Journal Club

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 Lessells, C.M. (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 Schwartz[1] 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.

