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Clutch size and the cost of incubation in the Bengalese finch (*Lonchura striata* var. *domestica*)

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Summary. By measuring daily intake of food, we compared the cost of incubation for small and large clutches in adult Bengalese finches (*Lonchura striata* var. *domestica*). Natural clutches of captive finches were experimentally manipulated to produce two egg or six egg clutches. While incubating large clutches, parents ate significantly more food and took longer to hatch their first egg than did the same birds when provided with small clutches. This supports the hypothesis that the cost of incubation increases with clutch size. This cost should influence other energy allocation decisions in birds such as determination of clutch size and parental investment decisions.

Introduction

During reproduction, an animal faces an array of interrelated energy allocation decisions, such as how large a clutch to make or how strongly to defend an offspring. In theory, animals should make these decisions to maximize the rate of return on their investment of time or energy (Sargent and Gross 1985; Coleman et al. 1985). To understand how these decisions are made, it is therefore important to identify both the benefit and the cost of the investment into the behavior. The benefit of a behavior is the contribution to lifetime reproductive success. The cost of a behavior refers to the time or energy allocated to a behavior that could have been allocated elsewhere. This recognizes that time or energy, once allocated, is no longer available for other uses (Williams 1966). Of particular importance is how these costs change with changes in other life history parameters of the animal, for example with changes in offspring number or age of the parent.

In this paper we examine whether the cost of incubation increases with clutch size in birds. While the benefits of incubation are well known, few studies have addressed whether clutch size influences the cost. Does it cost a parent more to incubate a larger clutch than a smaller one? If the cost of incubation increases with clutch size, then it will probably influence other energy allocation decisions of birds such as determination of clutch size.

There is good reason to predict that the cost of incubation should increase with clutch size. Each egg requires an input of heat energy to maintain a constant temperature (excluding the situation in hot environments where the function of incubation is to remove excess heat from the eggs, e.g. Walsberg and Voss-Roberts 1983), thus the heat requirements of the clutch must increase with clutch size (see Kendeigh 1963; Mertens 1977). If heat production is an active process costing energy, the cost of incubation should increase with clutch size.

However, several researchers have suggested that incubating birds can supply a large fraction of the heat required for incubation from that produced as a by-product of their basal metabolism (e.g. King 1973). If this is true, then the cost of incubation should not increase with clutch size. Others have assumed that because the cost of incubation is small, it must not differ substantially for different clutch sizes (e.g. Walsberg 1978; Robertson and Biermann 1979).

To resolve this controversy, we examined the incubation behavior of captive Bengalese finches, *Lonchura striata* var. *domestica*. Previous studies of the cost of incubation have suffered from small

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Offprint requests to: R.M. Coleman, Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1 sample size or inadequately controlled experiments (e.g. Gessaman and Findell 1979; Haftorn and Reinertsen 1985). Our test involved *ad lib* feeding under controlled conditions and assumed that birds expending more energy would eat more. To control for the numerous variables of reproduction, we always compared birds against themselves using a manipulative paired experimental design. This design reduced many possible sources of variation. It is important to manipulate clutch size when examining the cost of incubation and other costs of reproduction (see Reznik 1985) rather than using natural variation because if we use the latter (e.g., Finch 1984) we do not know whether a difference in energy expenditure or intake is due to different clutch sizes or merely the result of a correlated factor. For example, parents which lay large clutches may be in better condition than other parents and thus have more energy to expend on incubation (De Steven 1980). By varying clutch size and measuring food consumption and time to hatch of the first egg, we were able to test whether the cost of incubation increases with larger clutches.

The Bengalese finch

The Bengalese finch is a domesticated descendent of the wild sharp-tailed munia (*L. striata acuticauda*) (Eisner 1957). Adults are approximately 12 cm long, and breed readily and consistently in captivity. The breeding biology of the Bengalese finch is described in Eisner (1957, 1960a, 1960b, 1961, 1963, 1969), Slater (1970) and Henry (1971). Wild birds build a spherical nest with a side entrance (Henry 1971), but captive birds will readily nest in commercially available finch nests. Clutch size ranges from 2–9 eggs, with 5–6 most frequent (Eisner 1960a; Henry 1971). Eggs are typically laid every day in the early morning, although females occasionally skip a day. Both parents incubate the eggs although neither sex develops a true brood patch (Eisner 1960b). The parents equally divide the time invested in incubating the clutch (Eisner 1961) and one of the parents is always on the nest during incubation (Eisner 1961, 1969; Slater 1970). During both the incubation and nestling stages, the parent birds can often be observed together on the nest, particularly at night (Eisner 1961, 1963).

