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Increased daily work precipitates natural death in the kestrel

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Summary

1. Costs of reproduction have been assessed experimentally by measuring subsequent survival and reproduction of parent animals raising enlarged and reduced numbers of offspring. Reported effects on survival have so far always referred to local survival of marked individuals in the study population. They do not provide definitive proof of a cost of reproduction, since reduced local survival may be due either to reduced survival or to an increased tendency to emigrate from the study area. Therefore, it is important to assess mortality rates in connection with brood size experiments

2. We report an analysis of the time of death in 63 cases where kestrels, *Falco tinnunculus* L. had raised broods of manipulated size and were subsequently reported freshly dead. 60% of the parents raising two extra nestlings were reported dead before the end of the first winter, compared to 29% of those raising control or reduced broods. This result confirms our interpretation of the manipulation effects on local survival as due to mortality rather than emigration. The extra mortality occurred in the winter following the brood enlargement

3. Kestrel parents in these experiments have been shown to adjust their daily energy expenditure to the modified brood size. Increased parental effort in this species thus entails an increased risk of death half a year later.

Key-words: brood size manipulation, cost of reproduction, dispersion, recoveries, survival

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Introduction

A reduction in the residual reproductive value of parents as a consequence of their reproductive effort, as postulated first by Williams (1966), is one of the central theorems of life-history theory. This cost of reproduction in iteroparous animals leads to a trade-off between the number of offspring in the current brood (brood size) and expected future reproduction, and forms the basis of clutch size theory (Charnov & Krebs 1974). A cost of reproduction may be found in subsequent fecundity or in subsequent survival or in both. The method to evaluate such costs has generally been the manipulation of the number of young after birth of a litter or brood, and the subsequent assessment of survival and/or fecundity of individually marked parents in the study population. The most clearcut effects on subsequent fecundity have been those where the incidence of second broods was reduced following enlargement, or enhanced following reduction of the first brood (Smith, Källander & Nilsson 1987; Lindén 1988; Tinbergen 1987; Verhulst 1995; Verhulst & Hut

1996). In addition, long-term effects on reproductive success have been observed (Gustafsson & Sutherland 1988; Røskaft 1985; Verhulst 1995). Effects on fecundity may be viewed either as a physiological or as a strategic consequence of the experiment. For instance, the effects may be in the first place on a physiological condition affecting the probability of survival, which might alter the strategic decision of the animals whether or not to produce another brood.

Effects of brood size manipulations on survival itself have been less unambiguously demonstrated. Such effects have so far been reported in three species (*Ficedula hypoleuca* Askenmo 1979; *Parus caeruleus* Nur 1984, but see Pettifor 1993; *Falco tinnunculus* Dijkstra *et al.* 1990). In all cases the data refer to *local survival*, i.e. the relative frequency of return to the next breeding population of individually marked parents. Decreased local survival may reflect increased mortality or an increased tendency to leave the local area, or a combination of both. Increased emigration is a plausible alternative hypothesis for birds for whom reproduction has been more exhaustive, and which

may have experienced this as a poor situation. Thus, decreased local survival following brood enlargement by itself does not constitute evidence for a cost of reproduction. Along the same line of reasoning, the absence of an experimental effect on local survival is no evidence to refute a cost of reproduction. This is particularly true when the effort of parents raising the enlarged brood has not been assessed, as is frequently the case.

In view of this dilemma, we have undertaken to assess the rate of mortality in kestrels having raised manipulated broods. This was done by recording all ring recoveries of birds found freshly dead by the general public and calculating the proportion recovered more than one year after the experiment. We now report that after raising two extra nestlings, parents suffer increased mortality in the subsequent winter, and thus provide direct evidence for a physiological cost of reproductive effort.

