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**BROOD SIZE MANIPULATIONS IN THE KESTREL
(*FALCO TINNUNCULUS*): EFFECTS ON OFFSPRING
AND PARENT SURVIVAL**

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SUMMARY

(1) Brood reductions and enlargements were carried out in kestrel nests to evaluate the consequences of raising different numbers of nestlings for both the offspring and the parents.

(2) Brood enlargements caused increased daily hunting activity of the parents, reduced growth rate of the nestlings, increased nestling mortality and enhanced weight loss in the female parent. Brood reductions caused an increased food intake by the nestlings, in spite of (non-significantly) reduced parental hunting activity. Local survival of the parents was negatively correlated with the experimental change in brood size.

(3) A review of the literature on brood enlargements is presented, showing that parents were able to raise more young till fledging than their natural broods in twenty-nine out of forty altricial bird species investigated. Negative effects of brood enlargements on parental survival or future reproduction were established in eight out of twelve species investigated.

(4) The results are consistent with the theory that parental work for the offspring entails an inherent reduction in future reproductive output and that natural broods, by being smaller than the maximum number of nestlings that can be raised, maximize the total reproductive output.

INTRODUCTION

Lack (1947, 1948a, b) suggested that clutch size in birds has evolved through natural selection to match the maximal number of offspring that can be raised, and that the most common clutch size is also the most productive in the population. In contrast with this proposition, several studies have shown the largest clutch size to be more productive than the most common (Perrins 1964; Cavé 1968; Perrins & Moss 1975). Lack's hypothesis was extended by postulating adaptive interindividual variations in clutch size (Perrins & Moss 1975), such that the optimal clutch depended on differences in habitat quality or condition of the bird (Drent & Daan 1980; Högstedt 1980). In other words, individual birds phenotypically adjust clutch size to their own situation. Furthermore, Williams (1966) proposed a possible trade-off between current parental effort and future reproductive output. This trade-off would result in a smaller optimal clutch size than expected if only the current breeding attempt were taken into account (Charnov & Krebs 1974). Individuals reproducing submaximally, i.e. laying relatively small clutches, might enhance their own changes in survival and thereby increase their total fitness. A number

of brood manipulation experiments have been carried out to test whether the clutch size laid equals the most productive brood size (review by Lessells 1986). The majority of these studies did not support Lack's hypothesis since enlarged broods were more productive than control broods. In most studies productivity was measured in terms of numbers fledged (e.g. Hegner & Wingfield 1987; Tarburton 1987) or the number of offspring alive after 3 months (Nur 1984b). Ideally, survival of the juveniles at least until reproductive age should be taken into account to test the hypothesis thoroughly. Few studies have investigated effects of brood manipulation on adult survival (Askenmo 1979; Gustafsson & Sutherland 1988; Pettifor, Perrins & McCleery 1988) and on future adult reproductive output, either within the same year in multiple breeders (Finke, Milinkovich & Thompson 1987; Tinbergen 1987) or in subsequent years (Røskaft 1985). Parental effort in food provisioning to manipulated broods was estimated in some of these studies on the basis of food deliveries to the nestlings. The feeding rate is only a crude estimate of parental effort since variations in habitat quality or foraging efficiency affect parental energy expenditure. We have undertaken a study in the European kestrel (*Falco tinnunculus* L.), attempting to cover the effects on offspring prospects and on parental effort and survival as completely as possible.

In the European kestrel the largest clutch size is the most productive in terms of offspring surviving until reproductive age (Dijkstra 1988). Energy expenditure of male parents with complete broods, i.e. without preceding mortality, did not vary with respect to brood size (Masman *et al.*, 1989). Hunting yield, in terms of voles caught per hour flight-hunting, was positively correlated with brood size. Thus, clutch size seems to be adjusted to individual food availability, such that, at the time of highest parental effort the parents of broods of different sizes are able to feed their broods with the same effort. Nestling food deprivation experiments showed that estimated energy expenditure of the parents was considerably increased in response to enhanced food demand from the brood. Twice as much food was brought to the nest in these short-term experiments, which lasted 2–10 days, than under natural conditions (Masman *et al.*, 1989). These results strongly suggest that kestrels produce fewer young than they are actually able to raise if working at peak performance, but it is uncertain whether increased parental energy expenditure could be maintained throughout the nestling and fledgling stage. It is therefore of interest to analyse the consequences of artificial brood size changes on both parental behaviour and on survival. We manipulated brood sizes in such a way that the experimental broods contained two young more (enlargements) or two young less (reductions) than the original clutch size and assessed growth and survival of the nestlings as well as local survival of the juveniles till reproductive age. Also parental effort and estimated energy expenditure for manipulated broods was investigated and adult body mass during the experiment was recorded. In subsequent breeding seasons we established local adult survival and reproductive performance.

