

Costs of reproduction: egg production takes its toll

Clutch size varies considerably within and between species and, ever since David Lack's seminal work in the late 1940s, biologists have been trying to explain this variation. Central to this endeavour is the need to understand the 'costs of reproduction'; that is, the tradeoffs between current and future reproductive success. In a recent study of great tits *Parus major*¹, Marcel Visser and Kate Lessells have produced one of the most complete examinations to date of reproductive costs and their effect on optimal clutch size. Birds were assigned randomly to a control group or to one of three experimental treatments that manipulated the level of investment required to achieve the same enlarged brood size. Full-costs birds were induced to lay up to two extra eggs by the temporary removal of the first four eggs laid; the free-eggs group had their clutch augmented by two eggs at the start of incubation; and the free-chicks group had two chicks added at hatching. Thus, the treatments varied egg-production costs, incubation costs and brood-rearing costs.

Although there were no treatment effects on chick mortality, fledging mass or size, or on the probability of recruitment to the breeding population, female mortality rate was progressively increased by the extra costs of incubation (free eggs) and incubation combined with egg production (full costs). Inexplicably, the mortality of control birds (without any increased costs) was the highest of all groups in the first year



of the study, and this underlines the importance of conducting such experiments in more than one year. Visser and Lessells estimated the overall fitness of breeding females by combining survival and recruitment rates to calculate the number of gene copies entering the breeding population in the subsequent year. When compared with the control group, birds that were given more eggs or chicks to rear, without the cost of laying the necessary eggs, had a higher fitness than did birds whose clutch size was not manipulated. But, crucially, if the full costs of producing those extra eggs were considered, birds with enlarged clutches were less fit. Thus, the adaptive significance of clutch size was apparent only when costs incurred at the egg formation and laying stage were considered.

This paper is noteworthy for several reasons. It illustrates the importance of using a comprehensive measure of reproductive expenditure when trying to identify the costs of reproduction: simple

clutch or brood manipulations would have failed to reveal the costs associated with egg-laying, and no fitness cost of enlarged broods would have been detected. It highlights the need to quantify 'fitness' as completely as possible, because the cost of laying extra eggs was identified only after combining offspring fitness measures with female survival. Even this fitness measure is incomplete because it omits other long-term costs, such as retarded laying date, which reduced the survival and recruitment of the offspring of the subsequent year for full-cost females. Finally, Visser and Lessells note that fitness costs incurred at the egg laying stage might depend strongly on environmental conditions, such as ambient temperature. This might constrain the evolutionary response of a species to climate change and could result in disrupted breeding performance, as has been reported in recent studies. The challenge, if we are to understand the consequences of climate change, is to identify the mechanisms by which these newly demonstrated fitness costs operate.

1 Visser, M.E. and C.M. Lessells (2001) The costs of egg production and incubation in great tits (*Parus major*). *Proc. R. Soc. London B Biol. Sci.* 268: 1271–1277

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Praise for the great biocenotic proletariat

What is the contribution of less common species to communities and ecosystems? Most natural plant communities consist of one or a few very abundant species and a relatively large number of more rare species. Most of the matter and energy processing at any given time is made by the dominant species; therefore, it is not surprising that their loss from a community usually has a very strong impact on ecosystem functioning. The ecosystem role of rare species is much more elusive. A recent experiment by Kelly Lyons and Mark Schwartz¹ provides some evidence for the

loss of less common species increasing the susceptibility of herbaceous communities to invasion by exotic plants.

Lyons and Schwartz performed a removal experiment on a natural mountain meadow community in Sierra Nevada, CA, USA. In one treatment, they reduced species richness to a randomly chosen number of species (between two and seven) by removing the least common species in the community. In another treatment, they removed an equivalent biomass of the most abundant species. After species diversity was successfully reduced, they sowed the exotic

annual ryegrass *Lolium multiflorum* onto the experimental plots. The ryegrass established better in those plots in which the rare species were removed and, among these plots, the ryegrass was more successful when the richness of resident species was lower. Where the most abundant species was removed, species richness did not influence colonization by the ryegrass. The authors suggest that the loss of less common species might be accompanied by the release of resources or niche space that the dominant species are unable to fill in the short term, making the community more susceptible to invasion.

These findings become even more interesting in conjunction with those published earlier this year² from work on microcosms of Californian grassland species subjected to experimental invasion by the annual forb *Centaurea solstitialis*. It was shown that high species richness minimized the effects of the invader on the growth and water balance of resident communities.