Methods

Among pairs of nests, characterized by similar laying date and clutch size, nestlings were exchanged when around 7 days old; two nestlings were moved from one ('reduced') nest to an other ('enlarged') nest. Kestrel parents accept new nestlings as their own, and adjust their daily food provisioning rate to the changed demands from the brood, such that more young fledge from enlarged than from control broods (Dijkstra *et al.* 1990). This is achieved by an increase in daily time spent hunting for food (Masman *et al.* 1989; Dijkstra *et al.* 1990) and in daily energy expenditure as assessed by the differential in clearance rates of stable isotopes of oxygen and hydrogen, the 'Doubly Labelled Water' method (Deerenberg *et al.* 1995).

Altogether, 200 pairs of kestrels were involved, breeding in the years 1985–90 in two study populations in the Netherlands (Masman, Daan & Beldhuis 1988; Masman *et al.* 1989; Dijkstra *et al.* 1990; Daan, Dijkstra & Tinbergen 1990). In 373 of the 400 cases the parent was ringed, and the proportion of these cases in which the bird was observed alive in the study population at least 1 year after the experiment ('local survival') could be assessed. When surviving locally, an individual could enter the data set a second time, or a third, etc. In addition, 'global survival' was estimated from 63 cases of birds which had been involved in the experiment and were subsequently reported freshly dead in the years 1985–94. The fraction of these birds that died more than 1 year after the experiment gives an estimate of global annual survival. A small fraction, estimated at 0.14 for the 1990 birds, and down to 0.006 for 1985, on the basis of data from Dijkstra (1988), is probably still alive today (1995), and causes our data to slightly underestimate true survival rates. However, this bias should not cause a difference between experimental groups, as these were

equally distributed over the 6 years of experimentation.

Results

Reduced and enlarged nests did not deviate significantly from unmanipulated control nests in terms of laying data and clutch size, but they differed from controls in the numbers of fledglings raised (Table 1). In spite of a significant increase in nestling mortality in the enlarged broods, parents apparently were able to raise more nestlings than their own brood.

LOCAL SURVIVAL

Local survival of parents decreased with the number of nestlings ($\delta N = -2; 0; \text{ or } +2$) that had been added to their family (Fig. 1a, open symbols). The dependence of local survival on manipulation was tested by logistic regression and found to be significant at the $P < 0.05$ level (Table 3). Adding year of the experiment did not significantly reduce the deviance of the model. Including year in the model reduced χ^2 to 3.69, which still borders on significance. This confirms an earlier analysis based on part of these data (Dijkstra *et al.* 1990). The same effect was found when for each individual bird only the first experiment was taken into account (Fig. 1a, solid symbols). Again, the dependence of local survival on manipulation is significant (Table 3). Year did not significantly reduce the deviance, and including year in the model reduced χ^2 to 5.74, which is still significant ($P < 0.025$). The effect of manipulation on local survival can therefore not be attributed to the fact that some of the surviving birds re-entered the study population. The overall effect is not due to spurious year-to-year differences in local survival. Furthermore, the effect of the experiment was observed in both genders (Table 2).

GLOBAL SURVIVAL

The proportion of all experimental birds that was reported dead by the general public (see Table 2) was associated neither with gender (ANOVA $F_{1,371} = 1.08$) nor with experimental manipulation ($F_{2,370} = 0.88$). The proportion among these dead recoveries of birds that had survived at least 1 year decreased from birds raising reduced to those raising enlarged broods, while survival of control parents was intermediate, in birds of both genders (Table 2, Fig. 1b, open symbols). Logistic regression of the proportion of birds surviving 1 year yielded a significant contribution of experimental group to the explained variance ($\chi^2_1 = 5.00$; $P < 0.05$). In this case, including year in the model did significantly reduce the deviance, and reduced the χ^2_1 to 3.74, which borders on significance (Table 3). As with local survival, the same effect was found for global survival when for each individual bird only the first experiment was taken into account