METHODS

The data presented here were obtained in two different areas in the Netherlands: the Lauwersmeer polder and Flevoland. For a description of the areas we refer to Joenje (1977) and Cavé (1968). In both areas nestboxes were mounted on poles or against buildings and were regularly checked during the breeding season (Dijkstra *et al.* 1988). Kestrel pairs were caught during the breeding season using a *bal-chatri* trap away from the nest (Cavé 1968), or a net for catching them in the nestbox. The breeding population was

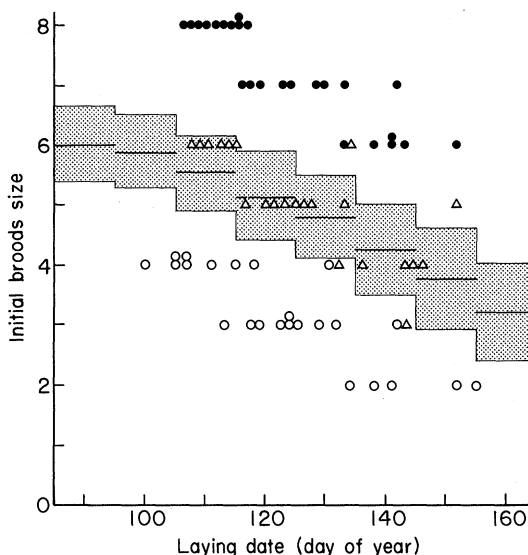


FIG. 1. Distributions of experimental brood sizes after brood manipulations, and laying dates (of the first egg of the clutch). Reduced broods (○) = two young less than original clutch size; enlarged broods (●) = two young more; control broods (△). Horizontal bars and shaded areas indicate mean clutch size \pm S.D. per 10-day interval of laying dates (Dijkstra 1988).

marked individually by colour rings in Flevoland and by wing-tags (Village 1982) in the Lauwersmeer area.

Manipulations of brood sizes were done in Flevoland in 1985 and 1986, and in the Lauwersmeer in 1986 and 1987. The experiments started when the nestlings were 5–10 days old. Brood size was changed in such a way that the number of nestlings was either two more (enlarged broods) or two less (reduced broods) than the original clutch size. In the control broods the brood size matched original clutch size. In these clutches failure to hatch was compensated by addition of chicks of appropriate age but the nests were otherwise unmanipulated. All broods were randomly placed in one of the three groups irrespective of preceding egg mortality. Experimental brood sizes of a subsample of seventy-two broods, i.e. twenty-five enlarged, twenty-five reduced and twenty-two controls) used for nestling growth analyses are shown in Fig. 1 as a function of laying date of the first egg of the clutch. The experimental broods were a representative sample of all nests with respect to laying date and clutch size (Fig. 1). The nestboxes were checked at intervals of 2–5 days until the young fledged at about 30 days of age. Nestlings were marked individually with flexible rubber rings and as soon as possible with aluminium rings from the Bird Ringing Centre (Heteren). Body mass was measured to the nearest gram using Pesola spring balances. Wing-length was measured and time of day recorded since body mass of nestlings of all ages was highly dependent on time of day (see Results). After fledging, a number of juveniles were caught by *bal-chatri* and weighed while still being fed by the parents. Recognition of the broods during the post-fledging phase was possible by marking the fledglings with colour dyes and the parents with wing-tags.

Parental effort in the experimental broods was investigated by continuous observation of selected individual kestrels throughout their daily activity period, from *c.* 0.5 h before

sunrise till 0.5 h after sunset. Age of the nestlings during observation ranged from 8 to 28 days. These data were obtained in 1986 in the Lauwersmeer. Only those days when the kestrels were in sight for more than 75% of the observation time were used for time and energy budget analyses. For a detailed description of the behavioural protocol see Masman, Daan & Dijkstra (1988a). Parental energy expenditure was estimated using data on basal metabolic rate, flight and perching costs, temperature regulation and heat increment of feeding, established for the kestrel (Masman, Daan & Beldhuis 1988b). Food provisioning of the nestlings was determined by electronic balances mounted at the bottom or in the entrance of the nestbox. Prey mass as well as the parent's body mass could be measured when the bird entered the nestbox with prey and left without.

Duration of parental care after the young had fledged was established by making behavioural observations of the parents every other day after the fledglings left the nestbox. The daily observation period for establishing the extent of parental care of fledglings started at about 06.00 h because feeding frequency was highest from 07.00 until 12.00 h, and was continued until at least one prey delivery to the young was seen. When no prey transfers were recorded for 8 h on one day, providing weather conditions were favourable and the parents had been in sight nearly continuously, we assumed they had stopped feeding the young.

Local survival of the parents of experimental and control broods was determined by identifying the whole breeding population a year later. This was done by recording tagged individuals (previous breeders) and catching untagged birds (local juveniles and immigrants of all ages). Pairs of which the complete clutch failed to hatch as well as cases of polygamy were excluded from analyses of survival until the next year. Statistical tests were two-tailed unless stated otherwise.

RESULTS

Parental effort and nestling provisioning

Male parents of enlarged broods in the Lauwersmeer in 1986 spent an average of 1.2 h d^{-1} (27%) more time in flight and flight-hunting than the controls (Table 1). Males from reduced broods hunted on average 0.8 h d^{-1} (17%) less than control males but this difference was not statistically significant. Daily flight time of males with enlarged broods was 2.0 h (50%) longer compared with those having a reduced brood ($P < 0.05$). Consequently, male estimated daily energy expenditure, determined by the time-energy budget model of Masman, Daan & Beldhuis (1988b), was significantly higher for male parents of enlarged broods compared with both the controls and the brood reductions. The females in the three groups showed the same trends in flight activity as the males, although in all cases they did less flying than the males. Hunting by females with reduced broods ceased almost completely (Table 1).

