

Why don't birds lay more eggs?

Pat Monaghan and Ruedi G. Nager

Elucidation of the relationship between reproductive effort and parental fitness remains a major, if elusive, goal of life-history theory. A central factor is the concept of trade-offs in the allocation of effort within and, in iteroparous species, between breeding attempts. Much of the work in this field has centred on birds, which offer the advantages of having three clearly recognized breeding phases (egg production, incubation and rearing chicks to independence) and of generally breeding more than once.

Theoretical and empirical studies have been strongly influenced by the early work of the ornithologist David Lack, who suggested that avian clutch size has been shaped by natural selection to correspond to the number of young that the parents can successfully provide with food¹. It has

since been found that the most common clutch size in unmanipulated avian populations is often less than that which gives rise to the most fledglings. That this effect operates at the individual level, rather than being a consequence of the elevated performance of a few, high-quality birds, is clearly demonstrated by the fact that random samples of parents given experimentally enlarged broods usually raise more young to fledging than do control pairs^{2,3}. These findings are contrary to Lack's predictions. So, if birds can rear more young than the number of eggs they lay, why don't they lay more eggs? This has been addressed to some extent by modifying Lack's hypothesis to encompass the concept of trade-offs^{2,4,5}. It is widely recognized that simply counting the number of young fledged in a single breeding attempt does not represent an adequate measure of parental fitness^{4,5}. Parental survival and future reproductive performance, as well as offspring recruitment rate and subsequent productivity, may be reduced as a result of increased parental effort in rearing the young to independence^{2,4,5}. In some bird species, there is good evidence that survival or subsequent reproductive performance is reduced in pairs given experimentally enlarged broods, as for example in kestrels (*Falco tinnunculus*)⁶; in others, no such effects are apparent⁷. Reduced offspring quality and recruitment rate have also been reported in some studies^{4,5,8}. However, there has been no assessment of the quantitative impact of any such trade-offs in accounting for the observed discrepancies between the most productive and the most common clutch sizes⁹. Furthermore, about 30% of studies have failed to find any evidence of effects on the fitness of parents or offspring after brood enlargement⁴.

The possibility that phases other than chick rearing may also play a part in limiting clutch size has only occasionally been mentioned¹⁰⁻¹². Studies of the breeding strategies of migratory wildfowl generally recognize that limitations can operate at the egg-laying stage¹³, but the overriding emphasis

Fifty years ago David Lack put forward a key hypothesis in life-history theory: that avian clutch size is ultimately determined by the number of young that parents can provide with food. Since then, a plethora of brood manipulations has shown that birds can rear more young than the number of eggs they lay, and prompted a search for negative effects of increased effort on future reproduction. However, recent studies have shown that the demands of laying and incubating eggs, generally omitted from experiments, could affect parental fitness. Lack's hypothesis, and the tests of its validity, need to be extended to encompass the full demands of producing and rearing the brood.

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in studies of optimal clutch size in birds has continued to be on the presumed all-important chick-rearing phase. Almost all experimental manipulations of reproductive effort have been carried out after the young hatch (Table 1). In this article we draw attention to the growing body of evidence that the amount of effort allocated to egg production and incubation may have an important role in determining parental fitness; this consideration must be taken into account in fully evaluating the evidence in support of Lack's hypothesis.

Egg production

Birds often replace eggs that are lost during laying, and lay repeat clutches if they lose the entire clutch after clutch completion. For this reason, Lack assumed that egg production was inexpensive and that many birds

could easily lay larger clutches than they actually do¹. Measurements of the energy content of the egg-production machinery and of the eggs themselves appear to corroborate this assumption. Peak daily energy expenditure during egg production depends on egg size and laying pattern. While the daily growth rate of the egg follicle in the female ovary affects the level of peak energy expenditure, clutch size influences only the number of days over which this peak needs to be sustained¹⁴.

