

# THE ADAPTIVE SIGNIFICANCE OF CLUTCH SIZE IN PRAIRIE DUCKS

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**ABSTRACT.**—Experimental manipulations of clutch size showed that neither incubation nor brood rearing constrains clutch size of Blue-winged Teal (*Anas discors*). Manipulated nests with small ( $\bar{x} = 4.9$ ), normal ( $\bar{x} = 9.9$ ), or large ( $\bar{x} = 16.0$ ) clutch sizes did not differ significantly in nest success (72.5%), hatchability (94.8%), or incubation periods (24.5 days). Survival of ducklings hatching from experimental nests was not related to the initial size of the brood, nor was duckling weight (at 35 days post-hatch) related to the initial brood size. Differences in duckling survival rates between years were associated with pronounced differences in habitat conditions. The variance of survival rates did not differ between the three brood size classes in either the wet or dry years. The variance in success among normal and large broods was significantly greater than that predicted from a binomial distribution. The size of the clutch being incubated did not affect the weight of females in late incubation, nor did brood size affect the weight of females accompanying nearly flying young. The results from this study are consistent with most of the limited data available for other waterfowl. Received 19 March 1984, accepted 29 October 1984.

LACK (1947, 1968) proposed that clutch size of birds is limited to the maximum number of young that parents can nourish. This hypothesis has seen at least two important modifications. The first suggests that clutch size may be lower than the maximum number of young that parents could raise because reduced reproductive effort increases the probability of parents surviving to breed again (Williams 1966a, b; Charnov and Krebs 1974; Askenmo 1979; De Steven 1980). Even more recently, Högstedt (1980) extended Lack's (1968) hypothesis by demonstrating that there are many optimal clutch sizes based on the variations of territory quality and differences between birds. His experiments showed that individual Black-billed Magpies (*Pica pica*) laid the number of eggs that was most productive for that pair's territory. Although there is ongoing interest in refining Lack's hypothesis, there is considerable agreement that provisioning nestlings or fledglings is the major determinant of clutch size in altricial birds (Klomp 1970, Ricklefs 1977).

Precocial development—defined here as reproduction wherein parents do not feed their young—is evident in 9 of the 25 extant orders of birds. The adaptive significance of clutch size

in the diverse assemblage of birds with precocial young has been neglected in comparison to the voluminous work on altricial birds (those that feed their young). Clearly, Lack's (1968) hypothesis for altricial birds cannot apply to birds that do not feed their young. Lack (1967) recognized this and suggested instead that clutch size of precocial birds is limited by the ability of females to produce eggs. This hypothesis is based on an inverse interspecific relationship between egg size and clutch size in precocial species, which suggests that limited nutrients can be allocated to many small or fewer large eggs. The correlation between body condition just prior to breeding and clutch size for arctic geese and eiders also suggests that clutch size has been limited by egg production in these precocial birds (Ryder 1970, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Davies and Cooke 1983).

Other hypotheses concerned with the adaptive limitations of clutch size in precocial species have received scant attention. Any aspect of either incubation or brood rearing that leads to declining reproductive output with increasing clutch size could influence the evolution of clutch size. Williams (1966b) and Cody (1966) have advanced such hypotheses, reasoning that the number of eggs laid by many precocial birds corresponds to the female's ability to incubate eggs or brood young. This study was designed to test two hypotheses concern-

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ing clutch size in prairie ducks, namely that the number of eggs laid corresponds to the number of eggs that the hen can incubate successfully, to the number of ducklings the female can raise after hatching, or to both.

To test these hypotheses, I altered clutch size and brood size to produce a range in numbers from well above to well below natural sizes. Incubation and brood rearing were monitored to determine success of the different size categories. Blue-winged Teal (*Anas discors*) were the main study species, although Northern Shovelers (*A. clypeata*) and Gadwalls (*A. strepera*) were also used in some tests.

*Predictions of the incubation limitation hypothesis.*—If some aspect of incubation limits clutch size, then those nests with experimentally altered clutch sizes that are larger than normal should produce fewer ducklings. Specifically, with increasing clutch size the incubation limitation hypothesis predicts that (1) nest success should decrease, (2) hatchability (the proportion of eggs hatching in successful nests) should decrease, (3) incubation periods should increase, and/or (4) the probability of the incubating female surviving to breed again should decrease. The first two predictions require no explanation. Longer laying and incubation periods (prediction 3) could influence clutch size by extending the risks of predation for both the eggs and the female. Delayed hatch, potentially caused by extended incubation, could cause a survival disadvantage for prairie waterfowl. Increased mortality of the incubating female (prediction 4) could be caused by large nests being easier for predators to detect. Such mortality would obviously result in nest failure and is covered by the first prediction. Female mortality rates could also increase if there are greater physiological demands for incubation of large numbers of eggs. Such mortality could be delayed so that any reduction in fitness caused by experimentally increased clutch size would be a result of decreased probability of breeding in subsequent years (Williams 1966a, Charnov and Krebs 1974).

