

Egg-Laying in Birds Remains a Hot Issue

High body temperature in birds may present a physiological barrier to egg retention and live births

EGG-laying really is for the birds, apparently, because no other class of vertebrates is so completely committed to this mode of reproduction.

Biologists have often suggested that birds lay eggs rather than produce live young because they are somehow "unable" to perform this "more advanced" function. Just recently Daniel Blackburn of Vanderbilt University and Howard Evans of Cornell University swept this notion aside and ventured the proposal that birds had simply not experienced selection for reproductive stages that are a prerequisite to the bearing of live young: egg retention and viviparity were just not advantageous to birds.

Now, however, Robert Ricklefs and his colleagues at the University of Pennsylvania respond to this notion and argue that there may indeed be something about birds in general that, for physiological reasons, precludes egg retention and subsequent viviparity. That something is an unusually high body temperature: the resting body temperature of most birds falls between 40° and 41°C, which is a good degree and more above that of the typical mammal. And it just so happens that developing embryos are particularly susceptible to elevated temperatures. Retaining the egg within the bird's body for longer than the usual day or so following ovulation and fertilization might therefore be harmful to the embryo.

Short-term egg retention as a potential prelude to viviparity would both increase the overall body weight of the mother and cut down the clutch size, two factors that could be disadvantageous to small birds but not necessarily to large birds, note Ricklefs and his colleagues. In fact, if the bird is large enough—as many pelagic seabirds are—then egg retention presents some potential benefits. These include reduction of certain risks—such as predation and parasitism—associated with spending time at the nest. In addition, a female might reduce energy expenditures by being temporarily freed from responsibility for the egg at the nest site: traveling to and fro between nest and feeding sites, for instance.

In the face of these potential benefits, "the absence of egg retention in birds remains

puzzling," say Ricklefs and his colleagues. The Pennsylvania researchers then note that the rate of passage of the fertilized egg through the oviduct is remarkably similar among bird species, which might be taken to imply some basic constraint. For instance, "chicken, turkey, and quail eggs all pass through the oviduct 24 to 26 hours after ovulation. . . . One possible barrier to the evolutionary extension of passage time is exhaustion of additive genetic variance in egg-passage rate by past selection for rapid oviposition."

That past selection may be related to the potential harm of the high body temperature in birds. Birds typically incubate their eggs at between 34° and 38°C. Experimental manipulation has shown that eggs incubated at temperatures above 40°C suffer high mortality and morbidity. For instance, at 40.5°C, 83.7% of embryos die and the remainder incur all kinds of organ malformation.

It is not just bird embryos that are susceptible to such temperatures: "Data from other classes indicate that developmental problems at or above 40°C may be common to all terrestrial vertebrates." The difference is that 40°C is in the normal range of body temperature in birds, a factor related to the metabolic demands of flight. "If this recurring pattern of regulation of embryonic temperature below 40°C and elevated embryonic mortality above 40°C represented a true physiological constraint, then it would seem to preclude egg retention in birds with typical avian body temperatures."

A second possible constraint on egg retention in birds is the poor gas exchange that is possible during passage. These various considerations lead Ricklefs and his colleagues to predict that if an egg-retaining bird were to exist it would have the following characteristics: "single-egg clutch, flightlessness and/or a small ratio of egg mass to female body mass, and a resting temperature below 39°." ■ **ROGER LEWIN**

ADDITIONAL READING

D. J. Anderson *et al.*, "Why are there no viviparous birds?" *Am. Nat.* 130, 941 (1987).



J. Cooke/Animals, Animals