ,  $P = 0.62$ ), suggesting that the quality of parental care provided to cross-fostered and non-cross-fostered nestlings was similar.

### Effects of brood size manipulations on parents

The mean 'brood mass gain index' was not significantly lower in reduced ( $-1 \pm 117$  g) than enlarged broods ( $30 \pm 108$  g) (Student  $t$ -test:  $t_{48} = 0.96$ ,  $P = 0.34$ ), although the median brood size was significantly smaller (Table 1). This suggests that parents did not adjust feeding rate to brood size manipulations. This interpretation is further supported by the fact that the quantity of prey items stored during the day in nestboxes was not significantly related to the brood size treatments. The mean mass of the prey storage in reduced broods was  $60 \pm 79$  g and in enlarged broods  $40 \pm 56$  g ( $t_{48} = -1.0$ ,  $P = 0.31$ ), and the mean mass of the entire prey items (i.e. not decapitated) was the same in both treatments (40 g;  $t_{25} = 0.25$ ,  $P =$

**Table 1.** Median brood size in the two experimental treatments before and after the manipulation of brood sizes and when the older nestling was 25 and 55 days of age.

	Median brood size		Statistics
	Reduced broods	Enlarged broods	
Before manipulation	5.5	5	$U_{26,24} = 375$ , $P = 0.21$
Just after manipulation	3.5	7	$U_{26,24} = 23$ , $P < 0.001$
When the older nestling was 25 days of age	3	5.5	$U_{26,24} = 62$ , $P < 0.001$
When the older nestling was 55 days of age	3	5	$U_{26,24} = 121$ , $P < 0.001$

0.80). We found respectively 41 and 33 Common Voles *Microtus arvalis*, 23 and 20 Water Voles *Arvicola terrestris scherman*, 27 and 7 field mice *Apodemus* sp. and 1 and 0 Bank Vole *Clethrionomys glareolus*.

The mean change in female body mass from the 20th day of incubation to the 18th day after the manipulation of brood size was not significantly different between reduced ( $-1.3 \pm 0.8$  g day $^{-1}$ ) and enlarged broods ( $-1.5 \pm 0.7$  g day $^{-1}$ ) ( $t_{33} = -0.65$ ,  $P = 0.52$ ). 18 days after the brood size manipulation females from reduced and enlarged broods did not significantly differ in body mass ( $332 \pm 18$  g, resp.  $331 \pm 21$  g;  $t_{33} = 0.17$ ,  $P = 0.87$ ) and in condition-index ( $1.11 \pm 0.07$  g cm $^{-1}$ ;  $1.12 \pm 0.06$  g cm $^{-1}$ ;  $t_{33} = -0.19$ ,  $P = 0.85$ ). Males involved in the rearing of a reduced brood had a similar body mass and condition-index ( $274 \pm 10$  g, resp.  $0.92 \pm 0.03$  g cm $^{-1}$ ) as males rearing an enlarged brood ( $277 \pm 22$  g, resp.  $0.93 \pm 0.08$  g cm $^{-1}$ ) ( $t_{24} = 0.43$ ,  $p = 0.67$ , resp.  $t_{24} = 0.17$ ,  $P = 0.87$ ). Brood size manipulations therefore had no detectable short-term effects on feeding rate, if we assume that the 'brood mass gain index' reflects it, and on body mass and body condition of female and male parents.

Potential effects of brood size manipulations on future reproductive success were tested in three ways. First, birds from the reduced group tended to produce more second clutches in 1996 (3 out of 26 males and 4 out of 26 females) than birds from the enlarged group (none of the 24 males and 2 out of 24 females), but the small number of double-brooded birds does not allow reliable

statistical analysis. Second, a similar number of birds from the two treatments bred in 1997: from reduced broods 19 out of 52 birds (37%) (12 males and 7 females), and from enlarged broods 18 out of 48 birds (38%) (9 males and 9 females) (males and females pooled:  $\chi^2_1 = 0.01$ ,  $P = 0.92$ ). And finally, laying date, clutch size, brood size at fledging, and feeding rate of parents involved in the rearing of an enlarged or a reduced brood in 1996 were not significantly different in 1997 (Table 2). This suggests that the residual reproductive value of adults was not affected by the manipulation of the size of their brood.

### Effects of brood size manipulations on offspring

The experiment conducted in 1996 did not increase overall mortality rates of nestlings. Six out of 56 (11%) experimental pairs failed to produce any fledgling. This proportion is the same as that found in unmanipulated pairs (data from 1990 to 1995, 29 failures out of 270 breeding attempts, 11%;  $\chi^2_1 = 0.00$ ,  $P = 1.0$ ). The number of dead nestlings per nest in experimental broods ( $1.2 \pm 1.2$ ,  $n = 50$ ) was smaller, but not significantly than in natural broods for which we know the number of hatchlings (data from 1990 to 1995,  $1.6 \pm 1.5$ ,  $n = 207$  successful pairs; Student  $t$ -test:  $t_{254} = 1.7$ ,  $P = 0.09$ ).