On the basis of egg composition data, estimates of the extra energy required for egg production range from 13 to 41% of basal metabolic rate (BMR) in passerines to more than 200% of BMR in waterfowl¹⁴. These estimates, however, are based only on analysis of the end product. They do not include the energy cost of acquiring and manufacturing the material^{14,15}, which has not been quantified in wild birds. The effort required to obtain the necessary resources may be considerable; birds usually form their eggs while both ambient temperatures and food availability are lower than during chick rearing and, as the nutrient balance in eggs generally differs from that in the natural diet¹⁶, more demanding foraging strategies may be required. Furthermore, in modelling the energetic requirements of egg production, a biosynthetic efficiency of around 75% has generally been assumed¹⁴. Estimates from laying hens (*Gallus gallus*) indicate that the true value may be much lower (30–37.5%, Ref. 17) – another reason why the energy expenditure associated with egg production could be much higher than has been suggested.

The daily energy expenditure of laying barn swallows (*Hirundo rustica*) has recently been measured directly, using doubly labelled water¹⁸. The daily accumulation of material into the egg accounted for only 4.5–4.9% of their total daily energy expenditure, apparently confirming earlier estimates of a relatively small energy demand for egg synthesis in passerines. However, the total daily energy expenditure during egg formation (averaging 370% of BMR) did not differ

significantly from that in chick rearing, which averaged 380% of BMR. Therefore to gain the material to produce eggs, the female barn swallows had to work just as hard as they did later in the season to provide food for their chicks.

That egg production is an expensive process is corroborated by many correlative and experimental studies in wild birds showing that it is closely linked to variation in food supply. Supplementary feeding affects clutch and egg size, timing of laying and laying intervals^{12,19,20}. Manipulation of energy demands via environmental temperature can alter egg size and the pattern of laying^{21,22}. The results of such experiments depend on both local food availability and on the quality of any supplement provided²³, with the availability of energy²¹, protein^{24,25} and calcium²⁶ all playing a part.

Incubation

It has often been assumed that the incubation period is a time of reduced energy expenditure, because of the relatively low level of parental activity and the low thermoregulatory demands that result from the favourable microclimate provided by the nest²⁷. However, the extent to which birds must expend additional energy in keeping their eggs warm is strongly influenced by the thermal environment. Early attempts to quantify incubation demands used calculations based on measurements that were made in thermoneutral conditions and thereby gave a misleading impression. Measurements made in more realistic temperatures below the thermoneutral zone show that metabolic rate in passerine birds increases by 19–50% above that in non-incubating controls²⁷. While body size, clutch size and incubation pattern all have important effects, the overriding conclusion is that the time and energy demands of incubation are far from trivial²⁷. For incubating birds, any energy savings resulting from reduced activity may be offset by the fact that nest attendance during incubation will markedly reduce the time available for foraging, even in biparental incubators, at a time when food supplies may be relatively low.

In many species the incubating partner, usually the female, has to incubate the eggs unassisted and must divide energy and time between the mutually exclusive behaviours of supplying heat to the eggs and foraging for self-maintenance. Furthermore, when uniparental incubators return from foraging trips the eggs will usually have cooled to some degree and need to be reheated, which considerably increases the energy expenditure of the incubating bird²⁷. Direct measurements of the energy consumption of unassisted incubators have revealed levels of energy expenditure as high as those in birds feeding young, and the energy requirements increase with increasing clutch size^{18,27–29}. In species where parents share incubation duties, or where males deliver most or all of the food required by the incubating female, eggs are covered almost continuously and reheating demands are low. Nonetheless, female energy expenditure during incubation in these species is increased over that of non-incubating females by 20–30% (Ref. 27). While such increases may seem relatively small, sustaining them over the whole incubation period may be particularly demanding. The consequences for males of the increased energy demands they may incur in providing food for their incubating partner have been little studied.

The demands of incubation are further demonstrated by manipulative studies. Reduction in the efficiency of incubation after an experimental increase in the number of eggs incubated has been reported in several species, including a prolonged incubation period^{29–32}, reduced hatching success^{30,33} and increased hatching asynchrony²⁹. Similarly, manipulation of food availability, through either removal of

the courtship-feeding partner³⁴ or supplementary feeding of the incubating bird³⁵, affects incubation performance.