Male flight-hunting yield, expressed as the number of voles caught per hour hunting, did not differ significantly between the groups. This suggests that a relaxed or increased food demand of the nestlings did not affect parental hunting yield. In control broods, there was a positive correlation between brood size and hunting yield as previously established (Masman *et al.*, 1989), and enlarged and reduced broods differed slightly in original clutch size. Therefore, we also tested observed yields for reduced and enlarged broods against those expected on the basis of original clutch size (Masman *et al.*, 1989;

TABLE 1. Parental effort, hunting yield and nestling food intake in a subsample of experimental broods. Means \pm S.D. (n = number of observation days). Comparison between groups by Mann-Whitney U -test one-tailed (hunting yield: two-tailed)

Number of broods	Reduced (R) 3	Control (C) 8	Enlarged (E) 4	Comparison		
				R-C	C-E	R-E
Original clutch size	5.0 \pm 1.0	5.1 \pm 0.8	5.3 \pm 1.0	N.S.	N.S.	N.S.
Experimental brood size	2.7 \pm 0.6	5.1 \pm 0.8	7.3 \pm 1.0			
Male flight (h day ⁻¹)	3.8 \pm 2.2 (7)	4.6 \pm 1.6 (27)	5.8 \pm 1.4 (10)	N.S.	*	*
Male energy expenditure (kJ day ⁻¹)	364 \pm 99 (7)	388 \pm 78 (25)	459 \pm 74 (10)	N.S.	*	*
Male hunting yield (prey h ⁻¹ hunt)	6.4 \pm 1.6 (7)	6.4 \pm 2.7 (29)	7.3 \pm 1.4 (11)	N.S.	N.S.	N.S.
Female flight (h day ⁻¹)	0.3 \pm 0.3 (4)	1.8 \pm 1.3 (5)	2.3 \pm 1.4 (14)	*	N.S.	**
Food intake per brood (g day ⁻¹)	205 \pm 78 (8)	325 \pm 82 (24)	486 \pm 63 (14)	***	***	***
Food intake per nestling (g day ⁻¹)	81 \pm 24 (8)	61 \pm 12 (24)	66 \pm 8 (14)	**	N.S.	*

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Fig. 1), and again found no significant differences (Wilcoxon matched-pairs test). The difference between observed and expected yields also did not differ between reduced and enlarged broods. Different parental effort with equal hunting yield resulted in different amounts of food brought to the nest (Table 1, Fig. 2). The parents brought more food to the enlarged broods and less to the reduced broods, compared with the controls. Food intake per nestling was the same for controls and enlarged broods, but was significantly higher in reduced broods.

In addition to daily parental effort, the duration of parental care after fledging is a major factor in determining total energy expenditure of the adults during reproduction. Duration of parental care of kestrels breeding late in the season is significantly curtailed compared with early breeders. Fledglings from both enlarged and reduced broods became independent at about the age expected for the time of year (Fig. 3).

Nestling growth and survival

Growth of those nestlings surviving until fledging in natural broods is shown in Fig. 4. Variation in body mass in the course of the day was controlled for by calculating mass increase during the day as a function of age and converting all body mass data to 12.00 h. Both sexes weighed about 16 g at hatching and reached peak weights around 24 days of age. Females grew faster and reached higher peak weights than males. Body mass decreased in the final days before fledging. This trend continued after fledging and both sexes attained minimum body mass around the age of independence. The age at independence varied among broods from about 44 to 62 days after hatching, depending on time of year (Fig. 3). Growth of the primaries showed a different pattern from body mass (Fig. 4b). At fledging, wing length was only 75% of the ultimate length. The flight

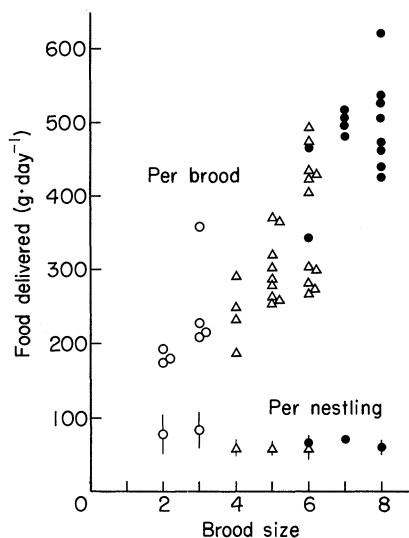


FIG. 2. Daily amount of food (g) delivered by the parents to the reduced (○), enlarged (●) and control (△) broods. Per brood: each symbol indicates one observation day. Per nestling: means \pm S.D.

feathers were fully grown at an age of approximately 50 days, 20 days after fledging. Variation in duration of parental care indicates that some parents stopped feeding the young before their flight feathers were fully grown, especially those breeding late in the season (Figs 3, 4).

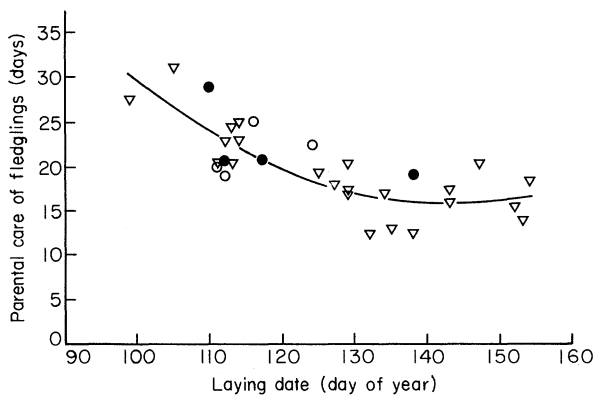


FIG. 3. Duration (days) of parental food provisioning of the young after fledging in natural (▽), reduced (○) and enlarged (●) as a function of laying date of the first egg of the clutch. Each symbol indicates one brood. Line is the quadratic regression fitted by least squares.