Methods

The study was conducted in an enclosed 3.2 m by 2.7 m laboratory at the Vancouver Public Aquarium, starting February 1985. The windows were fitted with 2.5 cm thick styrofoam to block external light and to minimize temperature gradients inside the room. The temperature averaged 24° C over the course of the experiment. The room was lit with fluorescent lighting from 0700 h to 1700 h.

Using vent characteristics and behavioral observations to sex the birds, we set up fourteen pairs of finches in the lab. Each pair was housed in a wood and wire-mesh cage (34 x 30 x 30 cm), visually separated from all other pairs. Each cage was equiped with the following: cuttlebone, pan with granite grit, water dispenser, food dish, and two perches. The food dish was located high on the side of each cage to minimize the possibility of the birds defecating in the dish. On the 15th day after pairing, a 10 cm diameter wicker finch nest was added to the back left-hand corner of each cage. Every few days after that, small strips of paper toweling and hay were added to the bottoms of the cages to encourage nest building activity. Bedding was removed from some nests as soon as the birds began to lay in order to make nests as similar as possible in insulating ability.

Diet

From preliminary experiments, we chose the following diet both for its nutritional qualities and for its resistance to scattering by the finches.

7.5 ml	Dibasic Calcium Phosphate USP (Hydrate) powder
15 ml	Vionate vitamin supplement (Rich Health Inc., Irvine CA)
15 ml	yeast culture
60 ml	water
200 g	Country Grains Bread
500 g	hard-boiled egg, with shells
100 g	carrot
350 g	Finch Seed (Borden Mercantile, Victoria, B.C.)

These ingredients were thoroughly ground together in a food processor with the seed added last and mixed in slowly, so as not to break the husks. It was then bagged in 400 g portions and refrigerated for a few days ahead of use.

Manipulations

Data were collected on 121 consecutive days after the final diet had been selected, from March through June 1985.

Nests were examined in the morning. If an egg had been laid overnight, it was numbered with a pencil, weighed, and returned to the parents within a few minutes. Once a clutch was complete, it was either reduced to two eggs (Small) or reduced to or left at six eggs (Large). In one case a clutch of five eggs was supplemented with a sixth egg from another pair. Parents that incubated Large clutches in their first brood cycle were given Small clutches the next cycle and vice versa. Half the pairs incubated a Large clutch first, and half incubated a Small clutch first.

Data collection

We used the daily food intake of the birds as a measure of the cost of incubation. Every morning between 0700 h and 0800 h, the food dishes were removed and any remaining food was weighed on a balance (accurate to 0.001 g). The dishes were then cleaned and the new day's allotment of food (25 g) was returned to the birds. Food intake was calculated as the difference between the 25 g and the weight of the remaining food. Some of the food was not actually eaten, but was picked out of the dish and dropped to the bottom of the cage. The amount of "scattering" was not quantified, but appeared approximately equal for all pairs. Because both parents fed from the same dish, this method of evaluating food intake combines the intakes for both parents. In this experiment this is desirable because both parents incubate the clutch (Eisner 1960b), and determining their relative contributions was not central to this research.

Food intake was measured for the first 10 days after manipulations. Since Eisner (1969) found that incubation began with the second to last or last egg, we were assured that full incubation was established by the time the clutch was completed. Only the first 10 days of the typical 16 day incubation period were used, to minimize the effects of embryo heat production.

The parent birds were weighed at the start of the experiment, eight days before the first female began laying eggs. For some of the breeding pairs, the weights of the male and female were taken both before and after the 10-day measured incubation time. Molting was not observed in any of the birds during the experiment.

