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Document Version

Publisher's PDF, also known as Version of record

Publication date:

1996

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Deerenberg, C. M. (1996). *Parental energy and fitness costs in birds*. s.n.

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CHAPTER 4

COSTS OF REPRODUCTION IN THE ZEBRA FINCH: MANIPULATION OF BROOD SIZE IN THE LABORATORY

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Submitted to: Journal of Avian Biology

ABSTRACT

Brood size of Zebra Finches *Taeniopygia guttata* was manipulated in an attempt to identify a trade-off between current and subsequent reproduction in a laboratory situation with *ad libitum* food availability. The birds were able to raise a larger brood than the most frequent brood size under the same conditions. Initiation of the subsequent clutch was advanced after raising a small brood, and delayed after raising an large brood. Size of the subsequent clutch was not affected by the previous, experimental brood size. Thus, a cost of reproduction was observed in modification of the reproductive interval. Brood size also affected the prospects of the current, experimental brood. Both nestling survival and nestling weight at independence decreased with increasing brood size. It has often been suggested that food availability limits reproduction in the field. This study shows that under unrestricted access to food, other factors limit reproduction. Time allocation, and energy expenditure of the parents are discussed as potential alternative constraints.

INTRODUCTION

Field experiments using manipulation of brood size have been applied widely to altricial birds to investigate the life history theory of a trade-off between current and future reproduction. Parents are often able to raise a larger brood than their original brood size, at the expense of their own residual reproductive value (Dijkstra *et al.* 1990). This reduction in fitness is the cost of reproduction (Williams 1966; Trivers 1974), and can be measured as a change in survival rate following the experiment, or as altered reproductive decisions at the subsequent reproductive events (*viz.* timing and/or size of the next clutch; reviews in Dijkstra *et al.* 1990; Stearns 1992). In addition to a cost of reproduction, parents raising more young than their original brood may be faced with a diminished fitness return from each of these young. Generally, a lower weight at fledging is observed in experimentally enlarged broods, and therefore a lower reproductive value per young may be expected (Gustafsson & Sutherland 1988; Tinbergen & Boerlijst 1990).

The mechanism through which the trade-off between current and future reproduction comes about in the field is largely unknown. Study of this mechanism is hampered by variation in the environment that may cause corresponding variation between individuals. The study of consequences of reproductive decisions of parents also requires prolonged observations and repeated measurements of, for example, body mass and survival on parents and young. Experiments conducted in the laboratory may solve some of these problems, but necessarily add other confounding factors, mainly through the *ad libitum* availability of food. A major problem is the difficulty of simulating costs and risks associated with foraging. Exactly these aspects of foraging may largely determine brood size in the field (Calow 1979; Drent & Daan 1980; Partridge 1987). However, in the laboratory we may be able to identify other, *i.e.*, intrinsic physiological constraints limiting brood size. Therefore, it is of primary importance to investigate whether parental costs of reproduction can be studied in the laboratory as well.

In a study on domesticated Zebra Finches *Taeniopygia guttata*, we carried out brood size manipulations under standard, controlled conditions that are favourable for breeding, and unrestricted access to food. We aimed at investigating effects of brood size on current reproductive output and on subsequent reproductive decisions of the parents.

METHODS

Experimental birds

Pairs of male and female zebra finches, originating from domestic stock, were kept in climate rooms at 25°C, and relative humidity 60%, in a LD cycle of 14:10 (lights on at 0800 h). Each pair was held in a cage of 40·80·40 cm (h·w·d) with two perches, and equipped with food and drinking water *ad libitum*. The food was a mixture of tropical and herb seeds (ratio 1:1). Each cage contained a nest box, and nesting material was available throughout.

Manipulation of brood size

Experiment 1 Daily checks of the nest box were carried out to determine the start of reproduction (= laying date of the first egg), clutch size, hatching date and hatching success. Clutch size ranged from 3 to 6 (mean 4.3, sd 0.9, n=84). Modal clutch size was 4 eggs (51% of all clutches). We created broods of 2, 4 and 6 young to represent small, intermediate and large

broods respectively. Nests of similar hatching dates were assigned to one of three categories, such that original clutch sizes were randomly distributed over the categories. Manipulation of brood size was carried out at three days after the first young hatched. All young were used to create experimental broods of similar age. The young were weighed at an age of 35 days. The fledglings appeared to be nutritionally independent around this age (Ten Cate 1982; personal observations). Therefore we considered them to have reached independence at the end of this period. The young were transferred to separate cages when they were 50 days old.

