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The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents

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Understanding the selective pressures shaping the number of offspring per breeding event is a key area in the study of life-history strategies. However, in species with parental care, costs incurred in offspring production, rather than rearing, have been largely ignored in both theoretical and empirical studies until relatively recently. Furthermore, the few experimental studies that have manipulated production costs have not yet teased apart effects that operate via the parental phenotype from effects on the quality of the resulting young. To examine whether increased egg production influences parental brood rearing capacity independently of effects operating via egg quality, we experimentally increased egg production in gulls and then examined their capacity to rear a control clutch. We found that the capacity of parents to rear the control brood was substantially reduced solely as a consequence of having themselves produced one extra egg. The paradox that, in many species, parents apparently aim for fewer young per breeding event than the experimentally and theoretically demonstrated optimum, has partly arisen from the failure to take into account the constraints imposed by production costs.

Keywords: egg production; reproductive costs; trade-offs; gulls; clutch size; life history

1. INTRODUCTION

In species with parental care, it has generally been assumed that the fitness costs of reproduction are to be found mainly in the costs of provisioning offspring after birth or hatching (Martin 1987; Lessells 1991; Roff 1992; Stearns 1992). This assumption has directed the focus of empirical research and underpinned the development of theories predicting the optimum number of offspring per breeding event (Godfray *et al.* 1991; Roff 1992; Stearns 1992). Nonetheless, it is recognized as a dangerous assumption (Partridge & Harvey 1985; Clutton-Brock 1991). Since the relative costs of different components of reproduction have been little studied, the importance of phases of the breeding cycle prior to provisioning young in the evolution of reproductive rates is largely unknown (Clutton-Brock 1991; Monaghan & Nager 1997). The development of clutch-size theory has largely been driven by research on birds (Godfray *et al.* 1991), in which the experimental manipulations of reproductive costs have generally ignored all stages other than chick rearing. However, this body of theory predicts a larger optimal reproductive rate than is commonly observed (Stearns 1992; Roff 1992). This difference between theory and observation may at least partly arise from the failure to take into account costs incurred by the parents in the actual production of the young, such as in egg formation (Monaghan *et al.* 1995; Heaney & Monaghan 1995) and incubation (Heaney & Monaghan 1996). In the few cases where production stages have been manipulated, the effects have been confounded with those of rearing the resultant enlarged brood, and/or the experiments have not separated the effects on the young from those on the parents (reviewed in Monaghan & Nager 1997). It therefore remains unclear to what extent the parent's capacity to rear a brood is in itself impaired independently of any effects of increased egg production on the quality of young produced; the key experiment to separate the two has not hitherto been carried out. In order to do this, the experiment needs to be carefully designed, to (i) separate the effects of increased rearing from increased production costs, and (ii) separate the effects on parental performance from any effects of increased production on the quality of the eggs themselves.

In this study, we carried out such an experiment by examining the effect of increased egg production on the capacity of lesser black-backed gulls, *Larus fuscus*, to rear a control brood within the same breeding attempt. We hypothesized that an increase in the resources required for egg production would alter the subsequent pattern of resource allocation in the same breeding attempt, and thereby reduce the number of offspring reared.

2. MATERIALS AND METHODS

The experiment was carried out at a large colony of *ca.* 24 000 pairs of lesser black-backed gulls on Walney Island, Cumbria, UK, in 1997. The modal and maximum clutch size of the lesser black-backed gull is three (Cramp 1983). Egg production in a random sample of 30 pairs, nesting in the centre of the