To be used in the analysis, a pair of finches had to lay two clutches of sufficient size to allow the manipulations. Of the 14 pairs of finches, 7 did so. Other pairs laid 15 other clutches but these could not be used for this experiment because on six occasions the parents did not incubate consistently and on nine occasions we did not obtain the corresponding data (i.e. Small or Large) to make up a paired set. Data from these other clutches were included in calculation of the average clutch size. Because we compared the same parents on each of two different clutch sizes, paired t-tests were used to compare samples, and the probability level for significant differences was set at 0.05.

Results

At the start of the experimental period, females weighed 14.8 g (SD = 0.9, $n = 6$) and males weighed 14.5 g (SD = 0.9, $n = 7$). The average clutch size was 5.3 eggs (SD = 1.7, $n = 29$), with clutches ranging from one to eight eggs. The average weight of a clutch was 6.15 g (SD = 0.44, $n = 26$) or 44.9% (SD = 12.0, $n = 24$) of each female's pre-reproductive body weight.

The mean duration of incubation to hatching of the first egg (using clutches which did not have any eggs added to them) was 15.7 days (SD = 1.7, $n = 15$) counting Day 1 as the day on which the second to last egg was laid. This agrees with Eisner (1960a). The eggs within a clutch usually hatched on the same day, with one or two hatching in the next couple of days.

Table 1. a Comparison of clutch size and weight in the two treatments before clutch size was manipulated. Two-tailed paired *t*-tests were employed to compare the two clutches laid by each pair of birds used in the experiment. **b** Comparison of parental food intake and time to hatch the first egg when given a Small clutch versus the same parents when given a Large clutch using one-tailed paired *t*-tests. Data are means ±SE

	Small	Large	t_6	*P*
a Before manipulations				
Number of eggs laid	6.0 ±0.4	6.3 ±0.4	1.00	0.36
Weight of clutch laid (g)	6.73±0.39	7.17±0.52	1.19	0.28
b After manipulations				
Food intake (g-day^{-1}-pair^{-1})	14.79±0.31	15.74±0.38	2.36	0.03
Time to hatch (days)	15.3 ±0.5	18.3 ±0.6	5.20[a]	0.01
Number hatched	1.6 ±0.3	2.7 ±0.6	1.33	0.12

[a] *df* = 3 due to missing data for some pairs

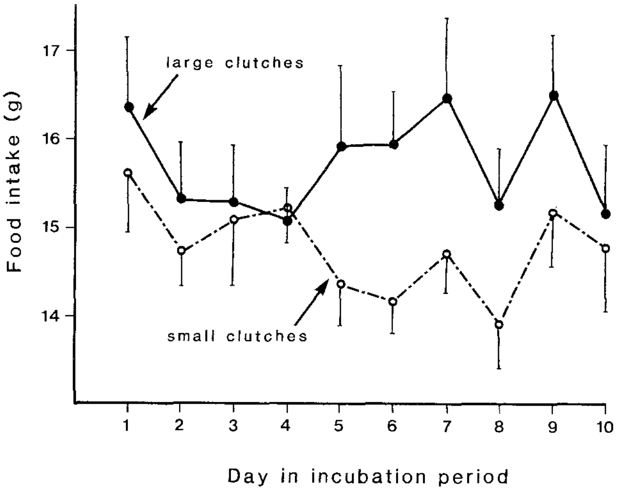

Fig. 1. The relationship between day after manipulation and food intake. Error bars indicate 1 SE

Before manipulation

For the two clutches laid by each female, there was no significant difference in the size or weight of the clutches before they were manipulated (Table 1a). In three cases, the pair laid exactly the same number of eggs in each of the two clutches, in the other four cases the two clutches differed by one egg. We concluded that the two clutches laid by each female were therefore equivalent before manipulations. Of these, three pairs were given their Large clutch first and four pairs incubated their Small clutch first.

After manipulation

Averaging food intake over the 10 days following manipulation, parents incubating Large clutches ate significantly more (6.5%) than when they were incubating Small clutches (Table 1b). For the four pairs on which we had hatching times for both clutch sizes, all took longer (an average of 3 days) to hatch their first egg of a Large clutch than the same parents when incubating Small clutches (Table 1 b).

