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Received 15 October 1985, accepted 12 December 1985.

Response to D. C. Duncan

FRANK C. ROHWER[1]

Duncan (1986) suggested that my experiments (Rohwer 1984) involved improper methods and were not appropriate tests of Lack's (1967) hypothesis that clutch size of waterfowl is limited by egg production. Perhaps of greater interest, Duncan used information on continuous laying (renesting without an interruption in laying) to conclude that "... clutch size in wild prairie ducks does not appear to be ultimately limited by a female's ability to produce eggs ...."

Duncan's (1986) initial criticism of my methodology involved the timing of egg removals. Duncan felt that removal of the fourth and subsequent eggs from wild birds may not have been early enough to allow the wild ducks to respond with extended egg laying. Two lines of evidence suggest that starting egg removals at the fourth egg should be early enough to induce extended laying, if such a response is a normal part of waterfowl breeding biology. First, there is a continuous progression of sizes of Blue-winged Teal (*Anas discors*) ovarian follicles up to about 4 days before clutch completion (Rohwer 1984). This situation applies also to Northern Shovelers (*A. clypeata*) and Mallards (*A. platyrhynchos*). Second, cases of continuation laying demonstrate that removal of the entire egg set later than the fourth egg can result in extended laying. Sowls's (1955) only record of continuation laying (where an excessive number of eggs was laid) involved a Blue-winged Teal that laid 13 eggs in a continuation nest after 5 eggs in an initial nest were taken. Gates (1962) had two Gadwalls (*A. strepera*) lay 17 and 22 eggs without skipping a day of laying. One female laid 11 eggs after the first nest of 6 eggs was destroyed; the other had two prior nests totaling 11 eggs interrupted before she completed an 11-egg clutch in a third nest. Finally, Strohmeyer (1967) had 9 records of continuation laying, 5 of which occurred after the destruction of first nests containing 5, 6, or 7 eggs.

Duncan implied that removals beginning earlier than the fourth egg may lead to extended laying in wild ducks. Unfortunately, it will be very difficult to test this idea. Initially, I tried removals on Mallards and Blue-winged Teal starting with the third egg. This earlier removal resulted in nest abandonment after hens had laid only 1–4 additional eggs. Abandonment was not caused by direct disturbance, because females were not disturbed at the nest after the initial flushing that allowed me to locate the nest. It is plausible that hens returning to a nest and finding only two eggs can perceive the egg reduction (Steen and Parker 1981). A few days of such stimuli could cause the females to abandon. Egg removals beginning with the second or third egg may be possible, if the female has not been disturbed. Flushing a female at the nest increases the likelihood of nest abandonment at subsequent disturbances (Rohwer pers. obs.). These subsequent disturbances may be only a perception that eggs are disappearing.

Duncan's (1986) second major point was that the laying skips shown by the captive Mallards rendered the experiments on captive birds invalid. In particular, he suggested that the extended laying of the egg-removal group may have been an artifact of skipped laying or egg "dropping." By this argument, it is not clear why extended laying was not observed in the nonremoval group, because those Mallards showed the same frequency of laying skips as did the removal birds. Duncan mentioned that two Northern Pintails (*A. acuta*) in his captive study laid "abnormally" large clutches. These anomalies of laying can be interpreted as extended laying by captive hens when they experience small numbers of eggs in their nest. In this case, the deficit of eggs that females could perceive was not due to removals, but was caused by laying in two nest sites or laying eggs outside of any nest ("dropped eggs"?). Duncan did not mention whether he had pintails that skipped or dropped eggs and did not extend laying. If so, his argument that anomalous laying leads to enlarged clutches in Northern Pintails is incorrect, as it appears to be for Mallards.

I realize that laying skips are not typical of wild

[1] Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA.

or captive birds. Batt and Prince (1979) had a much lower frequency of laying skips, and captive Mallards in their study laid clutches of comparable size to wild Mallards. The control birds in my study were housed in the same facility and were treated the same as the birds in Batt and Prince's (1979) study, so the skips in laying and the smaller final clutches are perplexing. The frequent laying skips precluded direct comparisons between clutch sizes of the captive and wild Mallards, but it is unclear how such comparisons would be useful in understanding the adaptive significance of clutch size.

Duncan concluded by rejecting Lack's (1967) hypothesis because some females have extended laying by producing continuation nests. I agree with Duncan that such continuation laying is the type of information that could be used to reject Lack's hypothesis (for a contrary opinion see Winkler and Walters 1983: 47). I am not convinced that the scant data allow a rejection of Lack's hypothesis. Gates (1962) observed 2 cases of extended laying, and Sowls (1955) and Strohmeyer (1967) had only 7 Blue-winged Teal lay exceptional numbers of eggs. To induce continuation laying, I took the partial clutches of 21 Blue-winged Teal (nests contained 4–8 eggs) and 12 Mallards (4–6 eggs). None of the Mallards, and only one teal, extended laying; the teal laid 20 eggs in 20 days. I am not aware of other cases of continuation layings that resulted in excessive egg production, but there have been many other studies of the renesting biology of ducks (see Bellrose 1980). The rarity of continuation laying I observed in Blue-winged Teal is consistent with Lack's hypothesis, because we might expect some females to be in particularly good condition or to experience exceptionally productive food supplies. Accordingly, only these females would be able to extend laying. Perhaps a larger sample of egg removals on wild birds also would show some exceptional females that laid larger-than-normal numbers of eggs.

I should make it clear that egg-removal experiments cannot provide strong support for Lack's hypothesis. The coupled observations of determinate laying by wild birds and extended laying by captive birds fed *ad libitum* is, at best, weak support for Lack's hypothesis (Rohwer 1984). Extended laying in captivity may be a response to abundant food, but it also could be caused by any number of unknown effects. It is interesting to note, however, that Moss and Watson (1982), working with another precocial bird with self-feeding young, also saw extended laying in captivity (see also Höst 1942) but no extension of laying when eggs were removed from the nests of wild Willow Ptarmigan (*Lagopus lagopus*).

I agree with Briggs's (1985) and Duncan's (1986) suggestion that additional experiments dealing with the laying patterns of birds with self-feeding young would be useful. Furthermore, a critical evaluation of all of the predictions of Lack's hypothesis would be timely, and of considerable interest.

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Received 5 December 1985, accepted 12 December 1985.