*Predictions of the brood-rearing limitation hypothesis.*—As with incubation, any aspect of brood rearing that causes decreased productivity with increased brood size could set the adaptive limits to clutch size. Three predicted mechanisms for brood-size limitation are: (1) decreased pre fledging survival with increased brood size, (2) decreased quality of ducklings

fledging from large broods, and (3) increased brood-rearing costs for a parent attending large numbers of ducklings. Immediately decreased duckling survival could result from inability to brood many ducklings, from increased predation caused by greater probability of detection for large broods (Safriel 1975), or from the negative effects of intrabrood competition, even though precocial young are not directly provisioned by parents. Intrabrood competition for invertebrate prey probably would have a greater impact on the quality of young at fledging than on pre fledging survival. Ducklings that were in poor condition at fledging would be less likely to survive to breed the next spring. Prediction 3 was based on the idea that maximum lifetime production of young is obtained by balancing expenditures between current and future events (Williams 1966a, Charnov and Krebs 1974). Experimentally enlarged Blue-winged Teal broods may decrease the chances of survival for the attending female.

#### METHODS

All experiments involved wild birds breeding in southwestern Manitoba in 1978–1980. Nests were experimentally manipulated to produce a range of clutch sizes from 3 to 19 eggs. Normal Blue-winged Teal nests average  $10.4 \pm 0.08$  eggs ( $n = 291$ ) in this area, and nearly the same number of young leave the nest. The range and mean size of small, normal, and large experimental nests are defined in Table 1, and sizes of small, normal, and large experimental broods are shown in Table 3. The manipulations involved exchanging eggs so that half the eggs in each nest were from one female and half were from another female. In almost all cases, the female incubating a manipulated clutch was the natural mother of half of those eggs. Nests used in the incubation experiment were all manipulated prior to the third day of incubation. Use of a field candler (Weller 1956) allowed matching of incubation stages (necessary to maintain hatching synchrony) up to at least the eighth day of incubation. Incubation was considered to begin on the day the last egg was laid and was complete when more than half the eggs had hatched. "Successful nests" were those where at least one egg hatched. All nests used in the incubation experiment were fenced to reduce predation (Sargeant et al. 1974). The fences were 15–20 m of 5-cm mesh wire that stood 75 cm high. I assumed that the fences would reduce predation by the same proportion for all clutch sizes.

Most of the broods in the rearing experiment were hatched from nests used for the incubation experiment. The remaining broods were hatched from nests that were manipulated at later stages of incubation.

TABLE 1. Mean nest success (%) and hatchability (%) of experimental Blue-winged Teal nests.

Clutch size		Nest success (n)	Hatchability $\pm 1$ SE (n)
Mean	Range		
4.9	3-6	62.1 (29)	97.5 $\pm$ 2.50 (8)
9.9	9-10	76.9 (52)	94.7 $\pm$ 3.21 (14)
16.0	14-19	73.6 (72)	93.9 $\pm$ 1.55 (24)

All of the experimental broods consisted of an equal mix of ducklings from eggs of two different females. Experimental brood size was randomly assigned to females; this resulted in experimental clutch sizes being randomized with respect to the numbers of eggs laid by females. Broods were identified by marking the female parent, prior to hatch, with a nasal saddle (Sugden and Poston 1968) and/or a back-mounted radio transmitter. The radio package had no discernable effect on the behavior of the brood hen. Broods were located and counted as frequently as possible. Any Blue-winged Teal duckling surviving to 20 days was considered fledged. This was justifiable because no ducklings were lost after 20 days in the 7 broods that were observed repeatedly up to flying age.

Means are reported  $\pm 1$  SE, and statistical significance was tested at the 0.05 level. Sample sizes that are not given in the text can be deduced from the tables.