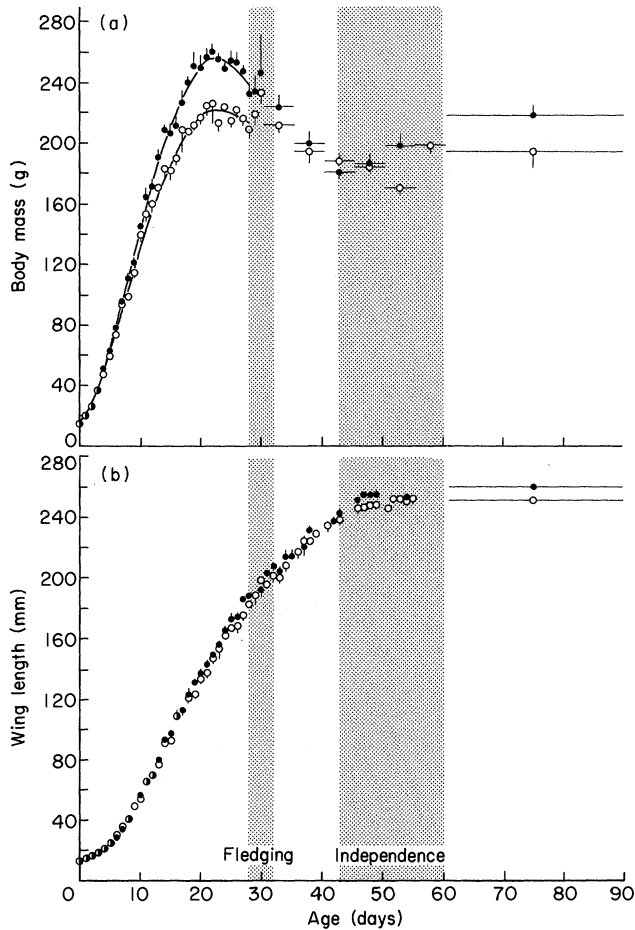


FIG. 4. Mean body mass (a), and wing length (b), of male (O) and female (●) nestlings from natural broods as a function of age and of birds recaptured after fledging. Means (g) \pm S.E. The curves in body mass indicate the 5-day running means of body mass for males and females in the nestling period.

Growth of chicks in the manipulated broods was analysed by calculating individual body mass increase per day between the first measurement after age 9 days, i.e. at the start of experiment, and the last measurement before age 20 days. As the rate of increase in wing length in natural broods was approximately constant from age 10 to 24 d (Fig. 4b), we used this interval in the analyses of wing-length growth in the experimental broods.

Growth rates of body mass as well as wing length in nestlings which survived until fledging were significantly lower in enlarged broods compared with reduced broods as well as controls, both for males and females (Table 2). The differences between reduced and control broods were not significant although body mass increase tended to be faster in reduced broods. To test whether the reduced growth in enlarged broods was due to some individuals within the brood or the result of slower development of the whole brood, variance in growth rates within broods was calculated for all nests (Table 2). The

TABLE 2. Nestling growth in manipulated broods. Individual body mass increase (g day^{-1}) was calculated from the first measurement after age 10 (days) and the last before age 20 (Fig. 4), and then averaged per brood. Means \pm S.D. (n) of brood averages and intra-brood variance are shown. Wing-length: age 10–24. Statistical comparison of groups by Mann–Whitney U -test, one tailed

	Reduced (R)	Control (C)	Enlarged (E)	Comparison		
				R–C	C–E	R–E
Body mass increase (g day^{-1})						
Males						
Mean	9.5 \pm 2.8 (17)	8.4 \pm 2.6 (15)	5.9 \pm 2.7 (25)	N.S.	**	***
Variance	1.7 \pm 1.7 (7)	3.1 \pm 3.4 (12)	4.6 \pm 5.5 (20)	N.S.	N.S.	N.S.
Females						
Mean	10.5 \pm 2.5 (15)	10.1 \pm 2.9 (19)	6.9 \pm 4.6 (23)	N.S.	**	**
Variance	1.8 \pm 2.9 (11)	6.0 \pm 11.9 (14)	3.9 \pm 5.6 (17)	N.S.	N.S.	N.S.
Wing-length increase (mm day^{-1})						
Males						
Mean	7.2 \pm 0.3 (20)	7.2 \pm 0.4 (19)	6.9 \pm 0.5 (25)	N.S.	*	**
Variance	0.05 \pm 0.04 (10)	0.1 \pm 0.2 (15)	0.13 \pm 0.2 (20)	N.S.	N.S.	N.S.
Females						
Mean	7.5 \pm 0.3 (21)	7.5 \pm 0.3 (20)	7.1 \pm 0.7 (23)	N.S.	*	*
Variance	0.06 \pm 0.06 (12)	0.07 \pm 0.06 (19)	0.12 \pm 0.2 (17)	N.S.	N.S.	N.S.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

differences in mean variance between the experimental groups were not statistically significant. This does not support the idea that the reduced growth rate of the enlarged broods was due to more uneven distribution of food over the brood.

The body mass increase was far from linear after age 20 and became negative shortly before fledging in the natural broods. We therefore calculated relative mass of the experimental nestlings for this age class. Expected mass for every day of age was determined by taking the 5-day running mean of nestling weight in natural broods (Fig. 4a). The same method was used for analyses of wing length during the last 10 days before fledging. Body mass before fledging in enlarged broods was significantly lower than in reduced broods, whereas mean relative wing length did not differ between the groups (Table 3). After fledging, only a fraction of the juveniles could be recaptured and no differences in body mass between the groups could be established in the females. The males from reduced broods were significantly heavier than the controls in age-class 31–40 days (Table 4). As neither sex from enlarged broods differed in mass from the other groups during the fledging period, initial arrears in growth before fledging were possibly made up by then.