Table 1. Standard reproductive parameters for experimental and control nests. Means \pm standard deviation (number of nests in parentheses). Laying date expressed as day of the year (121 = 1 May). Mortality is the proportion of nestlings dying between brood size manipulation and fledging. Parental DEE in kJ day⁻¹ (from Deerenberg *et al.* 1995) as measured in 25 parent kestrels in 1992 (number of individual parents in parentheses). Laying date and clutch size did not vary between experimental groups. Young fledged, nestling mortality and parental DEE were significantly affected by experimental manipulation

Experimental group	Reduced	Control	Enlarged	<i>F</i> , <i>P</i>
Laying date	116.0 \pm 11.7 (44)	115.9 \pm 15.0 (103)	118.7 \pm 12.6 (52)	$F_{2,196} = 0.78$; $P > 0.10$
Clutch size	5.44 \pm 0.73 (43)	5.31 \pm 0.89 (96)	5.42 \pm 0.82 (52)	$F_{2,187} = 0.80$; $P > 0.10$
Young fledged	2.95 \pm 0.96 (44)	4.61 \pm 1.18 (104)	6.35 \pm 1.69 (52)	$F_{1,198} = 165$; $P < 0.001$
Nest mortality	0.03 \pm 0.10 (44)	0.04 \pm 0.13 (104)	0.11 \pm 0.22 (52)	$F_{1,198} = 10.25$; $P < 0.002$
Parental DEE	368 \pm 60 (9)	428 \pm 65 (7)	449 \pm 70 (9)	$F_{1,23} = 7.24$; $P < 0.02$

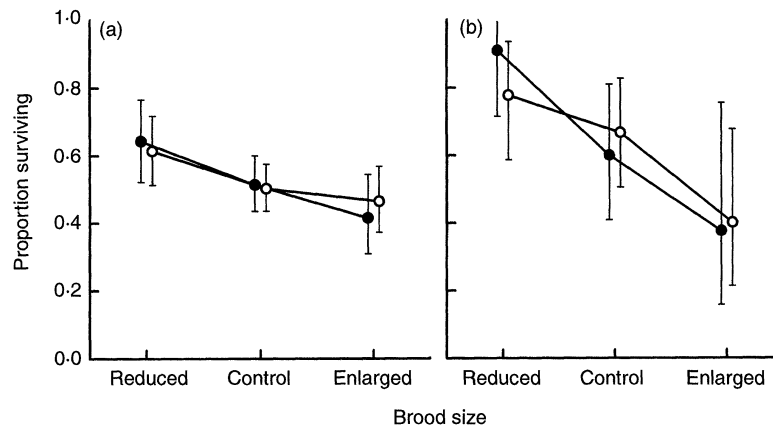


Fig. 1. First-year survival indices for kestrel parents after raising a modified brood. Proportions surviving \pm 95% confidence interval based on binomial distributions. Open symbols = proportions based on all cases (numbers of birds as in Table 2); closed symbols = proportions based only on the first case for each individual bird. (a) Survival based on local recoveries of live birds within the study population one or more years later. (b) Survival based on the fraction surviving 1 year among all recoveries reported freshly dead.

Table 2. Indices of survival and dispersion for kestrel parents raising experimental and control broods. Local survival is based on live recoveries in the study population after 1 year, global survival on the fraction of recoveries later than 1 year among all dead recoveries. Numbers in parentheses. For 'individuals' only the first case (with recovery distance only the last case) in which each individual participated in the study was regarded. For statistical analysis of survival see Table 3

Experimental group	Reduced		Control		Enlarged	
	Male	Female	Male	Female	Male	Female
Local survival						
Cases	0.62 (39)	0.61 (44)	0.57 (92)	0.44 (99)	0.50 (48)	0.43 (51)
Individuals	0.58 (24)	0.69 (32)	0.57 (65)	0.47 (75)	0.48 (31)	0.35 (34)
Global survival						
Cases	0.70 (10)	0.87 (8)	0.73 (15)	0.60 (15)	0.44 (9)	0.33 (6)
Individuals	0.86 (7)	1.00 (4)	0.57 (7)	0.61 (13)	0.25 (4)	0.50 (4)
Recovery distance (mean $^{\circ}$ log km)						
Individuals	0.69 (3)	2.17 (6)	1.34 (8)	2.18 (11)	1.09 (7)	2.56 (4)
Range (km)	0–3	2–94	0–10	1–185	0–20	0–37