Of a total of 42 pairs brood size was manipulated, resulting in 13 intermediate broods, 15 small and 14 large broods. All pairs were given the opportunity to renest (nest box and nesting material present) throughout the experiment. Laying date and size of the subsequent clutch was assessed from daily checks of the nestbox. The reproductive interval was measured as the number of days from hatching date of the first young till laying date of the first egg of the next clutch.

Experiment 2 In an additional experiment with 21 pairs (5 intermediate broods, 11 small and 5 large broods) that was carried out for other purposes, nest boxes were removed after fledging of all young. Upon removal of the young at 50 days of age, the nest box was replaced in the parental cage and subsequent laying date and clutch size were recorded.

Data analysis

The effects of experimental brood size, and of initial differences in pre-laying interval, clutch size and initial brood size among the three experimental groups were tested using analysis of variance. Post-hoc comparisons of means were carried out with Tukey HSD tests. Variables potentially explaining variation in reproductive interval were tested in a multiple linear regression model. Variables were omitted or added using a stepwise, backward elimination procedure, starting from an initial model including all variables. Significant contribution to the model was tested using F-ratio test on change in deviance (= residual sum of squares) between the final model and the model also containing the tested variable. All tests were two-tailed unless specified otherwise; significance was accepted at $P < .05$. We used the SX statistical package (version 4.0, NH Analytical Software Comp.) for the analyses.

RESULTS

Reproductive success of current brood

Data on timing, clutch size and original brood size prior to the brood size manipulation are listed in Table 1 per experimental category. There were no significant initial differences between the experimental categories. Data on pre-laying interval combined pre-laying intervals of first clutches ($n=33$), and replacement clutches ($n=9$) of first

Table 1. Descriptives of the experimental broods. Means \pm standard deviation, and test results of analysis of variance are given.

	Experimental Group			F	df	P
	Small	Intermediate	Large			
Sample size (no. of broods)	15	13	14			
Current reproduction:						
Pre-laying interval (days)	12.1 \pm 12.1	12.2 \pm 10.0	14.6 \pm 18.4	0.14	2	ns
Clutch size	4.3 \pm 0.7	4.3 \pm 0.6	4.1 \pm 0.9	0.25	2	ns
Brood size:						
original	3.0 \pm 0.9	3.5 \pm 1.1	3.4 \pm 1.5	0.86	2	ns
experimental	2	4	6			
at 35 days (independence)	1.9 \pm 0.3	3.8 \pm 0.4	4.8 \pm 1.7	30.8	2	<.001
Survival till 35 days (%)	96.7 \pm 12.9	96.2 \pm 9.4	79.8 \pm 27.9	4.37	2	=.02
Fledgling mass (g) at 35 days	13.2 \pm 1.0	12.5 \pm 1.0	11.7 \pm 0.9	8.65	2	<.001
Residual reproduction:						
Reproductive interval (days)	33.3 \pm 9.9	40.1 \pm 9.7	44.0 \pm 11.2	3.99	2	=.03
Clutch size	4.3 \pm 1.2	3.9 \pm 0.8	4.1 \pm 0.7	0.52	2	ns

clutches that failed to hatch. Most clutch failures were due to eggs not being fertilized. Average pre-laying interval was 7.9 days (sd 7.7, n=33), and 31.8 days (sd 14.8, n=9) for replacement clutches. Replacement clutches were assigned equally to the experimental categories: two to small broods, four to intermediate broods, and three to large broods.

Components of reproductive success of the experimental brood are also listed in Table 1. Mean body mass of the young at independence (day 35) decreased with experimental brood size. Young raised in small broods were significantly heavier than young from intermediate and large broods ($P < .05$). Mortality of young between manipulation and independence, and the number of young per brood that reached independence (day 35) increased with experimental brood size. Although nestling mortality was significantly higher in large broods in comparison with intermediate and small broods (test on arcsine transformed values, $P < .05$), still significantly more young reached independence in the large broods ($P < .05$). Despite differential nestling mortality rates during the experiment, we thus successfully manipulated current reproductive output, *i.e.*, number of young raised till independence, of the zebra finches.

Table 2. Variables, other than experimental brood size, explaining variation in post - experimental laying interval (days) in a multiple linear regression model. Variables that did not contribute significantly, are listed separately. Of these, the change in deviation (sum of squares) when the variable was added to the final model are given.