## RESULTS

The proportion of Blue-winged Teal nests that were successful (Table 1) did not vary significantly ( $\chi^2 = 2.21$ , NS) among the small, normal, and large clutch sizes. Failure of Blue-winged Teal nests was almost always due to predation. Nest abandonment by teal was rare and usually caused by my disturbance at the nest site. The proportion of eggs hatching from successful nests (Table 1) also did not differ significantly among the three clutch-size categories (Kruskal-Wallis test,  $H = 3.45$ , NS). Similarly, for Gadwalls the 87  $\pm$  3.6% hatchability in 6 enlarged nests (15-17 eggs each) did not differ significantly (Mann-Whitney  $U$ -test,  $U = 38$ , NS) from the 95  $\pm$  2.4% hatchability of 8 natural nests ( $\bar{x} = 10.5 \pm 0.32$  eggs). This comparison of natural and experimental Gadwall nests was not entirely valid because the experimentally enlarged nests had greater disturbance than unmanipulated nests. For Blue-winged Teal, the 95  $\pm$  3.2% hatchability of experimental nests of 10 eggs was not significantly lower

TABLE 2. Mean lengths of incubation periods and mean weights of incubating female Blue-winged Teal.

Mean clutch size	Incubation periods (days) $\pm 1$ SE (n)	Female weights	
		Stage <sup>a</sup>	Weight (g) $\pm 1$ SE (n)
4.9	23.8 $\pm$ 0.65 (6)	21.2	342 $\pm$ 6.4 (13)
9.9	24.4 $\pm$ 0.56 (9)	21.7	333 $\pm$ 3.4 (44)
15.9	24.8 $\pm$ 0.30 (17)	21.9	338 $\pm$ 6.1 (21)

<sup>a</sup> Number of days female had incubated prior to being weighed.

than the 99  $\pm$  0.7% hatchability of natural nests of 10 eggs (Mann-Whitney  $U$ -test,  $U = 136$ ,  $n = 31$ , NS). However, teal are much more tolerant of disturbances at the nest (i.e. fewer abandonments and less time away from the nest caused by human intrusion) than are Gadwalls (unpubl. data). In any case, the total hatch of enlarged nests greatly exceeds the hatch of normal-sized nests for both Blue-winged Teal and Gadwalls. Blue-winged Teal incubation periods (Table 2) were not significantly influenced by clutch size (ANOVA,  $F = 1.02$ , NS).

Weight of incubating females was used to index the physiological cost of incubation. The stage of incubation (Table 2) for the females captured during incubation was similar for the three clutch-size categories, so direct comparison of weights was legitimate. The weights, at 22 days of incubation, did not differ significantly among the females incubating the small, normal, and large clutches (ANOVA,  $F = 0.88$ , NS). This suggests that if incubation causes stress-induced mortality (Harris 1970), such mortality is not likely to be related to the demands of incubating different-sized clutches.

Enlarged Blue-winged Teal broods produced more young (Newman-Keuls test,  $q = 4.17$ ,  $P < 0.01$ , Zar 1974) than experimental broods of normal size (Table 3). The normal-sized broods fledged more young than small experimental broods (Table 3), but the difference was not significant (Newman-Keuls test,  $q = 1.79$ , NS). Duckling survival did not vary significantly (Kruskal-Wallis test,  $H = 0.92$ , NS) among the three brood-size classes. Brood success for Blue-winged Teal was recorded in years of extreme habitat conditions encountered by prairie ducks. Survival rate of ducklings did not vary between the three brood sizes in the drought of 1980 (Kruskal-Wallis test,  $H = 1.47$ , NS;  $n =$

8,  $n = 10$ , and  $n = 10$  for small, normal, and large broods, respectively), nor did survival rate vary for brood sizes in the wet years of 1978 and 1979 (Kruskal-Wallis test,  $H = 2.71$ , NS;  $n = 5$ ,  $n = 2$ , and  $n = 2$  for small, normal, and large broods, respectively). On the other hand, the  $82.6 \pm 6.03\%$  duckling survival of experimental teal broods in 1978 and 1979 was significantly greater than the  $56.2 \pm 6.12\%$  fledging success of all experimental teal broods in 1980 (Mann-Whitney  $U$ -test,  $Z = 2.18$ ,  $P < 0.05$ ).

The variance of brood survival rates for all years combined did not differ significantly between the three brood-size classes (Bartlett's test, proportions arcsine transformed,  $\chi^2 = 0.71$ , NS). Similarly, the variance of duckling survival rates between 1980 and the wet years of 1978 and 1979 did not differ significantly (arcsine transformed data,  $F = 2.72$ , NS). Based on the binomial distribution (Hastings and Peacock 1974), I calculated the expected variance in brood success ( $V = npq$ , where  $V$  is the expected variance,  $n$  is the brood size at hatch,  $p$  is the probability of survival, and  $q$  is  $1 - p$ ) for the small, normal, and large broods. The observed variance in brood success was significantly greater than the expected value for the normal- ( $F = 4.71$ ,  $P < 0.001$ ) and large-sized broods ( $F = 6.58$ ,  $P < 0.001$ ), but not for the small broods ( $F = 1.65$ , NS). This suggests that mortality of ducklings occurs with different probabilities within the different broods of equal sizes. Understanding why some broods do "unexpectedly" well, whereas other broods have low survival, will require detailed study of brood ecology.