Fitness consequences

There is considerable evidence that both egg production and incubation in birds are demanding processes in terms of energy, time and nutrients. What are the consequences of increasing these demands independently of those of chick rearing, and would their inclusion in brood enlargement studies influence the outcome? As is evident from Table 1, few experimental manipulations have addressed these issues.

In several studies, eggs have been added to a clutch to assess whether birds are able to incubate more eggs than they have produced. However, the independent consequences for the chick-rearing capacity of the parents of the increased incubation demand has, in most cases, either not been examined, or confounded with the costs of rearing the enlarged brood that resulted from the addition of eggs. To identify the effects of increased incubation effort on later stages in the reproductive cycle, we need to compare individuals that have experienced different incubation demands, but expended the same chick-rearing effort. This has so far been achieved in two ways:

(1) The breeding success of parents given additional eggs early in incubation has been compared with that of parents given the same number of additional young soon after hatching. Such data are available from three studies: gannets (*Sula bassana*, data extracted from Nelson's work)³⁶, collared flycatchers (*Ficedula albicollis*)³⁰ and common terns (*Sterna hirundo*)³⁷. In all three cases parents in which both incubation and chick-rearing demands were increased tended to fledge fewer young than parents that had only their chick-rearing effort increased (Box 1).

(2) The increased demand has been confined to the incubation period. This has been specifically addressed in two studies. In common terns (biparental incubators), birds laying two eggs were given an extra egg to incubate, and the extra egg was removed just before hatching. Thus both the experimental and control birds reared two chicks, and chicks of parents that had incurred the increased incubation demand grew less well³⁹. Incubation effort of barnacle geese (*Branta leucopsis*, uniparental incubators) was experimentally increased by prolonging the incubation period⁴⁰. This study found that increased incubation effort affected the body condition of the incubating female at hatching. The effect of this manipulation on breeding success was not examined, but return rate and arrival date the following season were not affected. It would have been interesting in the latter study to distinguish between experimental

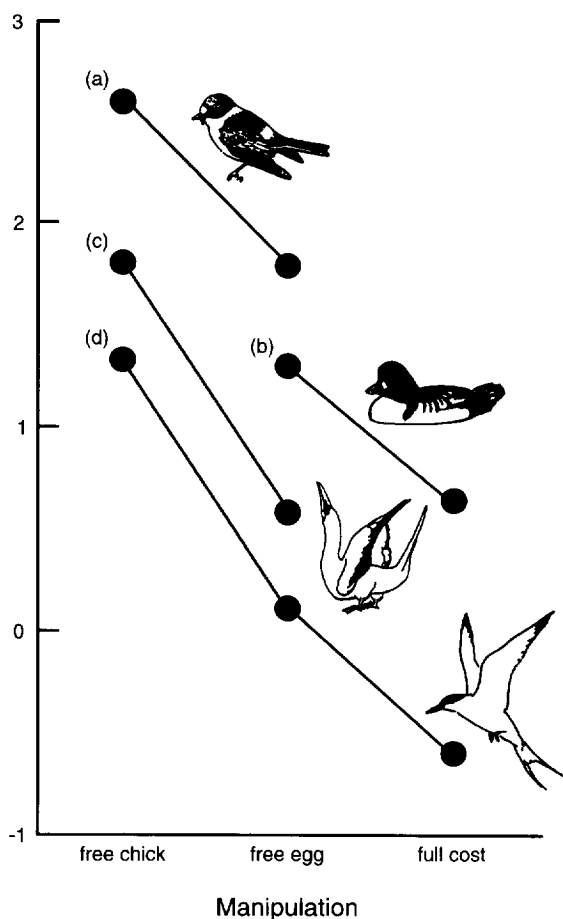
Table 1. Numbers of experiments on birds in which a brood manipulation was effected at different stages of the breeding cycle^a

	Manipulation		
	No. chicks after hatching	No. eggs during incubation	No. eggs laid per clutch
Number of studies	78 (80.4%)	24 (25.7%)	3 (3.1%)

^aWe have found 97 studies that manipulated reproductive effort in at least one breeding phase; a few manipulated effort in two or more phases. Independent manipulations of breeding stages were generally not carried out, so effects operating at different stages may have been confounded in some studies (but see Box 1). Source: Ref. 4, updated by the authors.