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colony, was manipulated during the early part of the breeding season (26 April to 18 May; laying continued in the colony until June). Egg removal was used to stimulate the birds to lay one egg more than the normal clutch (Parsons 1976; Monaghan *et al.* 1995). All study nests were visited twice per day during egg laying and at 30 experimental nests the first egg was removed (under licence from English Nature) within 12 h of it having been laid. The majority (80%) of the manipulated group produced a further three eggs, the females thus laying a total of four rather than three eggs: these 24 pairs constituted the experimental group. The remaining six pairs, which laid three eggs in total (to obtain a clutch of two), comprised mainly birds which would have laid two-egg clutches had one egg not been removed. The overall frequency of two-egg clutches in a large sample of non-manipulated pairs, laying over the same period in the same area of the colony, was 25% (out of 346 monitored pairs, 297 laid three eggs and 49 laid two eggs); not significantly different from the ratio found in the experimental group ($\chi^2 = 0.36$, $p < 0.05$). Egg size has been found to be an indicator of adult quality in lesser black-backed gulls (Bolton 1991). The fact that in the experimental group the birds laying only three eggs in total were relatively low-quality individuals was further confirmed as their first laid egg (produced prior to any manipulation) tended to be small (mean 79.65 ± 1.68 g, $n = 6$) in comparison with those from birds that laid four eggs (mean 83.07 ± 0.86 g, $n = 24$, $t_{28} = 1.78$, $p = 0.085$). In order to ensure that the control group was comparable to the experimental group, only birds laying a clutch of three were included in the control group, which comprised 34 pairs. The control group was also subjected to the same level of disturbance as the experimental group. Neither the size (*t*-test, $t_{56} = 0.92$, $p > 0.05$), nor the laying date (Mann–Whitney *U*-test, $Z = 0.24$, $p > 0.05$) of the first egg differed between the experimental and control groups, indicating no variation in the average quality of pairs between the groups. The total mass of eggs produced by pairs in the experimental group was increased by an average of 34% (80.1 ± 2.07 g). While the manipulation very slightly delayed the seasonal timing of clutch completion by the experimental birds (2.75 ± 0.114 d), this was extremely minor in relation to the overall spread within the study birds (spread of laying 21 and 19 d, respectively, in the experimental and control groups, and spread of hatching 22 and 23 d, respectively). Consequently, this did not give rise to any significant seasonal shift between the groups (timings of hatchings were not significantly different, Mann–Whitney *U*-test, $Z = 1.65$, $p > 0.05$). Furthermore, there were neither seasonal changes in the clutch or egg size, nor in breeding performance, within the control group.

To examine the capacity of parents to rear a standard clutch, we used a cross-fostering procedure to exclude any effects of increased egg production on clutch quality itself. On the day experimental pairs completed laying their own clutches, their eggs were replaced with three 'average-sized' eggs taken from non-manipulated birds that had completed a clutch of three eggs on that day. Clutches of the 34 control pairs, nesting in the same area and laying three eggs during the same period, were also exchanged in an identical manner (i.e. with three 'average-sized' eggs from another clutch completed that same day). There was no difference between the size of the eggs reared by the experimental and control pairs (first-, second- and third-laid eggs, *t*-tests, $t_{56} < 1.08$, all $p > 0.05$). The experimental protocol also ensured that all experimental and control pairs incubated and reared a 'normal' clutch of three eggs that was not their own, and that the treatment groups only differed in the number of eggs the pairs had produced, four in the experimental group and three in the control group.

We examined the effect of increased egg production on parental condition by measuring female body mass and estimating pectoral muscle size (a known source of protein used by birds in forming eggs: Bolton *et al.* 1993; Houston *et al.* 1995), once laying was complete, and compared it with birds in the control group. This was carried out 2–3 d after clutch completion by capturing incubating birds at a sample of experimental and control nests, using standard walk-in nest traps. A series of body measurements were taken and the pectoral muscle lean dry mass was estimated using the pectoral profiling technique as developed for use on live birds and detailed in Bolton *et al.* (1991). A droplet of blood was collected (under Home Office licence) from the leg of each of the birds, using a sterile lancet. The sex of the birds was identified from red blood cell DNA, using two *CHD* genes (Griffiths *et al.* 1996). All birds were released within 15–20 min, and resumed incubation.

All nests were subjected to the same level of disturbance throughout and followed through incubation until the chicks were five weeks old and about to fledge. The number of chicks hatched, hatchling size (tarsus) and mass, and the number and body mass of chicks at fledging, were recorded.