Unmanipulated Blue-winged Teal nests hatched  $10.2 \pm 1.01$  ducklings and produced  $5.8 \pm 0.46$  young in 1980 ( $n = 29$  unmarked broods). Eight experimental nests hatching 10 ducklings produced a mean of  $5.8 \pm 0.97$  young in 1980 (excluding total brood losses, since unmarked broods of zero cannot be observed). Lack of a significant difference (Mann-Whitney  $U$ -test,  $U = 135$ , NS) indicates that experimental broods were normal in brood success and supports my assessment that the radio packages had little effect on brood females.

I had trouble following Northern Shoveler and Gadwall broods, but these species also appear capable of raising enlarged broods. Two Gadwall broods that had 16 ducklings at hatch each produced 13 ducklings. Likewise, two shoveler broods of 16 fledged 11 and 12 young.

TABLE 3. Fledging success of experimental Blue-winged Teal broods.\*

Small broods		Medium broods		Large broods	
L	S	L	S	L	S
3	3	7	7	14	13
5	0	9	0	15	6
5	2	10	0	16	0
5	3	10	2	16	6
5	4	10	3	16	6
5	4	10	4	16	7
5	4	10	6	16	8
5	4	10	6	16	14
5	4	10	8	16	14
5	4	10	9	16	15
5	4	10	9	17	8
5	4	10	9	17	17
5	5				
$\bar{x} (\pm 1 \text{ SE})$ fledge		3.5 ( $\pm 0.35$ )		5.3 ( $\pm 0.98$ )	
$\%$ ( $\pm 1 \text{ SE}$ ) survival		72 ( $\pm 7.3$ )		60 ( $\pm 9.3$ )	

\* L = number of ducklings that leave the nest; S = number of ducklings that survive.

Broods of unmanipulated clutches produced an average of 6.7 and 5.6 young for Gadwalls and Northern Shovelers during the same year.

The best assessment of reproductive success is to determine the number of young surviving to breeding age, because survival of young between fledging and their first breeding can vary with clutch size (Lack 1968). Unfortunately, this was not feasible, nor was it possible to determine duckling survival once the young attained flight. To assess the "quality" of young from the different-sized teal broods, I collected as many young as possible at 35 days post-hatch (the minimum fledging time). Nested analysis of variance applied to the data summarized in Table 4 indicates that brood size did not significantly affect the weight of ducklings ( $F = 0.49$ , NS). Male ducklings were significantly heavier than female ducklings by 35 days of age ( $F = 16.6$ ,  $P < 0.001$ ). Brood size also had no apparent effect on the weight of the brood hen ( $F = 1.37$ , NS). The similarity of duckling weights between the brood sizes suggests that there is little difference in growth rates between different-sized broods. Dates of brood abandonment by females did not seem to be influenced by brood size. These data suggest that the physiological costs of brood rearing, if such costs occur, were not brood-size related.

TABLE 4. Mean weights (g)  $\pm$  1 SE of experimental Blue-winged Teal ducklings and brood hens at 35 days after hatch.

Brood size	Duckling weights		Brood-hen weights (n)
	Male (n)	Female (n)	
Small	334 $\pm$ 4.1 (9)	326 $\pm$ 3.1 (3)	357 $\pm$ 4.0 (4)
Normal	343 $\pm$ 8.2 (5)	314 $\pm$ 7.8 (10)	368 $\pm$ 17.9 (3)
Large	345 $\pm$ 17.4 (4)	301 $\pm$ 8.0 (8)	345 $\pm$ 9.6 (3)
Mean	339 $\pm$ 4.7	311 $\pm$ 5.0	357 $\pm$ 6.2