Offspring mortality occurred in 21 out of 24 enlarged nests (88%) and in 10 out of 26 reduced nests (38%) ( $\chi^2_1 = 12.8$ ,  $P < 0.001$ ). 45 (27%) of 169 hatchlings in enlarged broods died while in reduced broods 15 (16%) of 95 hatchlings died

**Table 2.** The 1997 breeding parameters of parents that produced a reduced or an enlarged brood in 1996.

	male			female		
	reduced	enlarged	statistics	reduced	enlarged	statistics
Mean laying date	25.4.	21.4.	$t_{19} = -0.59$ , $P = 0.56$	20.4.	27.4.	$t_{14} = 0.77$ , $P = 0.45$
Median clutch size	5	5	$U_{11,10} = 37$ , $P = 0.14$	5	5	$U_{7,9} = 35$ , $P = 0.69$
Median brood size at fledging	4	4	$U_{11,10} = 59$ , $P = 0.76$	5	4	$U_{7,9} = 46$ , $P = 0.11$
Feeding rate	$6.6 \pm 2.8$	$6.9 \pm 5.6$	$t_{15} = 0.15$ , $P = 0.90$	$2.8 \pm 1.8$	$3.1 \pm 3.3$	$t_{11} = 0.16$ , $P = 0.88$



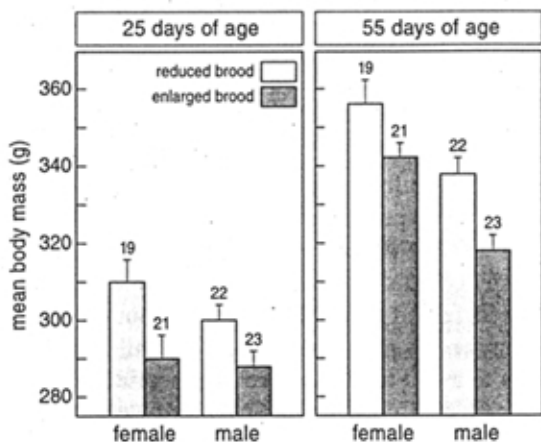


Fig. 3. Mean body mass ( $\pm 1$  SE) of female and male nestlings at (a) 25 and (b) 55 days of age, raised in reduced (light shaded bars) or enlarged broods (dark shaded bars). The numbers of nests available to calculate mean body mass, are indicated above the bars.

( $\chi^2_1 = 2.5$ ,  $P = 0.11$ ). In 56 out of 60 cases, mortality occurred before nestlings reached 25 days of age, and with two exceptions the nestlings that died were the youngest ones of the broods. We found 10 cannibalized nestlings (8 in enlarged and 2 in reduced broods), 9 non-cannibalized cadavers in nestboxes, and the circumstances of the disappearance of the 41 other dead nestlings were unclear.

Fledglings were more numerous in enlarged than reduced broods (Table 1), but of poorer physical condition as estimated by body mass (mean body mass at 25 and 55 days of age as repeated measures ANOVA with brood size treatment and sex as factors; treatment effect:  $F_{1,80} = 10.59$ ,  $P = 0.002$ ). Even if female nestlings were heavier (sex effect:  $F_{1,80} = 7.43$ ,  $P = 0.008$ ), brood size manipulations had a similar effect on the body mass of birds of the two sexes (no interaction between sex and brood size treatment:  $F_{1,80} = 0.0001$ ,  $P = 0.99$ ; Fig. 3).

## DISCUSSION

Before the present study brood size manipulations had been conducted in three avian predators, the

Tengmalm Owl *Aegolius funereus* (Korpimäki 1988), the Common Kestrel *Falco tinnunculus* (Dijkstra *et al.* 1990; Korpimäki & Rita 1996; Tolonen & Korpimäki 1996) and the American Kestrel *F. sparverius* (Gard & Bird 1990, 1993). Residual reproductive value of the parents decreased as a consequence of an enlargement of the broods in one out of three studies (Dijkstra *et al.* 1990 vs. Korpimäki 1988; Korpimäki & Rita 1996) and offspring appeared to always suffer in some way (Dijkstra *et al.* 1990; Korpimäki 1988; Gard & Bird 1993; Korpimäki & Rita 1996). Our results in the Barn Owl are in the same vein with a clear effect of brood size manipulations on offspring but not on parents. Nestling survival and body condition of the survivors was lower in enlarged than reduced broods. The 'brood mass gain index', body condition and future reproductive success of the parents did not significantly differ between the two brood size treatments suggesting that parents allocated same effort for rearing enlarged as reduced broods.

