SHORT COMMUNICATIONS

Patterns of Egg Laying in Prairie Ducks

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The hypothesis that clutch size is ultimately limited by the ability to lay eggs has been rejected for several species because it has been demonstrated that females continue to lay when eggs are removed from the clutch (Klomp 1970). A classic case involved a Northern Flicker (*Colaptes auratus*) that laid 71 eggs in 73 days (Phillips 1887). Few species exhibit such extended laying, and none fit Cole's (1917) definition of an indeterminate layer, one that both extends laying when eggs are removed and curtails laying when eggs are added to the nest. Numerous precocial species have been reported to extend laying when eggs are removed from the nest. These results are equivocal, however, having been based upon (1) species that feed their young (gulls, Parsons 1976; grebes, Fugle and Rothstein 1977); (2) anecdotal information, such as reports of natives increasing their total egg harvest by removing only one egg a day from each nest (Wagner 1957, Hori 1964); or (3) captive birds fed *ad libitum* (Mouquet 1924, Host 1942, Goodwin 1948, Romanoff and Romanoff 1949). There have also been reports that some female ducks reduced the number of eggs they laid when additional eggs were placed in their nest. These results were largely based upon the observation that parasitized nests contain fewer host eggs than do unparasitized nests (Weller 1959, Sugden 1980, but see Andersson and Eriksson 1982). Such natural experiments do not control for other possible factors that may explain the same phenomena, such as "high quality" females being able to avoid parasitism, and it is uncertain that all the host eggs displaced from the nests were found (most species were overwater nesters). To clarify the fragmentary information on laying by precocial birds, I did egg addition and removal experiments on wild, free-ranging Blue-winged Teal (*Anas discors*) and Mallards (*A. platyrhynchos*). To elucidate how food availability influences egg laying, I also removed eggs from captive Mallards that were of wild genetic stock (i.e. birds raised from eggs collected in the wild).

The work with wild, free-ranging birds was conducted in 1979 and 1980 in the prairie pothole region of southwestern Manitoba. Nests found in the laying stage with four or fewer eggs were experimentally manipulated. In the egg-removal experiments, egg number 4 and all subsequent eggs were removed while the female was absent during the late evening (2000–2300) of the day the eggs were laid. These removals limited the number of eggs in the removal nests to a maximum of four, with only three eggs present in the morning when females visited the nest to lay that day's egg. Removals continued until the hen was flushed off the nest. The nest was not checked again for 3–5 days. Incubation was usually initiated the day the last egg was laid, although in some cases it was a day after laying was terminated. Incubation for 3 days or more signaled the completion of laying. For Mallards I altered the above methods so that eggs were removed until the female had laid nine eggs or until I flushed her from the nest during an evening check. Nests were not checked again for 5 days. These precautions assured that Mallard females, which were very sensitive to disturbance at the nest site, did not abandon their nests. As laying progressed, Mallards spent increasing amounts of time at the nest and flushes on two successive evenings almost always caused abandonment.

The developing follicles in most Blue-winged Teal show an exponential weight hierarchy until egg 6 or 7 has been laid. Therefore, the egg removals should have been early enough to allow females to respond by continued development and ovulation of follicles that normally would have been suppressed. Beginning egg removals at the 2- or 3-egg stage would have increased the difficulty of locating an adequate number of nests and greatly increased nest desertion.

In the egg-addition experiment, 6 or 8 fresh Blue-winged Teal eggs were added to teal nests found with 2 or 3 eggs. Control nests were unmanipulated nests of the same seasonal phenology that were found during the laying stage in the same area. The control nests were found with 4–7 eggs already laid.

The experiment on captive Mallards was done in 1982 at the Delta Waterfowl Research Station in Manitoba, Canada. In mid-April, 54 pairs of captive Mallards were randomly assigned to either an egg-removal group or a control group. Pairs were visually isolated outdoors in 7-m cubicles with one-half swimming water and one-half dry concrete floor. Each cubicle had a nest box and was separated from other pens by a 0.7-m wall. Commercial chow (26% protein with a vitamin and mineral supplement) was supplied *ad libitum*. For further details of maintenance of captive birds see Ward and Batt (1973). For the removal group the third and all subsequent eggs were removed from the nest on the day they were laid.

Clutch sizes of addition, control, and removal nests (Table 1) for wild Blue-winged Teal did not differ

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TABLE 1. Number of eggs laid by wild Blue-winged Teal.

Treatment	Clutch size						n	Mean
	8	9	10	11	12	13		
Eggs added	—	2	6	4	—	—	12	10.2
Control	3	5	17	14	6	1	46	10.4
Eggs removed	—	2	3	3	2	1	11	10.7

significantly (Kruskal-Wallis test corrected for ties, $H = 1.25$, $P > 0.20$). Similarly, the removal and control clutches for wild Mallards (Table 2) did not differ significantly (Mann-Whitney, $U = 164$, $P > 0.20$). For neither wild Blue-winged Teal nor Mallards did the distribution of clutch sizes (Tables 1 and 2) for the treatment groups differ significantly (3×6 contingency table, $G = 7.02$, $P > 0.20$, and 2×5 contingency table, $G = 2.47$, $P > 0.20$, respectively; G-tests were calculated using William's correction, Sokal and Rohlf 1981). This demonstrates that not even a few experimental females produced an exceptional number of eggs.