## DISCUSSION

Comparisons of normal Wood Duck (*Aix sponsa*) nests with dump nests (where more than one Wood Duck laid eggs in the same nest) provide hatchability data from a "natural" experiment. Hatchability calculated from Heusmann's (1972) data shows that 16-20-egg dump nests have  $82.7 \pm 1.74\%$  hatch ( $n = 63$ ), which is significantly less (Mann-Whitney  $U$ -test,  $Z = 2.75$ ,  $P < 0.05$ ) than the  $86.4 \pm 1.89\%$  hatch of 8-13-egg normal nests ( $n = 85$ ). In a similar study of Wood Ducks, Clawson et al. (1979) observed 63% hatchability in 16-20-egg Wood Duck nests and 78% in normal nests. Leopold (1951) found hatchability in 16-20-egg Wood Duck nests was 91% vs. 86% for normal nests (7-12 eggs). Such natural experiments are a conservative test, because the reduction in hatchability of Wood Duck dump nests is largely a result of parasitic laying during incubation (Morse and Wight 1969). Late-laid eggs stand little chance of hatching because the hen and ducklings leave the nest within 2 days of hatch. Morse and Wight (1969) identified parasitic Wood Duck nests ranging from 4 to 28 eggs by using a more exacting definition of dump nesting than simply nests with more than 15 eggs. Hatchability was not correlated with clutch size (arcsine transformed proportions,  $r^2 = 0.02$ ,  $n = 95$ , NS). These data have fewer potential biases than comparisons of "normal" and dump nest hatchability.

Hori (1969) found no difference in hatchability between Common Shelduck (*Tadorna tadorna*) nests with 12 eggs or less ( $\bar{x} = 8.9$ ) and those with more than 12 eggs ( $\bar{x} = 17.9$ ). Likewise, hatchability of Common Goldeneye (*Bucephala clangula*) eggs was not related to clutch size for nests ranging from 3 to 14 eggs (Eriksson 1979). The larger clutches for both species represent intraspecific parasitism (Grenquist 1963, Hori 1969). Frederickson (1969) noted that

nest success of experimental supernormal clutches of American Coots (*Fulica americana*) was greater than nest success for normal or subnormal clutches. Hatchability of coot eggs was not influenced by clutch size up to at least double the normal number of eggs. Hills (1980) noted that adding an egg to shorebird nests disrupted nest symmetry and resulted in poor hatchability. The mean number of eggs hatching from 31 experimental 5-egg nests was only 2.6 vs. 3.9 hatched eggs from nests with 4 eggs.

It should be noted that my experiments and those I have referred to all involved adding fresh or slightly incubated eggs to the nest under observation. No eggs were held for extended periods prior to incubation. Perhaps viability markedly drops when eggs remain unincubated for 13 days (the maximal normal clutch size; laying rate is usually 1 egg/day).

The similarity of duckling survival rates for Wood Duck broods hatching from normal-sized nests and broods hatching from large (dump) nests is consistent with my results for Blue-winged Teal duckling survival. Heusmann (1972) and Clawson et al. (1979) obtained estimates of survival for ducklings in normal- and large-sized (dump nest) Wood Duck broods by web-tagging (Grice and Rogers 1965) ducklings just before nest exodus. Recapture rates for Wood Duck ducklings hatched in dump vs. normal nests were 26.4% vs. 25.5%, respectively (Heusmann 1972), and 13.4% vs. 10.9%, respectively (Clawson et al. 1979). Neither difference was statistically significant. Heusmann's (1972) recaptures were from trapping efforts months after fledging, and the recaptures of Clawson et al. (1979) were yearling females returning to the breeding grounds. Such late recaptures probably eliminate any biases that would be created if postfledging mortality was brood-size related. Both studies spanned several years and had impressive sample sizes.

Contrary to the findings for other waterfowl, Andersson and Eriksson (1982) found a significant negative correlation between brood size and duckling survival in the Common Goldeneye. These data were based on duckling counts of young, unmarked broods and the proportion of ducklings surviving for 20 days after the initial brood sighting (Eriksson 1979). This technique would have seriously biased Andersson and Eriksson's (1982: Fig. 5) result if the survival rate for large broods was based on broods that were initially sighted at a younger age than those ducklings in small broods. Most duckling mortality occurs in the first week after nest exodus (Keith 1961, Williams 1974, Ball et al. 1975, Street 1977). The small broods that Andersson and Eriksson (1982) observed may have been older ducklings than those in large broods and, therefore, may already have experienced a greater percentage of early post-hatching mortality. The brood-size related mortality of goldeneye ducklings may be a methodological artifact, or it may be typical of waterfowl breeding in relatively nonproductive habitat. Clearly, more studies of the relationship between brood size and survival of the young are needed for waterfowl and other precocial species.