Nestling mortality was significantly higher in the enlarged broods whereas reduced and control broods both showed the same low mortality rates (Table 5). In these enlarged broods, there was no difference between survival rates of nestlings raised by their own parents (80.6%) and those added to enlarge the brood (80.3%). In spite of increased mortality in the enlarged broods the brood sizes at fledging were still larger than in the

TABLE 3. Relative body mass and wing-length of nestlings from experimental broods during the last 10 days before fledging (age 21–30 days), expressed as percentage of the values obtained in natural broods in this age-class, Mean \pm S.D. Levels of significance as in Table 2. Mann–Whitney *U*-test, one-tailed

	Reduced (R)	Control (C)	Enlarged (E)	Comparison		
				R–C	C–E	R–E
Body mass						
Males	102.7 \pm 6.9 (19)	100.9 \pm 7.9 (21)	98.0 \pm 7.3 (23)	N.S.	N.S.	*
Females	101.3 \pm 8.7 (20)	99.8 \pm 5.6 (21)	96.4 \pm 7.3 (22)	N.S.	N.S.	**
Wing-length						
Males	98.0 \pm 2.4 (19)	98.9 \pm 3.4 (21)	96.9 \pm 3.9 (23)	N.S.	N.S.	N.S.
Females	99.1 \pm 3.9 (20)	98.5 \pm 3.6 (21)	96.81 \pm 4.6 (22)	N.S.	N.S.	*

TABLE 4. Body mass of male and female fledglings from manipulated broods. Means (g) \pm S.D. Age groups: 31–40 and 41–50 days, during parental care. Age group 51–90, at independence. Mann–Whitney *U*-test, one-tailed

Age (days)	Reduced (R)	Control (C)	Enlarged (E)	Comparison		
				R–C	C–E	R–E
Females						
31–40	238.4 \pm 12.4 (11)	224.0 \pm 20.7 (14)	232.5 \pm 11.7 (23)	N.S.	N.S.	N.S.
41–50	222.9 \pm 14.0 (3)	—	217.7 \pm 23.4 (14)			N.S.
51–90	187.7 (1)	206.0 \pm 19.6 (6)	197.9 \pm 17.9 (4)	N.S.	N.S.	N.S.
Males						
31–40	216.7 \pm 13.9 (12)	186.3 \pm 25.2 (10)	199.2 \pm 28.8 (33)	***	N.S.	*
41–50	206.3 \pm 20.6 (3)	192.3 \pm 9.90 (6)	190.1 \pm 20.2 (11)	N.S.	N.S.	N.S.
51–90	188.7 \pm 13.7 (9)	180.5 \pm 10.6 (9)	187.1 \pm 12.2 (8)	*	N.S.	N.S.

* $P < 0.05$.

*** $P < 0.001$.

other groups. This may have resulted in continued increased nestling food demand after fledging in the enlarged broods.

Out of 575 juvenile kestrels fledged from all broods in this study, forty-two were caught alive in the study area after 1 year. Hence, local survival amounted to 7.3%. Survival estimates based on ring analyses showed a mean survival during the first year of 36.6% in natural broods and local survival obviously underestimates overall survival because of dispersion of juvenile kestrels (Dijkstra 1988). Local survival of juveniles from fledging until the next breeding season did not differ between reduced (6/111), control (29/341), or experimental (7/123) broods (logistic regression of fraction surviving on manipulation categories ($-1 =$ reduced; $0 =$ control; $1 =$ enlarged; $t = 0.22$; N.S.).

Adult body mass and local survival

Mean body mass of adult male and female kestrels raising experimental broods is shown in Fig. 5 as a function of nestling age. Before the broods were manipulated mean

TABLE 5. Nestling survival and brood size at fledging in reduced, control and enlarged broods. Means \pm S.D. Mann-Whitney *U*-test, one tailed

	Reduced (R)	Control (C)	Enlarged (E)	Comparison		
				R-C	C-E	R-E
Number of broods	25	22	25			
Original clutch size	5.2 \pm 0.8	5.0 \pm 0.9	5.2 \pm 0.8	N.S.	N.S.	N.S.
Experimental brood size	3.2 \pm 0.8	5.0 \pm 0.9	7.2 \pm 0.8			
Brood size at fledging	3.1 \pm 0.8	4.9 \pm 0.9	5.7 \pm 1.9	***	*	***
Nestling survival (%)	98.0 \pm 10.0	98.5 \pm 0.9	80.6 \pm 26.5	N.S.	***	***

* $P < 0.05$.** $P < 0.01$ *** $P < 0.001$.

adult body mass did not differ significantly between the groups in either sex (Mann-Whitney *U*-test, N.S. in all cases). During the nestling period the females showed a decrease in body mass. Females raising reduced broods were consistently heavier than those with enlarged broods (Mann-Whitney *U*-test for females with broods aged 11–20 d, 21–30 d, 31–50 d all $P < 0.05$) and lost weight less rapidly than those with enlarged broods (ANCOVA, $F_{1,69} = 5.91$, $P < 0.05$). The rate of decrease in body mass of females raising complete broods was intermediate and did not differ from females with either reduced (ANCOVA, $F_{1,48} = 2.37$ N.S.) or enlarged broods (ANCOVA, $F_{1,69} = 0.75$ N.S.) The males showed no significant change in body mass in the course of the nestling period and no significant effects of brood manipulations on body mass could be found (Fig. 5).