3. RESULTS

At the end of egg laying, the body mass of the 10 captured experimental females was significantly less than that of the 11 control females (ANCOVA, comparison of body mass with body size as a covariate and treatment group as a factor; body size effect, $F_{1,18} = 14.88$, $p = 0.001$; treatment group effect, $F_{1,18} = 6.10$, $p = 0.024$, no significant interaction). The production of one egg more than the usual clutch of three resulted in the experimental females being, on average, 5.4% lighter (38.4 ± 15.5 g) than equivalent-sized control females. Following the production of four rather than three eggs, the depletion of the pectoral muscle was significantly greater in the experimental females (figure 1). Thus, females in the experimental group finished egg laying in poorer condition than they otherwise would have done. In a similar sample of males (eight experimental and nine controls), there was no evidence of any decline in the condition of the experimental birds.

We found no evidence that incubation performance was impaired following increased egg production: duration of incubation, hatching success, and size and mass of the newly hatched young did not significantly differ between the experimental and control groups (*t*-tests, $p > 0.17$ in all cases). Experimental pairs subsequently reared, on average, over 30% fewer chicks than control pairs (figure 2*a*), and a significantly greater proportion failed to rear any young at all (42% of the 24 experimentals compared with 12% of the 34 controls; $\chi^2 = 4.3$, 1 d.f., $p < 0.05$). The reduced young production in the experimental group resulted from an increase in post-hatching chick mortality. Dead chicks were generally found on the parental territory in an emaciated condition; predation rate on the young was low (less than 4% of the chicks disappeared), and did not differ significantly between the two groups (χ^2-test, $p > 0.5$). Surviving young in the experimental group weighed significantly less at fledging than the equivalent young of control pairs; this was

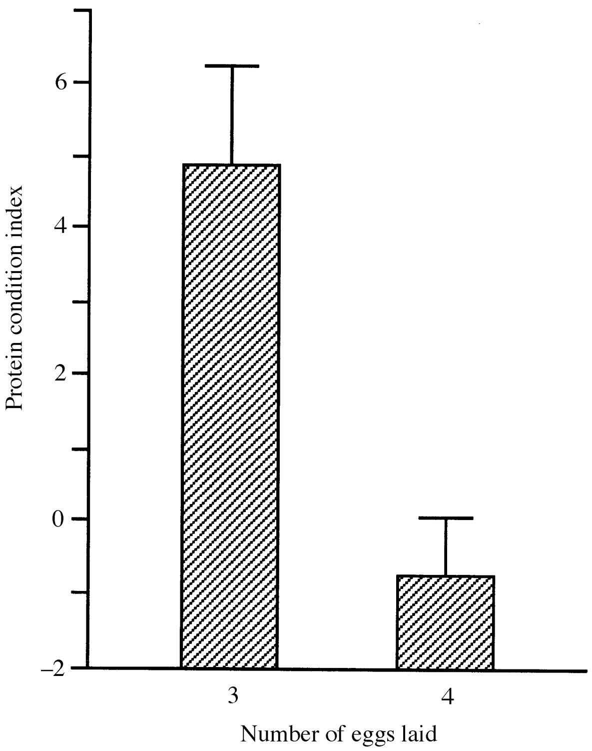

Figure 1. The relative condition of the pectoral muscle at the end of laying for 10 females that had laid four eggs in comparison with 11 control females that laid the normal clutch of three. Shown are the average deviations of each group relative to the expected values of pectoral muscle lean dry weight (PMLDW) produced in a covariance analysis. PMLDW increased with body size ($F_{1,18}=7.95, p=0.011$) but, for a standard body size, experimental birds had smaller pectoral muscles than control birds (1.06 ± 0.395 g, 5.3% less; $F_{1,18}=7.24, p=0.015$. No significant interaction, $p>0.05$).

particularly marked in pairs fledging one and two young, which were, on average, 16% and 22% lighter at this stage than the young in control broods (figure 2*b*). Such relatively light fledging mass is likely to translate into poor post-fledging survival of the offspring (Magrath 1991).