	(increase in) deviance	(increase in) df	P	coefficient	se
null model	4981.0	41			
final model	3611.2	39	<.01		
constant		1		35.58	2.10
pre-laying interval (days)	709.6	1	<.01	0.31	0.11
manipulation (∂N)	503.3	1	=.02	1.84	0.79
rejected terms:					
clutch size	230.9	1	>.10		
nestling mortality	131.1	1	>.10		

Subsequent reproduction

We examined only short-term effects of brood size on future reproduction of the parents: interval till the subsequent clutch, and clutch size of the subsequent clutch (Table 1). Size of the subsequent clutch did not vary with the previous, experimental brood size. Reproductive interval between the experimental clutch and the subsequent clutch increased with experimental brood size (Table 1). Parents raising a large brood significantly delayed the start of the next clutch when compared to parents of small broods, with on average 4.5 days per extra young that was raised till independence (Figure 1A). Reproductive interval in the intermediate group was intermediate, and did not differ significantly from either the small or the large group ($P < .05$). Reproductive interval was thus linearly dependent on experimental brood size (Interval = $28.4 + 2.7 \cdot \text{brood size}$, $r^2 = 0.17$, $P < .01$).

To identify whether the variation in reproductive interval was entirely due to experimental variation in brood size (no. of young added to or removed from the brood, ∂N) and experimental effects (no. of young that died after manipulation), or whether it was confounded by variation in pre-experimental components of brood size (pre-laying interval, clutch size), we combined all components of brood size in a multiple linear regression model of reproductive interval (Table 2). In addition to the main effect of experimental manipulation of brood size, pre-laying interval explained a significant part of the variation in reproductive interval. Neither clutch size, nor mortality of nestlings explained a significant part of the remaining variation in

reproductive interval (Table 2).

In experiment 2, new clutches were initiated within a few days after completion of

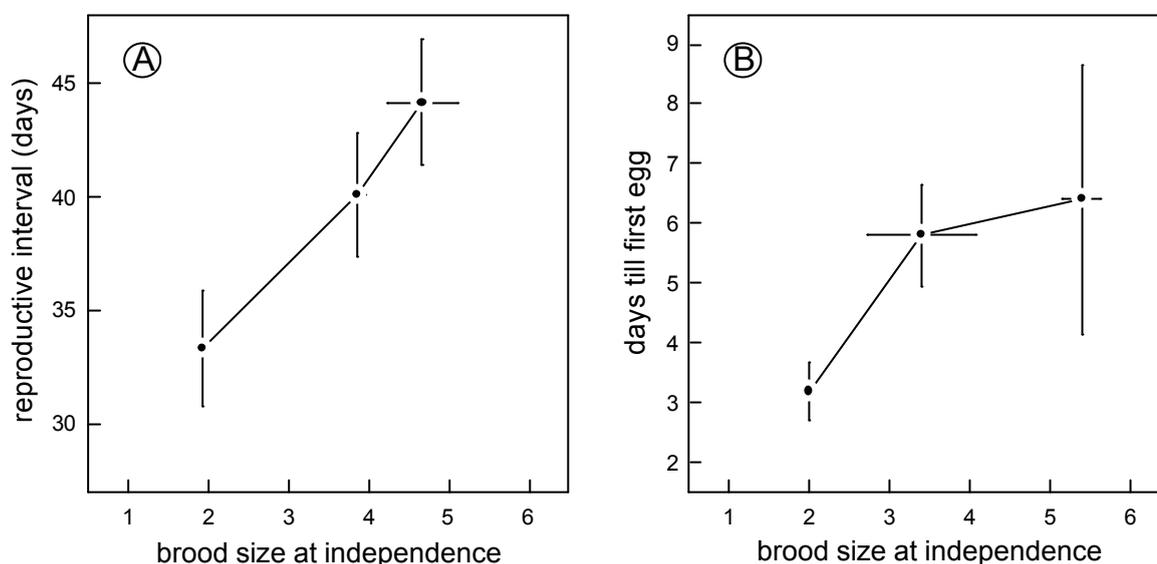


Figure 1. A. Reproductive interval (= days between hatching of experimental brood and first egg of subsequent brood) in relation to final brood size of the experimental brood. B. Days till first egg of subsequent brood after a forced interval of 50 days. Means and standard errors of both variables are depicted.

the forced interval of 50 days (Figure 1B). Parents of small broods initiated their next clutches after an additional 3.2 days (sd 1.6, $n=11$), parents of intermediate broods after 5.8 days (sd 1.9, $n=5$), and parents of large broods after 6.4 days (sd 5.0, $n=5$; nonparametric anova: $F_{2,18}=3.16$, one-tailed $P=.03$). Post-experimental clutch size did again not differ between the experimental categories (mean clutch size 4.1, sd 0.8; $F_{2,18}=0.63$, ns.). Thus, effects of experimentally manipulated brood sizes on subsequent reproduction appeared to be similar for both experiments. After 50 days, the effects of the experiments on reproductive interval were reduced, but still present.