Box 1. Experimental manipulations of egg production and incubation effort

The figure shows the effects on fledgling production of experimental increases in reproductive effort at different stages in the breeding cycle. The difference in fledgling production between parents whose reproductive effort was experimentally increased and unmanipulated control birds is expressed in units of standard deviation on the vertical axis. The experiments either added chicks after hatching (free chick), added eggs during incubation (free egg), or used egg removal to induce laying females to produce more eggs (full cost). (a) Comparison between effects of two free eggs and two free chicks in collared flycatchers³⁰. (b) Comparison between effects of free eggs and full cost in common goldeneye³⁸. While the differences were not statistically significant, in both studies the original clutch size of the parents was not controlled, nor were differences in the hatching success between treatment groups. The former will be linked to parental quality, which may affect the outcome, and the latter makes it difficult to separate effects occurring during the incubation and chick-rearing stages. (c) Comparison between free chick and free egg in gannets (extracted from Ref. 36). (d) Comparison between free chick, free egg and full cost in common terns³⁷. In these latter two cases all birds laid the same number of eggs (one and two eggs, respectively), and only birds that hatched all of the incubated eggs were included in the analysis. All four studies show a similar trend of decreasing fledgling production with increasing number of phases of the breeding cycle manipulated.



pairs that lost a significant part of their clutch during the prolonged incubation (and thus had a possibly compensatory reduction in demands during the chick-rearing phase), and pairs that paid the full energy cost of the increased incubation demand and raising the normal brood.

While numerous egg-removal experiments have shown that birds can often lay more eggs than they usually do, only three studies have followed the fate of these experimental eggs and parents^{37,38,41}. When lesser black-backed gulls (*Larus fuscus*) were induced (by egg removal) to lay a fourth egg to complete their normal three-egg clutch, the fourth-laid egg was much less likely to give rise to a fledged chick⁴¹. In contrast, goldeneye (*Bucephala clangula*) females

experimentally induced to lay three extra eggs in addition to their normal clutch of, on average, nine eggs showed no significant adverse effects on the outcome of this breeding attempt or on their return rate the next year³⁸.

However, it should be borne in mind that the extent to which increased demands translate into fitness costs may well be dependent on the state or quality of the parent⁴². Negative effects are most likely to be manifest in poorer quality individuals, as has been found in a number of studies^{39,42}. In the goldeneye study mentioned above³⁸, as is the case in many such experiments, birds that laid a range of clutch sizes and therefore were possibly of differing quality were pooled in the analysis. It would be interesting to examine the effects of such a manipulation on different categories of bird.

In the third experiment on the effects of increased egg laying, which involved common terns, only individuals of relatively poor quality (those laying a clutch of two eggs, rather than the modal clutch of three) were manipulated; birds that were made to lay an additional egg, and thus had increased egg-laying, incubation and rearing demands, were less efficient at chick provisioning and fledged significantly fewer young than birds that were given an additional chick just after hatching³⁷. The last experiment highlights how the demands of the earlier phases of reproduction can significantly alter the outcome of a brood-enlargement experiment, a trend that is clearly apparent in the few other studies where it is possible to examine such an effect (Box 1).

There is evidence that investment by birds of extra effort in egg production and incubation can adversely affect parental performance in chick-rearing in the same breeding attempt. Mechanisms whereby such an effect could operate are outlined briefly in Box 2. There is also evidence that the number of high-quality eggs or hatchlings that females can produce may be subject to physiological constraints (Box 2).

