COMMENTARIES

Does Food Limit Clutch Size in Prairie Ducks?

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What ultimately limits clutch size in precocial birds is, for the most part, unknown (Winkler and Walters 1983). Recently, Rohwer (1984) tested Lack's (1967) food-limitation hypothesis by examining the ability of wild and captive ducks to lay larger-than-normal clutches when eggs were removed during laying. When he removed eggs, captive birds with an unlimited food supply, but not wild birds, were induced to lay larger clutches. Because eggs had to be removed from the captive birds to induce greater egg production (although Rohwer did not actually compare clutch size in captivity with that in the wild), nutrition did not appear to be the proximate determinant of clutch size. Rohwer (1984: 604) stated that these results "... are consistent with Lack's (1967) hypothesis that clutch size in precocial species is limited by the female's ability to produce eggs given the average availability of food" and "... suggest that nutrition may be the ultimate determinant of clutch size." I believe there are a number of points that cast doubt on the applicability of Rohwer's data and the supportability of Lack's hypothesis.

First, Rohwer removed the fourth and subsequent eggs from wild birds but the third and subsequent eggs from captive birds. Winkler and Walters (1983) emphasized the need for a common experimental regime in egg-removal studies because there appears to be some point in the laying cycle at which a bird's clutch size is set and further follicular development is inhibited (Klomp 1970). Rohwer stated that developing follicles of Blue-winged Teal (*Anas discors*) had an exponential weight hierarchy until egg 6 or 7 was laid so that the birds "should" have been able to continue development of additional follicles when eggs 3 or 4 were removed. Although this assumption may be true, we do not know at what point in the laying cycle the clutch size of ducks becomes set.

In Rohwer's captive birds egg production was sporadic; birds often laid an egg and then delayed a number of days before producing another. The typical rate of laying in wild dabbling ducks is 1 egg/day (Bellrose 1976). The effect of the inclusion of the irregularly laying birds in Rohwer's data is unknown but was likely inappropriate for the following reason. During a study of reproduction in captive Northern Pintails (*A. acuta*), I recorded 2 hens that laid 14 eggs each in 14 and 15 days, respectively. One of these hens skipped 1 day and "dropped" a number of her eggs, whereas the other laid in 2 nest bowls. The largest first clutch of a captive hen that did not "drop" any eggs and laid in a single nest bowl was 11 (1 of 25). The largest clutch I found in the wild was 12 (1 of 290). Thus, ducks that lay in more than one nest or that "drop" eggs may produce abnormally large "clutches." I contend that egg production by birds that do not lay in a normal fashion, including hens that lay sporadically, should not be used in any analysis of clutch size.

My final point regarding the food-limitation hypothesis concerns the phenomenon of continuous laying. Sowls (1955) reported that ducks that were disturbed on their nests during laying may continue laying the next day in a new nest, maintaining the normal laying rate of 1 egg/day. The clutch in the second nest was of average size such that the birds had laid an unusually large number of eggs on consecutive days. Sowls termed this "continuous laying." The Northern Pintail that laid 14 eggs in 14 days would be classified as a continuous layer because she laid 4 eggs in her first nest and 10 in her second. Continuous laying in captivity could be attributed to the abundant food supply. Sowls, however, observed this phenomenon in the wild, and it has been reported in wild ducks by at least two others (Gates 1962, Strohmeyer 1967). Consequently, some wild prairie ducks both have the physiological capacity and breed in an environment that has sufficient food resources for the production of larger-than-normal clutches. Thus, clutch size in wild prairie ducks does not appear to be ultimately limited by a female's ability to produce eggs, contrary to Lack's (1967) hypothesis. The inability of Rohwer's egg-removal experiments to induce greater egg production in wild birds might have resulted from the birds not having been disturbed during laying and thus not having to construct a new nest. It is possible that disturbance during the laying cycle of a duck causes some physiological change whereby the entire nesting cycle is started anew, including construction of a new nest and laying of an entire new clutch. If so, this could have serious implications for the interpretation of egg-removal studies in general.

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Response to D. C. Duncan

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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

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