There was no clear relationship between day in the incubation phase and food intake for either sample (Fig. 1). Similarly, the weights of the parents did not change significantly over this period, when considered either by sex or as a pair (unpaired-*t*-tests, males: $t_7 = 1.47$, $P = 0.19$; females: $t_7 = 0.29$, $P = 0.78$; pairs: $t_7 = 0.65$, $P = 0.54$; paired *t*-tests could not be used due to missing data).

Discussion

The results support the hypothesis that the cost of incubation increases with clutch size. This agrees with previous investigations of the cost of incubation in other avian species. Blagosklonov (1977) manipulated clutch size in pied flycatcher (*Ficedula hypoleuca*) nests and found that time spent incubating increased with clutch size. Jones (1987) switched eggs between two incubating female swallows (*Hirundo rustica*) and also found a significant increase in time spent incubating a larger clutch. Biebach (1981, 1984) manipulated clutch size for starlings (*Sturnus vulgaris*) and using a gas exchange technique found an increase in energy consumption when the birds incubated larger clutches. Similarly, Haftorn and Reinertsen (1985) found an 18% decrease in the oxygen consumption of a single blue tit (*Parus caeruleus*) when its clutch of 13 eggs was reduced to 8 eggs and Weathers (1985) found an increase in metabolic heat production by three canaries (*Serinus canaria*) when incubating four or five egg clutches versus two egg clutches.

By contrast, Brisbin (1969) failed to detect an increase in daily food intake of pairs of ring doves (*Streptopelia risoria*) incubating normal two-egg clutches versus those incubating experimentally reduced clutches of one egg. As Brisbin (1969) pointed out, however, the two eggs of the ring dove weigh less than 7% of the female's body weight. In our study, the average clutch of 5.3 eggs was 45% of the female's body weight. The proportionately smaller eggs of the ring dove would make clutch size-dependent effects more difficult to detect than in Bengalese finches.

Some researchers have compared the resting metabolism of incubating birds against that of non-incubating birds outside the nest (e.g. Grant and Whittow 1983), and suggested that this is evidence against the existence of a cost of incubation (Walsberg and King 1978a, 1978b). Others have compared an incubating bird with a non-incubating bird in the nest (e.g. El-Wailly 1966; Vleck 1981; Haftorn and Reinertsen 1985). These studies are difficult to interpret because the non-incubating bird is not equivalent to an incubating bird without eggs (Walsberg 1983), and furthermore, their approach addresses a different question than the one we are concerned with here. They are asking which of a number of possible behaviors costs less for a bird to do. We are asking, given that a bird has to incubate its eggs for them to hatch properly, will the number of eggs it is incubating affect the cost to the parent.

Although we attempted to control the experiment as tightly as possible, a few potential sources of error remain. The most likely sources of error are failure to control for either past energy expenditures or anticipated future energy expenditures in the two treatments. We were able to control the immediate past energy expenditures of each pair by using only parents that laid two clutches of similar size. Although all Bengalese finch eggs are not the same size (egg size tends to increase with laying sequence, Coleman and Whittall, in preparation), the increase is small relative to total egg size. Since we compared clutches of two eggs versus six eggs these differences should not adversely affect our experiment. It is possible, however, that differences in more distant past expenditures such as clutch size in the previous brood were affecting the results. Similarly, the results may be confounded if a parent incubating a large clutch eats more in anticipation of feeding a larger number of hatchlings. However, if parental anticipation is important, it is most likely to show up in the latter stages of incubation. Partly for this reason we measured food consumption for only the first part of the incubation period. It is noteworthy that Fig. 1 shows no increase in feeding rate as hatching approaches. It therefore remains to be shown that parents do anticipate feeding hatchlings, especially several days before hatching.

Hatching success was low compared to many species of birds, however, this result is consistent with other studies of the Bengalese finch, both in captivity (Eisner 1960a) and in the wild (Avery 1978).

An important assumption of cost of incubation studies (including this one) is the use of short-term correlates of lifetime reproductive success (e.g. time spent incubating, weight loss or food intake, time to hatch) as measures of the cost of incubation. For practical reasons, these experiments assume that changes in these short-term allocations will have predictable consequences on lifetime reproductive success. This assumption is probably correct; however, an ideal test for a cost of incubation would examine directly the effect of different clutch sizes on lifetime reproductive success.