The brood-rearing results obtained in this study and for Wood Ducks (Heusmann 1972, Clawson et al. 1979) were markedly different from those obtained by Safriel (1975) on Semipalmated Sandpipers (*Calidris pusilla*). Enlarged sandpiper broods of 5 produced only 1.00 young vs. 1.74 young from experimental broods of 4. Safriel (1975) attributed this result to broods of 5 being easier for predators to detect. Once a predator found one young it concentrated its hunting in that vicinity, thereby reducing enlarged broods to well below the size of normal broods. The best data available on predation of ducklings are those for gull predation on Common Eiders (*Somateria mollissima*, Munro and Bédard 1977a). Large broods (creches) were attacked by gulls more frequently than small broods, but the duckling survival rate was higher in large broods. Similarly, gull attacks on White-winged Scoter (*Melanitta fusca*) ducklings were more successful on small than large broods; however, this result was confounded by different ages of the broods (Brown and Brown 1981). Creching is also common in the shelduck, but creche ducklings have lower chances of survival than ducklings in normal broods (Williams 1974, Patterson 1982). High

mortality of creche ducklings probably is not caused by the large brood size. Poor survival is likely caused by the inferior habitat that creches occupy and by increased predation, which results from parental inattentiveness due to frequent fighting between adults (Pienkowski and Evans 1982).

The results of nonexperimental studies on brood rearing (Heusmann 1972, Williams 1974, Munro and Bédard 1977a, Clawson et al. 1979, Brown and Brown 1981, Andersson and Eriksson 1982) should be interpreted with some caution. Munro and Bédard (1977b) have shown that dominant, aggressive Common Eider females are most likely to form creches. Therefore, high survival in large eider broods may be a function of above-average brood hen quality and not brood size. Similar biases caused by correlations between female quality and the size of her brood may have influenced the results of other studies where brood size was not randomly assigned to females.

My experimental alterations of clutch size and brood size provide data that clearly reject the hypothesis that incubation or brood rearing set the adaptive limits to clutch size in Blue-winged Teal. Females were very successful at incubating and caring for more eggs and young than is normal, and appear to achieve this success without incurring any alteration of their weight dynamics. These results are generally consistent with the limited data for other waterfowl (Fredrickson 1969, Hori 1969, Morse and Wight 1969, Heusmann 1972, Clawson et al. 1979, Eriksson 1979; but see Andersson and Eriksson 1982). This suggests that the adaptive limit of clutch size in most waterfowl is set by processes occurring in the laying stage, such as egg production (Lack 1967). The scarcity of experiments dealing with other precocial birds precludes generalizing these results to most precocial birds.