By monitoring tagged kestrels and capturing untagged individuals during the next breeding season, local survival of kestrel parents could be established. For natural broods local survival of the parents turned out not to be associated with final brood size (logistic regression by iterative maximum likelihood approximation, $t = 1.28$ $P > 0.1$). Mean local survival of parents raising enlarged broods was approximately 15% lower than in those raising complete broods, and 23% lower than in parents of reduced broods (Fig. 6). The logistic regression of local survival on brood manipulation category ($-1 =$ reduced; $0 =$ control; $1 =$ enlarged) was significantly different from 0 ($P < 0.05$). These trends were the same in both sexes, although not significant for either sex separately. However, the probabilities for female and male parents of the same nest to survive were not associated with each other ($\chi^2 = 2.37$; N.S.), so that pooling of the sexes seems acceptable. Female rates of local survival were lower than in males. Local survival of those parents in the same areas and years, which had an incomplete brood due to egg mortality (natural brood reductions), is also shown in Fig. 6. Local survival of these parents was not statistically different from the experimentally reduced broods (females $\chi^2 = 0.06$, males $\chi^2 = 2.2$, both N.S.). When we included the natural brood reductions in the experimentally reduced group, the effect of 'brood manipulations' on male local survival was statistically significant (logistic regression $P < 0.02$). The sexes combined again showed a pronounced effect of deviations from the complete brood size on adult local survival ($P < 0.01$).

Under the hypothesis that the differences in local survival were primarily determined by differences in rates of dispersion rather than in mortality, one might anticipate that parents from enlarged broods which did survive locally would more often be breeding away from the prior nest site than those from control and reduced broods. For the

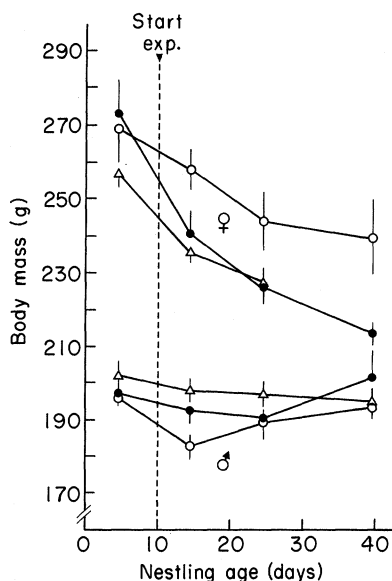


FIG. 5. Mean body mass (g) \pm S.E. of male and female parents of control (Δ), reduced (\circ) and enlarged (\bullet) broods during the nestling stage, per 10-day interval of nestling age. Dashed line indicates the start of the experiments.

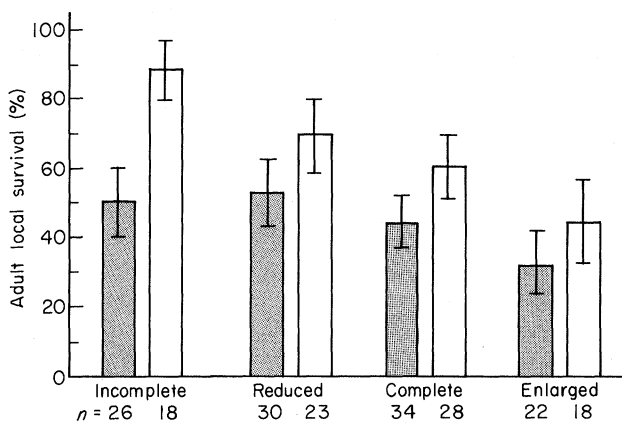


FIG. 6. Local survival till the next breeding season of kestrel female (\blacksquare) and male (\square) parents after brood manipulation. Means \pm S.E. Survival of those parents who raised a reduced brood due to egg mortality (natural brood reductions) is shown in the left panel. n below the figures indicates the number of identified parents over which local survival could be calculated.

experiments in the largest of our two study areas, Flevoland (about 575 km²), we analysed the distances between nest sites in consecutive years. Averages were 1.4 km (S.D. 2.2, $n=20$), 1.0 km (S.D. 1.9, $n=25$), and 1.4 km (S.D. 1.2, $n=8$) for parents of reduced, control and enlarged broods, respectively. There were no statistically significant differences between these groups (Mann-Whitney U -test). We finally analysed differences

between reproductive variables (clutch size, laying date) of those parents surviving in the local population until the following year, but did not find any significant relationship with brood manipulations.

DISCUSSION

Brood size manipulations in altricial birds have become a popular tool in avian reproductive ecology, ever since Von Haartman (1954) did the first experiments of this kind in the pied flycatcher (see Table 6). They are designed to evaluate the consequences for variables associated with individual fitness of raising more or fewer young than the natural brood size. The approach is based on the assumption that the parents of the manipulated broods are 'fooled' by the experiment and accept the extra nestlings as their own. In order to derive conclusions on the relation between brood size and fitness from such experiments it is necessary to evaluate the effects on both the brood and the parents. The analysis of repercussions on the parents is usually more difficult, and started much later (Harris 1970) than studies on the broods. In our study in the kestrel, we have attempted to cover influences on the prospects of both nestlings and parents. We realize that the proximate control of egg laying in the kestrel involves a close association between clutch size and laying date, probably based on a largely endogenous temporal programme (Meijer 1989). Since variations in clutch size and laying date appear to be adapted to the nutritional circumstances of individual pairs (Dijkstra 1988), they are likely to affect the results of experimental manipulations. Our data set is not large enough to differentiate between broods at different dates. Additional experimentation will be required to specifically study the effects of date *per se* on fitness. In any case, our experimental nests were representative of the natural distribution of clutch sizes and laying dates (Fig. 1).