Conclusions

Existing estimates of the costs of reproduction in birds appear to have underestimated the true costs of raising a larger clutch, because experiments have generally not included phases other than chick rearing. Empirical investigations of the fitness consequences of increases in these early costs are few, and there is a clear need for more, carefully controlled, experimental work in species that differ in the allocation of resources between the breeding phases. For example, we have mentioned that results for individuals of different quality are often pooled. In addition, the experimental protocol in many studies is such that all pairs are subjected to the same absolute level of egg or brood manipulation, usually addition of one or two eggs or chicks; thus, individuals of different quality may experience different proportional changes in demand. Neither has the timing of manipulation always been carefully controlled, so that birds that have incurred variable amounts of incubation and chick rearing costs may have been included within the same experimental groups. The diverse methodologies employed to date may have made it difficult to pick up consistent effects. Another factor that needs to be taken into account is background food levels²⁶, as the extent to which individuals can cope with increased demands will vary with the ease with which they can obtain food.

Five main areas in particular need further attention.

- (1) We need experiments that compare the effects of independent increases in the demands of each of the three stages of the breeding period – experiments that make separate increases in egg production, incubation or chick rearing demands.

Box 2. Possible mechanisms whereby increased early costs could adversely affect breeding performance

Increased effort in egg production and incubation could adversely affect subsequent performance in the same or in a later breeding cycle, via direct effects on the parents or indirectly on the eggs or hatchlings. Birds use stored protein to form eggs^{14,43} and show an increased depletion with increasing egg production^{13,44}. As most of the protein reserve is in the flight muscles⁴³, depletion of these muscles may reduce the female's flight performance and thereby her foraging efficiency and predator avoidance. A loss of condition at an early stage in the breeding cycle may also affect the level of effort a breeding bird is willing or able to invest at later stages⁴⁵, as parental body condition may be maintained at the expense of the condition of the young⁴⁶. Other, more subtle, effects may also be important. Increased egg production is associated with a higher incidence of disease in great tits, presumably reflecting a depressed immune function⁴⁷. The delay of only a few days needed to produce and incubate a larger clutch can have important consequences on the recruitment probabilities of the young⁸. Disrupted or protracted incubation might negatively affect the quality of the young at hatching, as a result of dehydration or resource depletion, and thereby jeopardize their survival. The egg-laying capacity of females may be subject to physiological constraints, such that producing more eggs may be at the direct expense of egg or hatchling quality, which negatively affects breeding success⁴¹.

(2) We need experiments that examine the cumulative effects of increased costs at each stage, as there may be interesting interactive effects – experiments that increase egg production only, egg production and incubation, and egg production, incubation and chick-rearing demands.

(3) We need to examine the effects of increased energy demands on individuals of different quality, as the capacity to compensate for costs at different stages may be dependent on the state of the individual.

(4) Cross-fostering studies are needed to distinguish between effects on reproductive performance that are mediated through effects on egg or chick quality and those mediated through effects on the parents themselves.

(5) More-detailed investigations of proximate mechanisms are required, to understand both the ways in which subsequent parental performance can be impaired by an increase in early costs, and how physiological constraints might influence the costs and benefits of increased offspring production. Physiological manipulations, for example of ovarian follicle number or female endocrine state⁴⁸, may be a useful addition to the experimental protocols. Providing links between proximate and ultimate factors in this way is likely to be an important future development in the study of life-history strategies.

Obviously, factors other than the parental capacity to produce and provision the brood may influence clutch size. For example, we do not know how the role of predation risk influences reproductive costs and interacts with food availability⁴⁹. However, three things are clear. First, the rearing of extra chicks given at hatching does not fully mimic the effort required to produce additional young, so the evidence that parents could rear an enlarged brood is equivocal. Second, Lack's hypothesis needs further revision to encompass the whole breeding period; that is, avian clutch size is tailored to the number of young that parents can successfully lay, incubate and rear to independence. Third, further theoretical and empirical work is needed to evaluate the relative importance of the early phases of reproduction in determining optimal clutch size.

