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Optimizing clutch size in birds

In July's *TREE*, Monaghan and Nager¹ reviewed literature relevant to David Lack's enduring question 'Why don't birds lay more eggs?'. The question is about optimality. It is reasonable, therefore, that discussions often focus on costs incurred by parental birds during the several stages of reproduction. Knowing the costs is necessary to calculate the optimal clutch size. Monaghan and Nager pointed out that few studies address all possible costs, so most estimates of reproductive costs in birds are too low. Knowing all the costs would presumably yield a lower expectation for the optimum.

Without taking anything away from the account by Monaghan and Nager, an important addition should be made. Calculating the clutch size that birds should produce requires knowing more than the optimal phenotypic value. Our expectation should also depend upon (1) the distribution of phenotypic error from single genotypes and (2) the overall shape of the fitness function. The clutch size problem was introduced in this context by Mountford² and was formally modeled by Yoshimura and Shields³.

This form of optimality thinking has been called the cliff-edge effect⁴, probabilistic optimization^{5–7}, and error-constrained optimization⁸. It works as follows. There is nearly always phenotypic noise around genotypic values. (A genotypic value is the mean phenotype produced by a genotype⁹.) The fitness consequences of the phenotypic noise depends on the shape of the fitness function. For traits under stabilizing selection, we rarely find a perfectly symmetrical fitness function. Rather, the function is usually asymmetric; fitness on one side of the function drops off rapidly ('the cliff') relative to the other side. Because genotypes produce phenotypes with error (in the statistical sense), then they often cannot code for a phenotypic mean near the optimum without potentially producing phenotypes with low or no fitness. The optimal genotypic value, assuming normally distributed phenotypic variance⁹, is located away from the side of the fitness function with the sharpest drop, in the skewed end of the fitness function. If the fitness function for clutch size is skewed to the left, then the optimal genotypic value is also to the left of (lower than) the phenotypic optimum. In such cases we should expect optimum-minded birds to 'underproduce' eggs relative to the phenotypic optimum. While Monaghan and Nager are probably right that we overestimate phenotypic optima, we should also concede not to expect birds to produce that optimum.

Thus, the question 'Why don't birds lay more

eggs?' relies not only on costs and benefits of the component parental tasks, but also relies on the shape of the fitness function and the probabilistic aspects of producing clutches of various sizes. Instead of pitching the question merely as a matter of costs and benefits, it should be pitched as a problem of probabilistic optimization. Instead of seeking optimal phenotypic values, we must seek optimal genotypic values. This is true for all evolutionary questions.

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Monaghan and Nager¹ stress that the demands of laying and incubating eggs may have an important role in determining parental fitness, and suggest that this consideration should be taken into account when evaluating the evidence in support of Lack's hypothesis². While we agree with their message, we would like to correct their misconceptions in interpreting the goldeneye (*Bucephala clangula*) experiment by Milonoff and Paananen³.

Monaghan and Nager (Box 1) used the goldeneye study³ as one example to show that there is a 'trend of decreasing fledging production with increasing number of the phases of the breeding cycle manipulated'. They divided manipulations into three categories according to the stage of the breeding cycle: 'free chick', 'free egg' and 'full cost'. In the case of the goldeneye, females would have faced 'full cost' if they had been made to lay and incubate a larger clutch including extra eggs and thus they would have reared a larger brood. However, in the goldeneye experiment the (three) extra eggs of females that were induced to lay more were removed and added to nests of other females. So, contrary to Monaghan and Nager's interpretation, there was no group of 'full cost' females with increased egg-laying, incubation and chick-rearing demands.

Also the calculation of goldeneye data points in their figure (Box 1) is unclear to us. Milonoff and Paananen³ did two manipulations: the first

increased egg production only and the other, with three eggs added, increased incubation and chick-rearing demands, and neither showed a reproduction cost. Manipulations did not prolong incubation period, nor did they affect hatching success³, indicating low incubation costs of enlarged clutches (e.g. Ref. 4).

When considering the non-significant result of the goldeneye experiment Monaghan and Nager (Box 1) claimed that the original clutch size of females and differences in the hatching success between treatment groups were not controlled. This is not true. While it is difficult to determine original clutch size of the females that were induced to lay extra eggs, the original clutch size of 'free egg' females did not differ from that of control females, nor were there differences in the hatching success between treatment groups³. As suggested by Monaghan and Nager, original clutch size may be linked to parental quality, which may affect the outcome of clutch-size manipulations. However, in the goldeneye, maternal effort, brood mortality, fledging success and recruitment rate are not associated with clutch or brood size (e.g. Ref. 5), indicating that clutch size is not closely linked to parental quality.

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Reply from P. Monaghan and R. Nager

The main purpose of our review was to draw attention to the fact that most studies of the cost of reproduction in birds have underestimated the true costs of raising a larger clutch, since the full costs of brood production are generally not included¹. DeWitt rightly emphasizes that this may result in a lower expectation of optimal clutch size, and that other processes may also yield an optimal clutch size lower than that predicted by the number of young that parents can successfully provision (the Lack Clutch). Asymmetric fitness functions (the cliff-edge effect) as well as temporal variation in optimal reproductive investment^{2,3} and gene flow preventing local adaptations⁴ can all result in clutch sizes smaller than the Lack Clutch.

At present it is difficult to distinguish between these alternatives. However, this might not be entirely achieved by finding the probabilistic optimal genotypic value. Various sources usually