Effects on offspring

The consequences of the manipulations for the nestlings may be summarized as follows: surviving nestlings from enlarged broods initially showed lower growth rates than both complete broods and reduced broods (Table 2). Shortly before fledging body mass was still relatively low in the enlarged broods whereas wing length was the same as in the other groups (Table 3). After fledging no effect of brood manipulation on fledgling body mass could be established. Increased nestling mortality in enlarged broods (Table 5) resulting in relaxed competition for food among survivors possibly caused compensation of initial areas in physical development. Brood size at fledging was still larger in the enlarged broods in spite of increased mortality (Table 5). Duration of parental care showed no relation with type of experiment. Survival of the offspring from independence till reproductive age cannot be exactly established. Due to a large fraction of the birds dispersing from the study area, local survival underestimates true survival rates until maturation. The experiments did not cause significant effects on local survival. Hence, we must conclude that kestrel parents, under the conditions of the experiment, were able to raise more offspring surviving till reproductive age than they do under natural conditions.

With respect to the offspring, the kestrel results are in line with the conclusions from the literature. Most studies have reported increased nestling mortality and/or reduced condition (usually body mass) in enlarged broods (Table 6). However, the majority of studies also demonstrated that altricial birds are usually able to raise more nestlings than the number they opted for themselves (Table 6, Lessells 1987). Reduced condition of fledglings in enlarged broods suggests that such increase might be offset by reduced

TABLE 6. Summary of brood enlargement experiments in altricial birds. Fitness components analysed: N_f =number of fledglings; M_f =body mass of fledglings; S_o =survival of nestlings till fledging; S_f =survival of fledglings till autumn or next breeding season; M_p =body mass of parents; S_p =survival of parents; B_p =future breeding performance of parents. Positive, negative and zero effects are indicated by +, - and 0, respectively

Order/species	Offspring				Parents			Author
	N_f	M_f	S_o	S_f	M_p	S_p	B_p	
(a) Non-passeres								
Procellariiformes								
<i>Diomedea immutabilis</i>	-		-					Rice & Kenyon (1962)
<i>Oceanodroma castro</i>	-		-					Harris (1969)
<i>Oceanodroma leucorhoa</i>	0	-	-					Huntington, in Lack (1966)
<i>Puffinus puffinus</i>	-	-	-		0			Harris (1966)
<i>Puffinus tenuirostris</i>	0	-	-					Norman & Gottish (1969)
Pelecaniformes								
<i>Sula sula</i>	-		-					Nelson (1966)
<i>Sula bassana</i>	+		-					Nelson (1964)
<i>Sula capensis</i>	+	-			0			Jarvis (1974)
Falconiformes								
<i>Accipiter rufiventris</i>		-	-					Simmons (1986)
<i>Falco tinnunculus</i>	+	-	-	0	-	-	0	this study
Strigiformes								
<i>Aegolius funereus</i>	+	0	0		0	0	0	Korpimäki (1988)
Charadriiformes								
<i>Stercorarius longicaudus</i>	+		0					Andersson (1976)
<i>Larus argentatus</i>	+	0	0					Haymes & Morris (1977)
<i>Larus glaucescens</i>	+	-						Ward (1973)
<i>Larus glaucescens</i>	+		0					Vermeer (1963)
<i>Larus glaucescens</i>					-	-	0	Reid (1987)
<i>Larus fuscus</i>	+	0	0					Harris & Plumb (1965)
<i>Rissa tridactyla</i>	+	-	0					Coulson, in Lack (1966)
<i>Creagrus furcatus</i>	+	0	0		0	0		Harris (1970)
<i>Fratercula arctica</i>	+		-					Corkhill (1973)
<i>Fratercula arctica</i>	-		-					Nettleship (1972)
<i>Cephus grylle</i>	+	0	0					Asbirk (1979)
<i>Alca torda</i>	+	-	-					Lloyd (1977)
<i>Alca torda</i>	+	-	-					Plumb (1965)
Columbiformes								
<i>Columba palumbus</i>	+	-	-	0				Murton, Westwood & Isaacson (1974)
Caprimulgi formes								
<i>Apus apus</i>	-		-					Perrins (1964)
<i>Aerodramus spodiopygius</i>	0	-	-					Tarburton (1987)
(b) Passeres								
Passeriformes								
<i>Delichon urbica</i>	+	0	0					Bryant (1975)
<i>Delichon urbica</i>	+	-	-					Bryant & Westerterp (1983)
<i>Iridoprocne bicolor</i>	+	-	0	0	0	0		DeSteven (1980)
<i>Troglodytes aedon</i>	+	0	0		0		0	Finke, Milinkovich & Thompson (1987)
<i>Ficedula hypoleuca</i>	0	-	-		-	-		Askenmo (1977, 1979)
<i>Ficedula hypoleuca</i>	+	-	0	0				Von Haartman (1954)
<i>Ficedula albicollis</i>	+			-*		0	-	Gustafsson & Sutherland (1988)
<i>Turdus pilaris</i>	+	0	0					Slagsvold (1982)
<i>Parus major</i>	+	-	-	-				Smith, Kallander & Nilsson (1987, 1989)
<i>Parus major</i>	+	-	-	-	0	0	-	Tinbergen (1987, unpublished)
<i>Parus major</i>	+					0		Boyce & Perrins (1987); Pettifor, Perrins & McCleery (1988)
<i>Parus caeruleus</i>	+		0	0	-	-	0	Nur (1984a, b, 1988)
<i>Plectrophenax nivalis</i>	+	0	-					Hussell (1972)
<i>Agelaius phoeniceus</i>	+	-	-					Cronmiller & Thompson (1980)
<i>Pyrrhula pyrrhula</i>	-	-	-	-				Newton, in Lack (1966)
<i>Passer domesticus</i>	+	-	-					Schifferli (1978)
<i>Passer domesticus</i>	+	-	0		0	0	-	Hegner & Wingfield (1987)
<i>Quelea quelea</i>	0	0	-					Ward (1965)
<i>Sturnus vulgaris</i>	+	-	-					Crossner (1977)
<i>Sturnus cinerareus</i>	+		-					Kuroda (1959)
<i>Pica pica</i>	-	0	-					Högstedt (1980)
<i>Corvus corone</i>	+	0	-					Loman (1980)
<i>Corvus frugilegus</i>	+					0	-	Røskaft (1985)

* In addition, there was a negative effect on offspring fecundity.