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References

- Lack, D. (1947) **The significance of clutch size**, *Ibis* 89, 302–352
- Lindén, M. and Møller, A.P. (1989) **Cost of reproduction and covariation of life history traits in birds**, *Trends Ecol. Evol.* 4, 367–371
- Vander Werf, E. (1992) **Lack's clutch size hypothesis: an examination of the evidence using meta-analysis**, *Ecology* 73, 1699–1705
- Stearns, S.C. (1992) *The Evolution of Life Histories*, Oxford University Press
- Roff, D.A. (1992) *The Evolution of Life Histories*, Chapman & Hall
- Daan, S., Deerenberg, C. and Dijkstra, C. (1996) **Increased daily work precipitates natural death in the kestrel**, *J. Anim. Ecol.* 65, 539–544
- Orell, M. *et al.* (1996) **Brood size manipulations within the natural range did not reveal intergenerational cost of reproduction in willow tit *Parus montanus***, *Ibis* 138, 630–637
- Pettifor, R.A., Perrins, C.M. and McCleery, R.H. (1988) **Individual optimization of clutch size in great tits**, *Nature* 336, 160–162
- Hochachka, W. (1992) **How much should reproduction cost?** *Behav. Ecol.* 3, 42–52
- Partridge, L. (1989) **Lifetime reproductive success and life history evolution**, in *Lifetime Reproduction in Birds* (Newton, I., ed.), pp. 421–440, Academic Press
- Lessells, C.M. (1991) **The evolution of life histories**, in *Behavioural Ecology: an Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 32–68, Blackwell
- Martin, T.E. (1987) **Food as a limit on breeding birds: a life history perspective**, *Annu. Rev. Ecol. Syst.* 18, 453–487
- Cooke, F., Rockwell, R.F. and Lank, D.B. (1995) *The Snow Geese of La Pérouse Bay*, Oxford University Press
- Carey, C. (1996) **Female reproductive energetics**, in *Avian Energetics and Nutritional Ecology* (Carey, C., ed.), pp. 324–374, Chapman & Hall
- Perrins, C.M. (1996) **Eggs, egg formation and the timing of breeding**, *Ibis* 138, 2–15
- Houston, D.C., Donnan, D. and Jones, P.J. (1995) **The source of the nutrient required for egg production in zebra finches *Poephila guttata***, *J. Zool.* 235, 469–483
- Van Es, A.H.J. (1980) **Energy costs of protein deposition**, in *Protein Deposition in Animals* (Buttery, P.J. and Lindsay, D.B., eds), pp. 215–224, Butterworth
- Ward, S. (1996) **Energy expenditures of female barn swallows *Hirundo rustica* during egg formation**, *Physiol. Zool.* 69, 930–951
- Boutin, S. (1990) **Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future**, *Can. J. Zool.* 68, 203–220
- Nilsson, J.A. and Svensson, E. (1993) **The frequency and timing of laying gaps**, *Ornis Scand.* 24, 122–126
- Nager, R.G. and van Noordwijk, A.J. (1992) **Energetic limitation in the egg laying period of great tits**, *Proc. R. Soc. London Ser. B* 249, 259–263
- Yom-Tov, Y. and Wright, J. (1993) **Effects of heating nest boxes on egg laying in the blue tit (*Parus caeruleus*)**, *Auk* 110, 95–99
- Nager, R.G., Rügger, C. and van Noordwijk, A.J. **Nutrient or energy limitation on egg formation: a feeding experiment in great tits**, *J. Anim. Ecol.* (in press)
- Bolton, M., Houston, D.C. and Monaghan, P. (1992) **Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study**, *J. Anim. Ecol.* 61, 521–532
- Ramsay, S.L. and Houston, D.C. **Nutritional constraints on egg production in the blue tit: a supplementary feeding study**, *J. Anim. Ecol.* (in press)
- Graveland, J. *et al.* (1996) **Poor reproduction in forest passerines from decline of snail abundance on acidified soils**, *Nature* 368, 446–448
- Williams, J.B. (1996) **Energetics of avian incubation**, in *Avian Energetics and Nutritional Ecology* (Carey, C., ed.), pp. 375–416, Chapman & Hall
- Haftorn, S. and Reinertsen, R.E. (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