Table 3. Logistic regression of first-year parental local and global survival (0 = not survived; 1 = survived) on manipulation (nestlings added: -2 = reduced; 0 = control; 2 = enlarged) and year of experiment (dummy variable). Cases refer to all experiments, individuals only to the first experiment in which an individual participated. *P*-values for the significance of the contribution to the explained variance were taken from the χ^2 distribution. Coefficients were taken from the model containing manipulation only

	(Increase in) deviance	(Increase in) d.f.	<i>P</i>	Mean coefficient	SE
Local survival: cases					
Null model	516.63	372			
Final model	512.73	371			
Constant	—	1		0.083	0.104
Manipulation	3.90	1	0.048	-0.148	0.075
Rejected: Year	8.83	5	0.116		
Local survival: individuals					
Null model	361.51	260			
Final model	355.27	259			
Constant	—	1		0.087	0.126
Manipulation	5.74	1	0.017	-0.231	0.094
Rejected: Year	10.90	5	0.053		
Global survival: cases					
Null model	82.69	62			
Final model	54.96	56			
Constant	—	1		0.561	0.273
Year	22.73	5	0.0004		
Manipulation	3.74	1	0.053	-0.421	0.196
Global survival: individuals					
Null model	50.92	38			
Final model	29.45	32			
Constant	—	1		0.584	0.365
Year	15.16	5	0.010		
Manipulation	4.76	1	0.029	-0.663	0.291

(Fig. 1b, solid symbols). For the individual birds, the dependence of global survival on manipulation category remains significant after including year in the model ($P < 0.05$; Table 3). Again, the effect can not be attributed to the fact that some birds surviving locally re-entered the study population.

If birds from the three experimental groups had a different tendency to disperse to areas varying in the probability of reporting, then the proportion reported dead after more than 1 year would represent a biased index of survival. We therefore analysed the distribution of distances of dead birds from the experimental area. This was done by first log-transforming these distances (in view of the skewness of the distributions) and then regressing \log distance on gender and the last received experimental treatment. Mean recovery distances and ranges are shown in Table 2. Females were reported further away from the experimental area, and this difference was significant ($F_{1,37} = 8.30$; $P < 0.01$). After controlling for gender, \log distance was not associated with experimental group ($F_{1,36} = 0.25$; $P > 0.1$). Controlling for year of the experiment does not change these results. Therefore, there appears to be no valid ground for explanations invoking differences in behaviour and reporting rates causing the drastic effects of the experiments

on survival. Using the log-survivorship curve derived from all birds reported dead, we can further identify the timing of the enhanced mortality among birds having raised increased broods. A breakdown of first year survival rates with respect to time of year shows that mortality was most severe during the winter (Fig. 2). Survival during the summer and autumn following

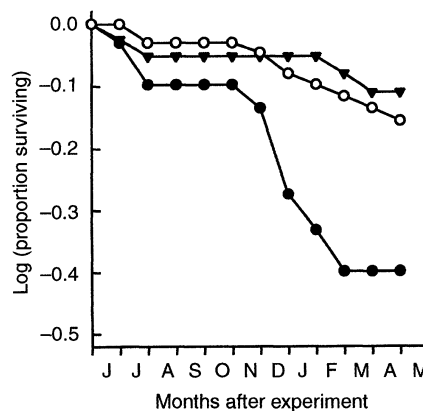


Fig. 2. Fraction surviving plotted as a function of time of year for kestrel parents after having raised experimental or control broods.

the experiment (June–October) was 0.89 (56/63) and was not associated with experimental manipulation. Survival rates in the subsequent winter (November–March) were significantly affected by the experiment, as demonstrated by logistic regression: $y = \ln [S/(1-S)] = 1.149 - 0.513 \delta N$ (null model: deviance 62.98, d.f. 55; final model 58.03, d.f. 54; change in deviance by including δN : 4.95; $P = 0.027$).