DISCUSSION

Trade-off between current and subsequent reproduction

In a laboratory situation, zebra finches were able to raise a larger brood than the most frequent natural brood size under the same conditions, although large broods suffered from increased nestling mortality rates. Also, weight of the young at independence was negatively affected by brood size, with distinctively heavier young in small broods. Similar trade-offs have been demonstrated in natural populations of birds (Dijkstra *et al.* 1990; Stearns 1992). Natal brood size may affect potential quality of the young in terms of sexual attractiveness (De Kogel & Prijs 1995) or post-fledging survival (Tinbergen & Boerlijst 1990).

Raising a manipulated brood bore a time cost to the parent zebra finches. Nestling

mortality in large broods obviously counteracted experimental manipulation. As a result, the costs of brood size enlargement in absolute terms seem quite small. The relative effects of brood size enlargement on the timing of subsequent reproduction (3.9 days delay per extra young raised till independence, see Figure 1A) are rather similar to the effects of a reduction in brood size (3.6 days advance per young less).

Costs of reproduction to the parent may be of temporary nature, and thus recoverable, or they may be persistent. The observed change in reproductive interval represents only a time cost, and is thus temporary. After a forced interval of 50 days in experiment 2, the average delay of the subsequent clutch of pairs having raised a large experimental brood was much smaller (0.3 days per extra young), even compared to the average advance after raising an experimentally reduced brood (1.8 days per young less). This reduced relative time cost of the additional experiment indicates that the effects of experimental brood size on the parents soon faded away. The fact that we still found an effect of previous, experimental brood size on timing of the subsequent clutch after removal of first brood fledglings means that the effect can not be ascribed to interaction of first brood fledglings only. This is consistent with findings on Great Tits *Parus major* from Slagsvold (1984), who removed the experimental broods before fledging, and still found effects on the initiation of second clutches.

Persistent costs of reproduction may appear from an overall decrease in performance, either by a reduction in subsequent breeding performance (*e.g.*, clutch size: Gustafsson & Sutherland 1988; Gustafsson & Pärt 1990) or by a shortened life span that appears from, *e.g.*, altered survival rates (reviews in: Dijkstra *et al.* 1990; Stearns 1992). In this study, there was no evidence of a permanently decreased reproductive performance, because there were no effects on size of the post-experimental clutch.

Other work carried out in the laboratory on effects of experimental brood size of Ring Doves *Streptopelia risoria* also showed adjustment of reproductive interval (Ten Cate & Hilbers 1991). The main body of field data on this subject is available from work on the Great Tit, a facultative multiple breeder. In that species, as well as in several other species, manipulation of brood size has been reported to affect the subsequent reproductive interval, *i.e.*, clutch or breeding interval (*e.g.*, Smith, Källänder & Nilsson 1987; Tinbergen 1987). Thus, experimental manipulation of brood size carried out under controlled laboratory conditions yielded results that are similar to findings characteristic of brood size experiments in multiple brooded species carried out in the field.

Potential constraints on reproduction

It seems rather astonishing to find clear effects of brood size manipulations in *ad libitum* food conditions on both current reproductive success, and on subsequent parental breeding performance. Apparently, parent zebra finches raising young under laboratory conditions are still operating under constraints. This points at the causal interference of factors other than food availability in determining reproductive decisions. Of the current conditions, time and energy are two general factors that should be considered as potential constraints.

Brood size may affect parental time budgets through the amount of brooding required early in the nestling phase, and by the required amount of food that has to be collected and transported to the young. Therefore, available foraging time may have limited the amount of food that can be collected and transported to the young, and thereby restricted brood size. A time constraint did not seem to apply, because parents spent *c.* 30 % of their time on apparently inactive behaviour, *i.e.*, sitting (Chapter 5). The absence of ecological risk factors (*c.f.* Partridge 1992) in this laboratory experiment renders unlikely that an altered time budget itself caused the

observed delays in reproductive interval.

On the other hand, the average brood size observed in the laboratory may already be at the physiological limits of the parents' ability to care for young. If parental care is energetically costly even under laboratory conditions, maximum energy expenditure of parents may have limited brood size (Drent & Daan 1980). Parental energetics of zebra finches have been studied, and are reported elsewhere (Chapter 5). That study showed adjustment of female, but not male, daily energy expenditure (DEE) to experimental brood size. The same study also indicated a potential causal involvement of DEE in relation to costs of reproduction (Chapter 5).

ACKNOWLEDGEMENTS

Critical comments on earlier versions of the manuscript by S.Daan, J.Komdeur and S.Verhulst are most appreciated. We thank J.Prijs for valuable assistance in taking care of the animals and in data collection. The study was supported by NWO-BION grant 436.912P to S.Daan and J.M.Tinbergen. The experiments were carried out under license BG00891 from the University of Groningen.