- 29 Moreno, J. and Carlson, A. (1989) **Clutch size and the costs of incubation in the pied flycatcher *Ficedula hypoleuca***, *Ornis Scand.* 20, 123–128
- 30 Moreno, J. *et al.* (1991) **The cost of incubation in relation to clutch size in the collared flycatcher *Ficedula albicollis***, *Ibis* 133, 186–193
- 31 Smith, H.G. (1989) **Larger clutches take longer to incubate**, *Ornis Scand.* 20, 156–158
- 32 Székely, T., Karsai, I. and Williams, T.D. (1994) **Determination of clutch size in the Kentish plover *Charadrius alexandrinus***, *Ibis* 136, 341–348
- 33 Siikamäki, P. (1995) **Are large clutches costly to incubate – the case of pied flycatcher**, *J. Avian Biol.* 26, 76–80
- 34 Lyon, B.E. and Montgomerie, R.D. (1985) **Incubation feeding in snow buntings: female manipulation or indirect male parental care?** *Behav. Ecol. Sociobiol.* 17, 279–284
- 35 Nilsson, J.A. and Smith, H.G. (1988) **Incubation feeding as a male tactic for early hatching**, *Anim. Behav.* 36, 641–647
- 36 Nelson, J.B. (1964) **Factors influencing clutch size and chick growth in the North Atlantic gannet, *Sula bassana***, *Ibis* 106, 63–77
- 37 Heaney, V. and Monaghan, P. (1995) **A within-clutch trade-off between egg production and rearing in birds**, *Proc. R. Soc. London Ser. B* 261, 361–365
- 38 Milonoff, M. and Paananen, P. (1993) **Egg formation, brood survival, and cost of reproduction as clutch-size-determining factors in common goldeneyes**, *Auk* 110, 943–946
- 39 Heaney, V. and Monaghan, P. (1996) **Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity**, *Proc. R. Soc. London Ser. B* 263, 1719–1724
- 40 Tombre, I.M. and Erikstad, K.E. (1996) **An experimental study of incubation effort in high Arctic barnacle geese**, *J. Anim. Ecol.* 65, 325–331
- 41 Monaghan, P., Bolton, M. and Houston, D.C. (1995) **Egg production constraints and the evolution of avian clutch size**, *Proc. R. Soc. London Ser. B* 259, 189–191
- 42 McNamara, J.N. and Houston, A.I. (1996) **State-dependent life histories**, *Nature* 380, 215–221
- 43 Houston, D.C. *et al.* (1995) **Changes in the muscle condition of female zebra finches *Poephila guttata* during egg laying and the role of protein storage in bird skeletal muscle**, *Ibis* 137, 322–328
- 44 Bolton, M., Monaghan, P. and Houston, D.C. (1993) **Proximate determination of clutch size in lesser black-backed gulls: the roles of food supply and body condition**, *Can. J. Zool.* 71, 273–279
- 45 Erikstad, K.E., Bustnes, J.O. and Moum, T. (1993) **Clutch size determination in precocial birds: a study of the common eider**, *Auk* 110, 623–629
- 46 Mauck, R.A. and Grubb, T.C., Jr (1995) **Petrel parents shunt all experimentally increased reproductive costs to their offspring**, *Anim. Behav.* 49, 999–1008
- 47 Oppliger, A., Christe, P. and Richner, H. (1996) **Clutch size and malaria resistance**, *Nature* 381, 565
- 48 Sinervo, B. and Licht, P. (1991) **Hormonal and physiological control of clutch size, egg size, and egg shape in side-blotched lizards (*Uta stansburiana*): constraints on the evolution of lizard life histories**, *J. Exp. Zool.* 257, 252–264
- 49 Martin, T.E. (1992) **Interaction of nest predation and food limitation in reproductive strategies**, in *Current Ornithology*, Volume 9 (Power, D.M., ed.), pp. 163–197, Plenum Press

Indiscriminate altruism – time for a more discriminating approach?