† In this study, the number of offspring recruited was evaluated (= $N_f S_f$).

prospects for the offspring. However, effects on fledgling survival have been documented in only three species: the bullfinch (Newton in Lack 1966) where the data concern local survival until autumn, which may well reflect differential dispersal, the collared flycatcher (Gustafsson & Sutherland 1988) and the great tit (Smith, Källander & Nilsson 1989), where the probability of recruitment into the breeding population was shown to be reduced in enlarged broods.

Effect on parents

Turning now to the parents, the kestrels clearly increased daily hunting effort to nourish the enlarged broods, and estimated energy expenditure was increased correspondingly. Yields per hour hunting were the same in all groups. This confirms our conclusions from nestling food deprivation experiments (Masman *et al.*, 1989). Females with reduced broods almost completely stopped hunting. Body mass decrease in this group averaged 30 g during the nestling phase which is the same as in *ad lib.* fed females breeding in captivity (Dijkstra, *et al.* 1988) and contrasts with an average weight loss of 60 g in females with enlarged broods (Fig. 5). This result supports the notion that female raptors build up fat reserves functioning as a buffer for nestling food provisioning during periods of food shortage (Wijnandts 1984). Males did not show differences in body mass in relation with brood manipulations (Fig. 5). They probably attain low body reserve levels during the nestling phase independent of variations in nestling food demand.

Local adult survival was negatively correlated with the change in brood size (Fig. 6). Parents from reduced broods survived best. Their local survival rates were 23% higher than in parents with enlarged broods. Female kestrels had lower local survival rates than males. This is true both in experimentally manipulated and control broods, and may reflect sex differences in dispersal rather than in true survival. Survival analyses based on ring recoveries of all nestlings ringed in the Netherlands from 1967 to 1986, compared with local survival in our study area from 1979 to 1987, indicated that 16 to 42% (depending on age) of the local natural breeding population disappeared due to dispersion rather than death (Dijkstra 1988). Insufficient data have so far accumulated for an analysis of ring recoveries of the manipulated parents (1985–87). Thus, although local survival reflects only one aspect of the future reproductive prospects of the parents, the results suggest that there may be rather important repercussions for the parents of raising more young than they 'intended' to. The behavioural analysis suggests that reduced local survival in parents of enlarged broods may be related to increased activity and estimated energy expenditure in providing food for the young. The daily time spent in flight hunt, a major determinant of daily energy expenditure (Masman & Klaassen 1987) was affected in both sexes. Although kestrels can compensate, within limits, for increased work loads by raising energy intake (Masman *et al.*, 1989), we surmise that the increased parental energy turnover in the brood enlargements is involved in the reduction in survival.

Effects of brood enlargements on parental prospects have been evaluated so far in only twelve altricial species (Table 6). Effects on the parents' condition during brood raising have been examined in thirteen studies, five of which report reduced body mass following brood enlargement. The kestrel results are in agreement with those of Hussell (1972) in the snow bunting, where the sexes differed. However, body mass may be equivocal in this respect, and the absence of any conditional response does not preclude long-term impacts on future reproduction. Such impacts have now been documented for eight altricial species. In the pied flycatcher (Askenmo 1979), the blue tit (Nur 1984a, 1988), the

glaucous-winged gull (Reid 1987) and the kestrel, there were effects on parental local survival rates. In the house sparrow (Hegner & Wingfield 1987), great tit (Smith, Källander & Nilsson 1987, 1989; Tinbergen 1987), rook (Røskaft 1985) and collared flycatcher (Gustafsson & Sutherland 1988), the effects were on rates of future reproduction of those parents surviving. A further four studies (Harris 1970; DeSteven 1980; Korpimäki 1988; Pettifor, Perrins & McCleery 1988) did not demonstrate long-term effects on parental survival (Table 6). We emphasize that in all of these studies, including our own, estimates of survival concern birds returning to the local population under study, and reflect losses due to migration as well as to death. For the kestrel no differences in the tendency to disperse *within* the study area was found between parents locally surviving after a brood manipulation, as might be expected if variations in dispersion rather than mortality were primarily involved. However, this is no more than circumstantial evidence, and a definitive demonstration of effects of parental effort on survival awaits the analysis of true instead of local survival.

Thus, while the ability of altricial birds to raise additional young beyond the natural brood size, albeit at the expense of increased brood mortality, has been amply documented, the repercussions of raising enlarged broods for the parents have been shown convincingly in only few cases. We further remain in the dark as to which aspects of parental care are causally involved in such repercussions. Our experience with the kestrels suggest that neither time nor food was in short supply, and increased energy expenditure in the males, who have the major share in food provisioning, can be made up for by increased intake. Yet, the increased energy turnover, at levels probably approaching the maximum sustainable (Masman *et al.*, 1989), may have resulted in reduced adult survival till the next breeding season.

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