Parents that tended a reduced brood probably did not allocate less effort than they were initially willing to devote and hence produced a brood of high quality nestlings. If they had decreased hunting effort the production of lower quality young would have probably not outweighed the marginal gain in parental residual reproductive value. This is so because a large decrease in effort only slightly improves parental reproductive value while strongly reducing the condition of the offspring (Stearns 1992), since a reduction in feeding rate affects the few nestlings. For instance, in the Kestrel, Dijkstra *et al.* (1990) showed that males are more strongly involved in the feeding of the young than females and did not decrease hunting effort after the size of their brood was reduced. Consequently, the food intake per nestling was significantly higher in reduced than control broods. This suggests that when the rearing conditions improve Kestrel and Barn Owl parents maintain constant effort. This may explain why in the Barn Owl prey remains are frequent and often not eaten at all (pers. obs.).

Parents that tended an enlarged brood also

probably did not allocate more effort than they initially decided to devote or at least not to a sufficiently high level to have prevented nestling mortality and lowered their residual reproductive value. Following life-history theory it can be very costly in terms of future reproductive success to slightly elevate effort above the normal rate (Stearns 1992). Field experiments have confirmed this view as an increased parental investment measured by feeding rate negatively affected parental condition or residual reproductive value in five out of six cases (Reid 1987; Dijkstra *et al.* 1990; Källander & Smith 1990; Martin & Wright 1993; Richner *et al.* 1995 vs. Orell *et al.* 1996). Assuming that owls tending unmanipulated broods are not already hunting at maximum effort (Drent & Daan 1980), they may have been reluctant to adjust reproductive effort if the production of extra young could not compensate for a loss in residual reproductive value. In the Barn Owl late-hatched nestlings have a relative low fitness value as they are almost always in poorer condition than early-hatched siblings. Because this difference in condition accentuates with increasing brood size (Wilson *et al.* 1987; Roulin 1998), when food supply declines parents are probably selected to direct resources to themselves than to late-hatched offspring, leading to brood reduction.

Most nestlings that died were the youngest ones of the broods and brood reduction events were more frequent in nests where the rearing conditions were stressful (enlarged broods). This pattern of mortality events fits the 'brood reduction hypothesis' which states that poor quality late-hatched young die when parents are no more able to bring enough food to rear all young (Lack 1947). In other words, under unpredictable adverse periods the rare food items collected by parents would be shared among a larger number of nestlings in nests where all nestlings survive compared to nests where partial losses of nestlings occur; thus, if brood reduction does not occur young may be in a so poor condition that all can rapidly die or nevertheless fledge but will never be recruited in the breeding population. We are aware of only one study that has tested experimentally

the brood reduction hypothesis. In the Magpie *Pica pica*, Husby (1986) found that fledglings survived less well when reared in nests where dead chicks were replaced by chicks from other nests compared with nests where dead chicks were not replaced. Unfortunately, in that study feeding rates, survival prospect and future reproductive success of the parents were not measured. Thus, Husby could show that the brood reduction strategy increased reproductive success but could not examine the possibility that it also allowed parents to avoid trading current against future reproduction (O'Connor 1978; Stenning 1996). If brood reduction is experimentally prevented, parents may be forced to increase their investment in the current brood at the expense of future reproductive success. Given that in the Barn Owl brood reduction occurred more frequently in the enlarged than reduced treatment and that the residual reproductive value of the parents was not affected by the experiment, brood reduction may be the potential mechanism that allowed parents to not jeopardize their residual reproductive value.

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## SAMENVATTING

Wanneer de totale voedselbehoefte van nestjongen groter is dan verwacht, kunnen de oudervogels al dan niet besluiten harder te gaan werken. Harder gaan werken heeft mogelijk gevolgen voor het toekomstige reproductiesucces van de ouders, bijvoorbeeld door een verhoogde sterftekans. Niet harder gaan werken kan daarentegen leiden tot de dood van een of meer jongen. Als de 'fitness' van soorten met een lange levensduur vooral gerelateerd is aan het totale aantal broedpogin-

gen, zullen de ouders er goed aan doen hun toekomstig reproductiesucces niet in de waagschaal te stellen en niet harder gaan werken. Deze hypothese werd onderzocht door de legselgrootte van Kerkuilen *Tyto alba* experimenteel te manipuleren. Sommige legsels werden met twee jongen verkleind, andere met twee jongen vergroot. De gevolgen van deze manipulaties werden zowel voor de ouders als voor de jongen bepaald. De gewichtstoename van alle nestjongen samen, gemeten op de 25ste dag na uitkomst van het eerste ei, is gebruikt als maat voor de inspanning die de ouders leverden. Deze maat bleek niet te verschillen tussen vergrote en verkleinde legsels. Ook het gewicht en de conditie van de ouders tijdens het experiment, het voorkomen van een tweede legsel en het reproductiesucces in het volgende jaar bleken niet te verschillen tussen de twee experimentele behandelingen. Daarentegen was de sterfte van de nestjongen in de vergrote legsels hoger dan in de verkleinde legsels. Bovendien was het lichaamsgewicht van de overlevende jongen in de vergrote legsels lager. We kunnen dus concluderen dat de manipulaties van de legselgrootte wel effect hebben gehad op de jongen, maar niet op de ouders. Kerkuilen leveren kennelijk niet de gevraagde extra inspanning en stellen dus hun toekomstig reproductiesucces niet in de waagschaal.

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