Laurent Keller's recent *TREE* review¹ of the challenges posed by 'indiscriminate altruism' to kin selection is a very clear presentation of the problems faced by adherents of the selfish-gene approach to explanations of social behaviour. Two aspects of the ideas presented strike us with particular force: (1) The increasingly subtle nature of the hypotheses presented to save the kin selection hypothesis in the face of apparently contradictory evidence, combined with the increasing difficulty of testing these hypotheses; and (2) the fact that none of the hypotheses offered addresses the problem of explaining the observed behaviour at the level of the colony.

Keller presents the logic of indiscriminate altruism in insect colonies with either multiple queens or a multiply-mated queen in terms of the costs and possible errors involved in recognition of kin, which could lead to losses in colony efficiency. The benefits of the group as a whole may then be greater than the sum of the selfish interests of each group member. While this logic may well be sound, we seem to have reached the point of seriously diminishing returns due to the difficulty of testing these hypotheses experimentally. Is this where major research effort should be concentrated?

Secondly, the approach to the fascinating problems of social behaviour via the selfish-gene hypothesis, or indeed any genetic analysis, necessarily fails to explain the collective social behaviour that is observed. It is not genes that are tending the queen and the brood, for example, but ants that behave in particular ways. Genes influence this behaviour, but no amount of detailed knowledge about different aspects of

fitness can explain how coordinated behaviour arises from the interactions of individuals in a colony, whether they are related or unrelated, capable of nepotism or not.

For instance, observations on a collective periodicity of activity in the brood chamber of *Leptothorax acervorum*² raises the question of how this behaviour arises from individuals whose activity patterns in isolation appear to be chaotic³. Explaining this emergent behaviour requires a model that is based on the activities of interacting ants^{4,5}. The model can then focus attention on the critical interaction parameters involved in generating the collective behaviour, leading to experimental testing of the hypothesis⁶. Having identified the origin of the emergent behaviour pattern as a phenomenon of distributed control over the colony as a whole (all members of the group participate) by using an explanatory model, one can then ask questions about the role of natural selection acting on individuals, and whether indiscriminate altruism is a viable strategy or not.

A phenomenon has to arise first before natural selection can affect its frequency, so explanations of origins at the level of interacting individuals must always be included in any full account of the phenomenon. It seems to us that this is often forgotten by adherents of genetic reductionism. Perhaps it is time for an approach that includes organisms as well as genes.

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References

- 1 Keller, L. (1997) *Trends Ecol. Evol.* 12, 99–103
- 2 Franks, S. *et al.* (1990) *Bull. Math. Biol.* 52, 597–612

- 3 Cole, B.J. (1991) *Proc. R. Soc. London Ser. B* 244, 253–259
- 4 Hemerik, L., Britton, N.F. and Franks, N.R. (1990) *Bull. Math. Biol.* 52, 613–628
- 5 Solé, R. *et al.* (1993) *J. Theor. Biol.* 159, 469
- 6 Cole, B.H. and Cheshire, D. (1996) *Am. Nat.* 148, 1–15

Reply from L. Keller

Goodwin and Harding's letter reflects the view of an increasing number of scientists who believe that complexity cannot be the product of natural selection alone. Instead, they suggest that complex systems such as the highly coordinated behaviour of workers in an ant colony is an 'emergent property'. For some of these scientists 'emergent properties' arise completely independently of natural selection, whereas others are more cautious and do not deny the role of natural selection.

Goodwin's position is clearly expressed by some of his statements in Roger Lewin's book¹, for example: 'The creative principle of emergence is a deep mystery in many ways...and that's a property of complex dynamical systems. But ultimately, it is intelligible. You can't say that about Darwinism' (pp. 116–117, my italics). Goodwin's distrust of the theory of natural selection is again apparent when he says that Darwin's theory cannot be amended with footnotes but that 'we need a new book' (p. 35) or when he states that, on a scale of one to ten, he would rate the importance of natural selection – in the context of the generation of forms – as close to one (p. 41).

It would be of limited value to reiterate the wealth of evidence for the role of natural selection in *TREE*, particularly since this has been well done