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## LITERATURE CITED

- ANDERSSON, M., & M. O. G. ERIKSSON. 1982. Nest parasitism in goldeneyes (*Bucephala clangula*): some evolutionary aspects. *Amer. Natur.* 120: 1-16.
- ANKNEY, C. D., & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459-471.
- ASKENMO, C. 1979. Reproductive effort and return rate of male Pied Flycatchers. *Amer. Natur.* 114: 748-753.
- BALL, I. J., D. S. GILMER, L. M. COWARDIN, & J. H. RIECHMANN. 1975. Survival of Wood Duck and Mallard broods in north-central Minnesota. *J. Wildl. Mgmt.* 39: 776-780.
- BROWN, P. W., & M. A. BROWN. 1981. Nesting biology of the White-winged Scoter. *J. Wildl. Mgmt.* 45: 38-45.
- CHARNOV, E. L., & J. R. KREBS. 1974. On clutch-size and fitness. *Ibis* 116: 217-219.
- CLAWSON, R. L., G. W. HARTMAN, & L. H. FREDRICKSON. 1979. Dump nesting in a Missouri Wood Duck population. *J. Wildl. Mgmt.* 43: 347-355.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20: 174-184.
- DAVIES, J. C., & F. COOKE. 1983. Annual nesting productivity in Snow Geese: prairie droughts and arctic springs. *J. Wildl. Mgmt.* 47: 291-296.
- DE STEVEN, D. 1980. Clutch size, breeding success, and parental survival in the Tree Swallow (*Iridoprocne bicolor*). *Evolution* 34: 278-291.
- ERIKSSON, M. O. G. 1979. Aspects of the breeding biology of the goldeneye (*Bucephala clangula*). *Holarct. Ecol.* 2: 186-194.
- FREDRICKSON, L. H. 1969. An experimental study of clutch size of the American Coot. *Auk* 86: 541-550.
- GRENQUIST, P. 1963. Hatching losses of the Common Goldeneye in the Finnish Archipelago. *Proc. 13th Intern. Ornithol. Congr.*: 685-689.
- GRICE, D., & J. P. ROGERS. 1965. The Wood Duck in Massachusetts. Final Rept. Proj. No. W-19-R, Massachusetts Div. Fish and Game.
- HARRIS, H. J., JR. 1970. Evidence of stress response in breeding Blue-winged Teal. *J. Wildl. Mgmt.* 34: 747-755.
- HASTINGS, N. A. J., & J. B. PEACOCK. 1974. Statistical distributions. New York, Wiley.
- HEUSMANN, H. W. 1972. Survival of Wood Duck broods from dump nests. *J. Wildl. Mgmt.* 36: 620-624.
- HILLS, S. 1980. Incubation capacity as a limiting factor of shorebird clutch size. *Amer. Zool.* 20: 774.
- HÖGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210: 1148-1150.
- HORI, J. 1969. Social and population studies in the shelduck. *Wildfowl* 20: 5-22.
- KEITH, L. B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. *Wildl. Monogr.* 6.
- KLOMP, H. 1970. The determination of clutch-size in birds. A review. *Ardea* 58: 1-124.
- KORSCHGEN, C. E. 1977. Breeding stress of female eiders in Maine. *J. Wildl. Mgmt.* 41: 360-373.
- LACK, D. 1947. The significance of clutch size, parts I and II. *Ibis* 89: 302-352.
- . 1967. The significance of clutch size in waterfowl. *Wildfowl* 19: 125-128.
- . 1968. Ecological adaptations for breeding in birds. London, Methuen.
- LEOPOLD, F. 1951. A study of nesting Wood Ducks in Iowa. *Condor* 53: 209-220.
- MORSE, T. E., & H. M. WIGHT. 1969. Dump nesting and its effect on production in Wood Ducks. *J. Wildl. Mgmt.* 33: 284-293.
- MUNRO, J., & J. BÉDARD. 1977a. Gull predation and crèche behaviour in the Common Eider. *J. Anim. Ecol.* 46: 799-810.
- , & ———. 1977b. Crèche formation in the Common Eider. *Auk* 94: 759-771.
- PATTERSON, I. J. 1982. The shelduck—a study in behavioural ecology. Cambridge, England, Cambridge Univ. Press.
- PIENKOWSKI, M. W., & P. R. EVANS. 1982. Breeding behaviour, productivity and survival of colonial and non-colonial shelducks (*Tadorna tadorna*). *Ornis Scandinavica* 13: 101-116.
- RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* 96: 234-252.
- RICKLEFS, R. E. 1977. A note on the evolution of clutch size in altricial birds. Pp. 193-214 in *Evolutionary ecology* (B. Stonehouse and C. Perrins, Eds.). London, MacMillan.
- RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82: 5-13.
- SAFRIEL, U. N. 1975. On the significance of clutch size in nidifugous birds. *Ecology* 56: 703-708.
- SARGEANT, A. B., A. D. KRUSE, & A. D. AFTON. 1974. Use of small fences to protect ground bird nests from mammalian predators. *Prairie Natur.* 6: 60-63.
- STREET, M. 1977. The food of Mallard ducklings in a wet gravel quarry, and its relation to duckling survival. *Wildfowl* 28: 113-125.
- SUGDEN, L. G., & H. J. POSTON. 1968. A nasal marker for ducks. *J. Wildl. Mgmt.* 32: 984-986.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *J. Wildl. Mgmt.* 20: 111-113.

- WILLIAMS, G. C. 1966a. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Amer. Natur.* 100: 687-690.
- . 1966b. *Adaptation and natural selection.* Princeton, New Jersey, Princeton Univ. Press.
- WILLIAMS, M. 1974. Creching behavior of the Shelduck (*Tadorna tadorna* L.). *Ornis Scandinavica* 5: 131-143.
- ZAR, J. H. 1974. *Biostatistical analysis.* Englewood Cliffs, New Jersey, Prentice-Hall, Inc.

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(continued from p. 353)