Although our study was performed on captive birds, the cost of incubation is applicable to free-living birds as well, though it may be manifested in a different way than in captivity. In our experiment the cost of foraging was small. In the wild, where there may be a substantial cost to increased foraging, birds incubating larger clutches will probably lose more weight than birds on smaller clutches (e.g. Jones 1987), rather than compensating for the cost of incubation by increasing food intake.

How important is the cost of incubation? We found a difference of 6.5% between the food intake of parents incubating large clutches versus small clutches. It is possible that this difference would be intensified at lower temperatures (see Mertens 1987). Some studies have assumed that because the cost of feeding nestlings is large, the smaller cost of incubation is unimportant (e.g. Robertson and Biermann 1979; Walsberg 1978). In Lack's (1947) discussion of the evolution of clutch size, he suggested that a parent's ability to produce and raise offspring is limited by its ability to feed the nestlings, not by its ability to incubate the eggs. This fails to recognize that no matter how small the difference between incubation costs for large and small clutches, provided this difference is significant and consistent, then natural selection can act upon it, and it will be a component in the evolution of avian life history. In fact, Nur (1986) recently concluded from his extensive study of clutch size in the blue tit that parents do not appear to adjust their clutch size according to their ability to rear nestlings, rather, he suggests that incubation may be important. Yom-Tov and Hilborn (1981) concluded from their model of the energetic constraints on avian breeding that the first period of energetic stress occurred at the end of incubation and that this stress was independent of clutch size. However, their model assumed that the cost of incubation was independent of clutch size, in contrast to our findings. Their model may yield different results if a clutch-size dependent cost of incubation were incorporated.

Determining whether the cost of incubation increases with clutch size is important not only for our understanding of avian parental investment, but it has become vital to testing general models of parental investment theory. Recently, Sargent and Gross (1985) determined that to resolve the tradeoff between investment into present and future reproduction, a parent should invest according to the value of its brood relative to its expected future reproduction. To test this theory, they proposed an experimental design that compared parental willingness to invest under different experimental treatments. A key assumption of the design was that parents with larger clutches perform some behavior that causes them to invest at a higher rate than parents with smaller clutches. To apply the design to birds, Sargent and Gross suggested that the cost of incubation increases with clutch size. By contrast, in an earlier test of parental investment decision rules, Robertson and Biermann (1979) assumed that the cost of incubation does not increase with clutch size. In both cases the assumption is critical to interpretation of the results. The present study suggests that Robertson and Biermann (1979) were incorrect in their assumption. Because of this, their experimental design will not uncouple the correlation between past investment and brood size: parents with large broods will also have large past investment because of their expenditures on incubation. Thus we cannot determine whether it is past investment or brood size (expected future benefits) that is responsible for parental investment allocation decisions in their experiment. By contrast, the experimental design of Sargent and Gross (1985) can be used for testing general models of parental investment in birds, as has been done for fishes by Coleman et al. (1985).

Future research should determine the exact nature of the relationship between clutch size and the cost of incubation, i.e. does the cost accelerate, decelerate or increase linearly with increases in clutch size. Mertens' (1977) model of incubation predicts a deceleration of the curve at larger clutch sizes because eggs may partially insulate one another in large clutches. The only data that have examined this, those of Biebach (1984) for starlings, found a linear increase in parental energy expenditure with increases in clutch size. Biebach suggests that the need to re-warm eggs not in contact with the brood patch increases in larger clutches and may counteract the insulating effect in Mertens' model. Further tests will be needed to examine these factors to construct more realistic life history models of avian parental investment.

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References

Avery ML (1978) Nesting sharp-tailed munias, *Lonchura striata*, in Northern Province Wellesley, West Malaysia. Malayan Nat J 31:85–101

Biebach H (1981) Energetic costs of incubation on different clutch sizes in starlings (*Sturnus vulgaris*). Ardea 69:141–142

Biebach H (1984) Effect of clutch size and time of day on the energy expenditure of incubating starlings (*Sturnus vulgaris*). Physiol Zool 57:26–31

Blagosklonov KN (1977) Experimental analysis of the rhythm of incubation in the pied flycatcher (*Ficedula hypoleuca*). Sov J Ecol 8:340–344