According to these pieces of evidence, minor species might have the potential to minimize the impact of biological invasions

on native communities by making native communities less prone to invasion and/or by minimizing the impact of the invaders. This helps to establish solid arguments for the conservation of rare species. Hurlbert³ called them the 'great biocenotic proletariat'. In the light of recent findings, this metaphor is more accurate than ever: however humble their individual contribution at any given time, the collective role of rare species in the face of a changing environmental and biotic context might be far from irrelevant.

1 Lyons, K.G. and Schwartz, M.W. (2001) Rare species loss alters ecosystem function – invasion resistance. *Ecol. Lett.* 4, xxx–xxx

2 Dukes, J.S. (2001) Biodiversity and invasibility in grassland microcosms. *Oecologia* 126, 563–568

3 Hurlbert, S.H. (1997) Functional importance vs keystone-ness: reformulating some questions in theoretical biocenology. *Austr. J. Ecol.* 22, 369–382

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Rapid colonization of polar waters by diving birds

The development of highly specialized insulation is generally presumed to have been a prerequisite for exploitation of cold polar waters by diving birds and mammals. This view is challenged by a new study of Arctic cormorants *Phalacrocorax carbo* by David Grémillet and co-workers¹. Cormorants are large diving birds, found from the tropics to the high arctic. The Arctic birds have no more insulation than do conspecifics from temperate regions, yet some spend their winters in Greenland, where water temperatures often dip below 0°C. Grémillet *et al.*¹ suggest that colonization of polar waters by diving birds might have been more direct than was previously imagined, and that there is no reason why diving birds should have evolved first in temperate regions and then slowly expanded their range into higher and higher latitudes as their body insulation became more and more effective.

The authors found no evidence that arctic cormorants have any specialized morphological adaptations to the thermal challenges of their environment. In fact, at first sight, they appear remarkably unsuited to the harsh Arctic environment, with partially waterproof plumage and very poor body insulation. However, unlike other extant

diving birds that use peripheral vasoconstriction and regional hypothermia to reduce heat losses in cold waters, such as penguins, cormorants maintain their internal body temperature by using intense central thermogenesis to balance peripheral heat losses. To do this, they must generate heat by burning energy reserves, and Grémillet *et al.*¹ estimated the energy expenditure of these birds in deep cold water to be fourteen times the resting metabolic rate. In comparison, swimming metabolic rates for penguins vary between two and eight times the resting metabolic rate. This rate of energy expenditure by the cormorants clearly cannot be sustained for long, and the authors found that birds wintering in Greenland foraged for an average of only nine minutes per day. The birds are able to reduce the amount of time they spend in the water because they can achieve very high prey capture rates – capturing over 50 g of fish per minute for those nine minutes. This is put into perspective by estimates for a similarly feeding species (the European Shag, *Phalacrocorax aristotelis*) in Scotland of 12 g per minute, and King penguins (*Aptenodytes patagonicus*) in the Antarctic of 7 g per minute. Hence, we can see that a

prerequisite for the success of the cormorant in the Arctic is the guaranteed availability of dense fish stocks.

Why has the cormorant not developed the insulation that would allow it to spend longer in the water and so colonize other high latitude areas where fish stocks are less bountiful or predictable? In the Arctic, it is unlikely that competition from other better-insulated species provides the answer. More plausible alternatives are that cormorants have only recently invaded the arctic and adaptations will follow, or that gene flow between cormorants in arctic and temperate zones restricts adaptation. The second of these should be particularly amenable to empirical testing. But, no matter the outcome of such studies, these unusual birds will remain illuminating tools for consideration of the avian invasion of high latitudes.

1 Grémillet, D. *et al.* (2001) Foraging energetics or arctic cormorants and the evolution of diving birds. *Ecol. Lett.* 4, 180–184

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Did *Wolbachia* cross the border?

Wolbachia is an obligate intracellular bacterium, widespread in arthropods, that is vertically transmitted from mothers to offspring. Owing to this mode of inheritance, selection favours *Wolbachia* variants that increase the fitness of infected females, regardless of a possible detrimental effect on infected males. Under such a selective pressure, *Wolbachia* have evolved a wide

variety of interesting phenomena (e.g. male killing; MK; feminization, F; thelytokous parthenogenesis, TP; and cytoplasmic incompatibility, CI) that favour the initial spread, and then maintenance of *Wolbachia* in uninfected populations. The evolutionary stability of *Wolbachia*–host associations strongly depends on which phenotype is induced. TP is probably the most irreversible:

male functions tend to degenerate, because they are not subject to any selective pressure in parthenogenetic lines. Once males are nonfunctional, a loss of *Wolbachia* (i.e. a return to sexual reproduction) is impossible. For MK, F and CI, selection (if resistance host genes evolve) or drift, can eventually lead to a loss of *Wolbachia* infection. However, a new study suggests that *Wolbachia* can become