- Charles D. MacInnes\*, Henry L. Marks, Richard L. Marsh, Carl D. Marti, Dennis J. Martin\*, Elden W. Martin, L. D. Martin, Steven Martindale, Paul Mason, Paul F. Matray, Ronald H. Matson, Brian A. Maurer\*, Harold F. Mayfield, Patrick D. McArthur, Donald A. McCrimmon, Jr\*, Mary McDonald, Sam McDowell, Christopher McGowan, Frank McKinney, M. Robert McLandress, Albert H. Meier, Bruce Menge, Robert M. Mengel\*, Joseph A. L. Mertens, Alex L. A. Middleton, David B. Miller, Don E. Miller\*, E. H. Miller\*, Richard S. Miller\*, Brian A. Millsap, Douglas W. Mock, Andrew Moiseff, Burt L. Monroe, Jr\*, William A. Montevecchi, Janice Moore\*, Michael C. Moore, Ralph D. Morris\*, Michael L. Morrison, Eugene S. Morton, James A. Mosher, Robert Moss, Helmut C. Mueller\*, John N. Mugaas, Dietland Müller-Schwarze, Ronald Mumme\*, Edward C. Murphy, Mary Murphy\*, Peter Myers, Bryan Nelson, Robert W. Nero, Stephen A. Nesbitt, David N. Nettleship\*, James D. Nichols, Gerald Niemi\*, Sven G. Nilsson, Ian Nisbet\*, Erica Nol, Val Nolan, Jr., Barry R. Noon, A. J. van Noordwijk, R. A. Norberg, Ulla Norberg, Gary Nuechterlein, Janet C. Ollason\*, Storrs L. Olson, John P. O'Neill\*, Gordon H. Orians\*, Lewis W. Oring\*, Myrfyn Owen, Theodore A. Parker, Kenneth C. Parkes\*, Linda Partridge, Robert B. Payne\*, Raymond A. Paynter, Jr., David B. Peakall, David L. Pearson, Danny B. Pence, Colin J. Pennycuik, C. M. Perrins\*, Marion Petrie, O. S. Pettingill, Jr., Jaroslav Picman, Nina Pierpont, Bob Pietruszka\*, Frank A. Pitelka, William Post, Wayne K. Potts, Dennis M. Power\*, Harry W. Power III, Kevin D. Powers, Peter W. Price\*, Harold H. Prince, H. Ronald Pulliam\*, Robert L. Pyle, Robert Raikow\*, John H. Rappole, John T. Ratti, Susan St. Clair Raye, Harry Recher, James V. Remsen, Jr., Jake Rice\*, Douglas Richards, W. John Richardson, James D. Rising, Carolyn A. Ristau, Marc Robbins, Thomas H. Roberts, William B. Robertson, Jr., Scott K. Robinson, Sievert A. Rohwer, John T. Rotenberry\*, Roland R. Roth, Stephen I. Rothstein, Mark R. Ryan, D. B. Sachs, Edward I. Saiff, Paul Samollow, Ralph W. Schreiber\*, Donna J. Schroeder, D. M. Scott\*, Spencer G. Sealy, William A. Searcy, Roger S. Seymour, Christine D. Sheppard, David F. Sherry, William Shields\*, Jennifer M. Shopland, Lester L. Short, Gary W. Shugart, Eyal Shy, Walter R. Siegfried, Alexander F. Skutch, W. J. L. Sladen, Norman F. Sloan, James N. M. Smith\*, Kimberly G. Smith\*, David W. Snow, Noel F. R. Snyder, Lennart G. Sopuck, Tex A. Sordahl\*, Paul R. Sotherland, William E. Southern\*, Alexander Sprunt IV, Peter B. Stacey, Cynthia A. Staicer, Mark V. Stalmaster, John B. Steen, Karen Steenhof, Robert C. Stein, Peter Stettenheim, Henry M. Stevenson, F. Gary Stiles, Joseph G. Strauch, Jr., Bill Sydeman, Robert C. Szaro\*, J. B. Tatum, Stanley A. Temple\*, John W. Terborgh, Jack Ward Thomas, William L. Thompson, Diana F. Tomback, Michael W. Tome, Harrison B. Tordoff\*, Elliot J. Tramer, John L. Trapp, Melvin A. Traylor, Angela K. Turner\*, Robert S. Unnasch, R. A. Väisänen\*, James C. Vanden Berge, Stephen B. Vander Wall, Gerald F. Van Tets, Sandra L. Vehrencamp, Nicholaas A. M. Verbeek\*, Jared Verner\*, A. Village, Carol Vleck, Fred H. Wagner, Glenn Walsberg, Jeff Walters\*, Edward C. Waltz\*, John Warham, Adam Watson, George E. Watson, Patrick J. Weatherhead\*, Wesley W. Weathers, Thomas Webber, Milton W. Weller\*, David R. Wells, Klaas Westerterp, Nathaniel T. Wheelwright, Clayton M. White, Bob Whitmore, G. Causey Whittow\*, James W. Wiley, R. Haven Wiley, David E. Willard, Anthony J. Williams\*, Joseph B. Williams\*, Timothy C. Williams\*, Edwin O. Willis, Mary F. Willson, W. Wiltschko, Peter H. Wimberger, John C. Wingfield\*, Larry L. Wolf, Bruce Woodward, Paul W. Woodward, Glen E. Woolfenden, Andrea Worthington, S. Joseph Wright, R. H. Yahner, Ken Yasukawa\*, Terry Yates, R. C. Ydenberg, Reto Zach, Steve Zack\*, Jerrold H. Zar, John L. Zimmerman, Richard L. Zusi, and Fred C. Zwickel.