Brisbin IL Jr (1969) Bioenergetics of the breeding cycle of the ring dove. Auk 86:54–74

Coleman RM, Gross MR, Sargent RC (1985) Parental investment decision rules: a test in bluegill sunfish. Behav Ecol Sociobiol 18:59–67

De Steven D (1980) Clutch size, breeding success, and parental survival in the tree swallow (*Iridoprocne bicolor*). Evolution 34:278–291

Eisner E (1957) The Bengalese finch. Avicult Mag 63:101–108

Eisner E (1960a) The biology of the Bengalese finch. Auk 77:271–287

Eisner E (1960b) The relationship of hormones to the reproductive behaviour of birds, referring especially to parental behaviour: a review. Anim Behav 8:155–179

Eisner E (1961) The behaviour of the Bengalese finch in the nest. Adrea 49:51–69

Eisner E (1963) A quantitative study of parental behaviour in the Bengalese finch. Behaviour 20:134–206

Eisner E (1969) The effect of hormone treatment upon the duration of incubation in the Bengalese finch. Behaviour 33:262–276

El-Wailly AJ (1966) Energy requirements for egg-laying and incubation in the zebra finch, *Taeniopygia castanotis*. Condor 68:582–594

Finch DM (1984) Parental expenditure of time and energy in the Abert's towee (*Pipilo aberti*). Auk 101:473–486

Gessaman JA, Findell PR (1979) Energy cost of incubation in the American kestrel. Comp Biochem Physiol [A] 63:57–62

Grant GS, Whittow GC (1983) Metabolic cost of incubation in the Laysan albatross and Bonin petrel. Comp Biochem Physiol [A] 74:77–82

Haftorn S, Reinertsen RE (1985) The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). Auk 102:470–478

Henry GM (1971) A guide to the birds of Ceylon, 2nd edn. Oxford University Press, London

Jones G (1987) Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balances. J Anim Ecol 56:229–245

Kendeigh SC (1963) Thermodynamics of incubation in the house wren, *Troglodytes aedon*. Proc 13th Internat Ornithol Congr 884–904

King JR (1973) Energetics of reproduction in birds. In: Farner DS (ed) Breeding biology of birds. National Academy of Sciences, Washington, pp 78–120

Lack D (1947) The significance of clutch size. Ibis 89:302–352

Mertens JAL (1977) The energy requirements for incubation in great tits, *Parus major* L. Ardea 65:184–196

Mertens JAL (1987) The influence of temperature on the energy reserves of female great tits during the breeding season. Ardea 75:73–80

Nur N (1986) Is clutch size variation in the blue tit (*Parus caeruleus*) adaptive? An experimental study. J Anim Ecol 55:983–999

Reznik DN (1985) Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267

Robertson RJ, Biermann GC (1979) Parental investment strategies determined by expected benefits. Z Tierpsychol 50:124–128

Sargent RC, Gross MR (1985) Parental investment decision rules and the Concorde fallacy. Behav Ecol Sociobiol 17:43–45

Slater PJP (1970) Nest building in the Bengalese finch. I. External factors affecting it and its relation to other behaviour early in the breeding cycle. Behaviour 36:300–319

Vleck CM (1981) Energetic cost of incubation in the zebra finch. Condor 83:229–237

Walsberg GE (1978) Brood size and the use of time and energy by the Phainopepla. Ecology 59:147–153

Walsberg GE (1983) Energetics of some prominent activites and events in the avian life cycle. In: Farner DS, King JR, Parkes KC (eds) Avian biology. vol VII. Academic Press, New York, pp 164–220

Walsberg GE, King JR (1978a) The heat budget of incubating mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. Physiol Zool 51:92–103

Walsberg GE, King JR (1978b) The energetic consequences of incubation for two passerine species. Auk 95:644–655

Walsberg GE, Voss-Roberts KA (1983) Incubation in desert-nesting doves: mechanisms for egg cooling. Physiol Zool 56:88–93

Weathers WW (1985) Energy cost of incubation in the canary. Comp Biochem Physiol [A] 81:411–413

Williams GC (1966) Natural selection, costs of reproduction and a refinement of Lack's principle. Am Nat 100:687–690

Yom-Tov Y, Hilborn R (1981) Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia (Berlin) 48:234–243