Similar egg removals from a smaller sample of other prairie ducks gave the following results: 4 Gadwalls (*Anas strepera*) laid clutches of 11, 10, 10, and 9 eggs; 2 Northern Shovelers (*A. clypeata*) laid 8 eggs; a Green-winged Teal (*A. crecca*) laid 9 eggs; and 2 Canvasbacks (*Aythya valisineria*), neither of which was parasitized by Redheads (*A. americana*), each laid 9 eggs. These nests were all within the normal range of clutch sizes.

The results of the experiment with captive Mallards (Table 3) were different from those of the experiment with wild Mallards (Table 2). Removal nests had 11.9 eggs, a number that differed significantly from the 7.6 eggs of control females (Mann-Whitney test, $U = 72$, $P = 0.005$). The distributions of clutch sizes were significantly different between the removal and control Mallards (2×6 contingency table, $G = 11.07$, $P < 0.005$). Still, it was apparent that about half of the females did not extend laying when eggs were removed. For the captive study, a full clutch was defined as the number of eggs laid before a laying skip of 3 days or more. Clutch size was so defined for captive birds, because egg production continued at a sporadic rate (i.e. control and experimental groups had frequent skips in egg laying) throughout the 43 days of the experiment, and few birds incubated. Using 2 days as the criterion for a single clutch resulted in nearly equivalent laying rates for the females in the control and removal treatments. Using a definition that allowed 3-day skips would have caused larger clutch sizes in the removal group but not the control group.

TABLE 2. Number of eggs laid by wild Mallards.

Treatment	Clutch size					n	Mean
	7	8	9	10	11		
Control	1	7	12	6	2	28	9.0
Eggs removed	2	2	4	1	1	10	8.7

Extended laying by some individual, captive (wild stock) Mallards is consistent with the results of other studies (Mouquet 1924, Romanoff and Romanoff 1949) of captive Mallards, which presumably used stock that was several generations removed from wild birds. Some captive, wild-stock Canvasbacks also extended laying when eggs were removed from nests (Kostow and Bluhm pers. comm.). Extended laying by captive birds may be a consequence of the abundant and available food supply. Unlike captive ducks with unlimited food supply, none of the wild ducks exhibited extended laying. This suggests that some wild ducks have the physiological capability of extending laying past normal clutch sizes but lack the nutrients required for extended laying. Such 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.

It is interesting to note that in captive birds, eggs must be removed in order to extend laying. This suggests that nutrition is not the proximate determinant of clutch size in prairie ducks (see also Batt and Prince 1979), although data presented here and elsewhere (Lack 1967, Drobney 1980, Krapu 1981) suggest that nutrition may be the ultimate determinant of clutch size. Unfortunately, egg-addition experiments are not very useful as tests of Lack's (1967) egg-limitation hypothesis. The results of my egg additions with Blue-winged Teal are consistent with the egg-limitation hypothesis, but so is the curtailment of laying, as was observed by Andersson and Eriksson (1982) in the Common Goldeneye (*Bucephala clangula*). Their results can be interpreted as a rejection of Lack's hypothesis only if both the proximate and the ultimate determinants of clutch size in waterfowl are assumed to be nutrition. Curtailment of laying when eggs are added to the nest early in laying suggests that Common Goldeneye females are laying a predetermined (optimal) number of eggs but does not clarify what factors lead to that optimal clutch size.

In summary, I have demonstrated that wild ducks do not lay indeterminately as has been reported (Delacour 1964, Andersson and Eriksson 1982: 8). Egg removals did not increase clutch size in several prai-

TABLE 3. Number of eggs laid by captive Mallards.

Treatment	Clutch size 6	7	8	9	10	11	12	13	14	15	...	20	*n*	Mean
Control	2	3	2	1	1	—	—	—	—	—		—	9	7.6
Eggs removed	—	1	1	—	2	1	—	2	—	1		1	9	11.9

rie ducks, nor did egg additions decrease the number of eggs laid by Blue-winged Teal. Some captive Mallards of wild genetic stock did extend laying when eggs were removed from their nests. Thus, Mallard females have the physiological ability to produce excessive numbers of eggs, and some females can be induced to extend laying when food is freely available.

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Experiments on Nestling Recognition by Brown Noddies (*Anous stolidus*)

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Davies and Carrick (1962) suggested that adults should distinguish their own young from offspring of neighboring conspecifics by the time their young become mobile enough to leave the nest and mix with other young birds. The influence of the type of nest in shaping recognition behavior is illustrated by members of the family Laridae, which show diversity in nest sites and structure and in the age at which