Discussion

The data presented in Fig. 1 represent the first evidence for increased mortality of individuals tricked into an increased rate of daily work in the field. It confirms our earlier tentative interpretation (Daan *et al.* 1990) that reduced 'local survival' is due to increased mortality, and not a result of increased dispersal from the study area. There is indeed reasonable quantitative correspondence between the trends observed in local and in global survival (Fig. 1). The data thus provide solid evidence for a life history cost of reproduction in the kestrel.

The mechanisms mediating these effects of the rate of parental work on mortality remain to be unravelled. The fact that the increased mortality is found during the winter months, long after the breeding season, suggests that it is not due to instantaneous hazards to the animals, such as increased predation (Magnhagen 1991) or disease during the episode of (manipulated) parental care.

An alternative hypothesis would be a temporary suppression of vitality, for instance due to interference of the rate of work with functioning of the immune system (Apanius 1993; Deerenberg 1996). Such a hypothesis would be in line with the original suggestion by Cavé (1968) that increased brood size may aggravate a 'risk of death by exhaustion' in kestrels. The consequences for mortality might then be measurable only several months after the experiment, when conditions of weather and food availability have deteriorated.

There is still a third hypothesis which might explain long-term changes in survival, the 'rate of living' theory. This theory, originally due to Pearl (1928), and later developed by Sacher (1978), states that the rate of degenerative cell destruction underlying ageing, senescence and death is proportional to the rate of metabolic energy turnover. The theory has derived correlative support from comparative studies on life span and metabolic rate (Pearl 1928; Sacher 1978; Calder 1984), and from the association between life span and the incidence of torpor in hibernators (Lyman *et al.* 1981), as well as experimental support from observed increments in life span following the reduction of metabolism through ambient temperature (Lyman *et al.* 1981; Miquel *et al.* 1976) and food restriction (McCay & Crowell 1934; Masoro, Yu & Bertrand 1982). However, the interpretation of experimental results is still controversial (e.g. Rose

1991). This theory has potentially important implications for the theory of life-history optimization (Stearns 1992). It would predict a non-temporary, cumulative effect of energy metabolism on rates of survival. Our data do not allow us to distinguish between mortality rates of the experimental groups more than a year later. Too few individuals survive 1 year after raising increased families to assess subsequent survival. The study can therefore not be conclusive on the cumulative aspect of the association between work rates and survival. The rate of living hypothesis would yield a rate of mortality which is roughly proportional to energy expenditure. The effect of the experiments on first-year mortality seems disproportionately large compared to the effect on Daily Energy Expenditure. Annual mortality increased from 0.22 for parents of reduced broods to 0.60 for enlarged broods (Table 2), a nearly threefold increase. DEE during parental care increased from 368 to 449 kJ day⁻¹ (Table 1), an increase of only 22%, and much less if integrated over a year, if we assume that DEE would revert to normal levels in all experimental groups after the time of parental care. Since it might be anticipated that effects of experimentally increased metabolic rates beyond optimal levels precipitate the ageing process and shorten life span in a non-linear fashion we cannot rule out the possibility that a temporarily enhanced DEE would lead to disproportionately increased mortality. The results are therefore neither inconsistent with the rate of living theory nor provide any support for it.

Regardless of the mechanism, the assay of mortality following brood size manipulations provides strong evidence for long-term detrimental effects of excess parental effort as have been postulated by Drent & Daan (1980), and which play a key role in the theory of optimal reproductive decisions (Williams 1966; Charnov & Krebs 1974; Daan *et al.* 1990; Stearns 1992).

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