4. DISCUSSION

In the control group, 57% of eggs gave rise to fledged chicks, which represents a high breeding success for this species (Cramp 1983). Thus, our study procedures did not in themselves have a detrimental effect on breeding performance. However, as predicted, increased egg production in the experimental group came at a price: the laying of one additional egg substantially reduced the capacity of parents to rear a normal-sized brood from cross-fostered control eggs. This lowered breeding performance occurred independently of any effect of increased egg production on egg quality itself, which may also be reduced when extra eggs are laid (Monaghan *et al.* 1995). In this study, at least 80% of pairs were capable of laying four eggs. Six pairs were excluded from the experimental group since they only laid three eggs in total, presumably having intended to lay a clutch of two. It is possible that amongst these six were one or two pairs that, while intending to lay a clutch of three, could not replace the

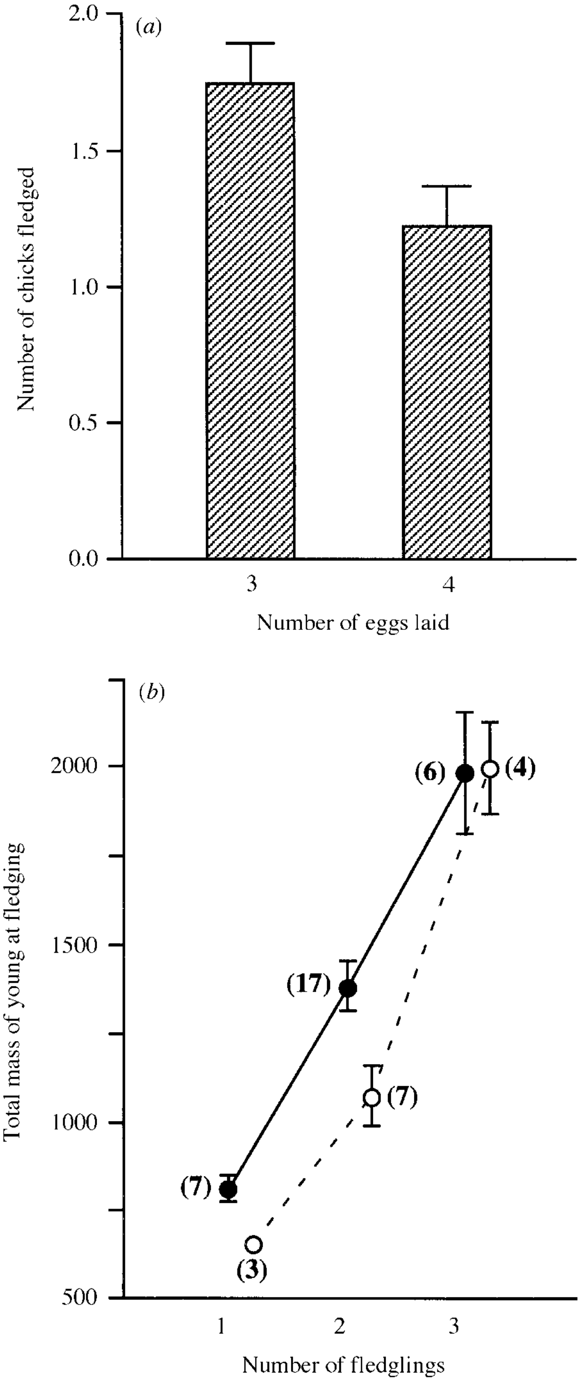

Figure 2. (*a*) The number of fledged young in relation to the number of eggs laid. All pairs started with a foster clutch of three 'normal' eggs. A generalized linear model with binomial error distribution (0, 1, 2, or 3 young fledged) was fitted to the data. Adding a factor for the treatment group (experimentally increased egg production or control) explained a significant part of the variation $\chi^2=5.24$, 1 d.f., $p<0.025$). There was no seasonal trend in fledgling production over the observation period (effect of fledging date: $\chi^2=0.31$, 1 d.f., n.s.). (*b*) Mean total brood mass (g) (±s.e.) at fledging of experimental pairs incurring increased egg production demands (open symbols), and control pairs (closed symbols). Young of experimental pairs were significantly lighter at fledging than young from control nests, independent of brood size (ANOVA: effect of brood size, $F_{1,41}=53.74, p<0.001$; effect of treatment, $F_{1,41}=4.91, p=0.032$; interaction term, $F_{2,38}=1.23, p>0.05$). Fledging date had no effect on the body mass of the chicks. Sample sizes for broods of one, two and three fledglings are 7, 17 and 6 for control pairs and 3, 7 and 4 for experimental pairs, respectively.

removed egg, and thus only laid the remaining two eggs of their intended three-egg clutch. This could have resulted in a very slight bias in the experimental group towards relatively high-quality females. If so, the very marked depression of average reproductive performance, compared to the controls, may, in fact, be a slight underestimate of the magnitude of the effect.

Our data suggest that the parental effect is mediated through the negative influence of increased egg production on female condition. The fact that this influences breeding performance during the subsequent chick-rearing period, several weeks later, suggests that the capacity of the parents to compensate for increased demands incurred during egg laying is limited, and that the relatively poor condition of the female at the end of laying has reduced her ability to obtain resources and/or to allocate these to the offspring. Although only one extra egg was laid, this does represent an increase of one-third of the normal clutch. Gull eggs are produced from a combination of stored reserves and dietary intake (Bolton *et al.* 1992, 1993). Mobilization of material from the pectoral muscle during egg production may in itself be a relatively costly process (Suarez 1996), and the recovery of depleted pectoral muscle protein during incubation appears to be slow (Houston *et al.* 1983). This will be influenced by the time constraints on foraging that incubation and chick provisioning impose, coupled with any negative effects of reduced pectoral muscle mass on flight (Marden 1987), and thereby foraging performance. It is also possible that a shortage of a specific nutrient, required for both egg production and somatic maintenance, is involved. Parental condition has an important influence on reproductive decisions in iteroparous breeders such as gulls (Clutton-Brock 1991; Monaghan *et al.* 1992; Weimerskirch *et al.* 1997), and it is interesting to note that the fledging mass of the young in the few experimental pairs that reared three chicks appears not to have been reduced (figure 2*b*). This suggests that the capacity to withstand the demands of increased egg production may be state-dependent (McNamara & Houston 1996), thereby varying with adult quality. It is perhaps surprising that the males in the experimental pairs, whose condition does not appear to have been affected by the increased egg production, did not compensate for the reduced performance of their mates.

Previous experiments on Laridae have shown that parents can rear more than the maximum natural brood size when extra chicks are placed in the nest (Harris & Plumb 1965; Haymes & Morris 1977; Winkler 1985), as is generally the case in birds (Lindén & Møller 1989). Gulls clearly have the physiological capacity to produce more eggs per breeding event than they actually do; most pairs can produce at least one extra egg, and some many more than this (Parsons 1976). Why then do they not produce a larger clutch? In trying to explain such perplexing observations, the focus of attention in experimental studies has generally been on inter-brood and intergenerational effects (Partridge & Harvey 1985; Roff 1992; Stearns 1992; Vander Werf 1992). Reduced subsequent survival or fecundity of parents or their chicks following post-hatching brood enlargement, clearly cannot account for the predominance of three-egg clutches in gulls. The growth and survival of chicks in broods enlarged after hatching are generally good (Harris & Plumb 1965; Haymes & Morris 1977; Winkler 1985). Where the effects of brood enlargement on subsequent parental survival have been found, they are very small and insufficient to explain the almost total absence of natural four-chick broods (Reid 1987). However, when the full egg laying, incubation, and chick-rearing demands are included and combined with the possible effects on the quality of additional eggs, the capacity to rear an enlarged brood can be negated (Heaney & Monaghan 1996). Intra-brood trade-offs between production and rearing costs are likely to be much more important than has hitherto been realized. As shown here, simply producing one more egg in itself makes parents less able to rear a normal brood, demonstrating that in order to maximize reproductive success, parents must optimize the allocation of resources across all components of reproduction. Such intra-brood trade-offs must therefore be taken into account in future theoretical and empirical investigations of reproductive trade-offs. Their exclusion in the evaluation of optimal offspring number may explain why observed clutch size generally seems to be less than the predicted optimum (Lindén & Møller 1989; Roff 1992; Stearns 1992; Van der Werf 1992).

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