

THE SIGNIFICANCE OF BODY MASS TO FEMALE DABBLING DUCKS DURING LATE INCUBATION¹

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Abstract. Allocation of nutrients to eggs and to costs of incubation in waterfowl may be constrained by the need to maintain nutrient reserves to complete incubation. This hypothesis predicts that body mass of successfully nesting females is greater than that of unsuccessful females. This prediction was tested by comparing the body masses of successful and unsuccessful female dabbling ducks captured late in incubation. Successful Mallards (*Anas platyrhynchos*) and Northern Shovelers (*A. clypeata*) were significantly heavier than unsuccessful females, and this process constituted evidence of directional selection. Body masses of successful and unsuccessful Blue-winged Teal (*A. discors*) did not differ.

We calculated residual (observed-predicted) body masses using published regression equations relating mass and stage of incubation in independent samples of shovelers and teal to test whether successful females in our study were relatively heavy. Residual body mass estimates of successful shovelers were significantly greater than those of unsuccessful ones; in teal, no relationship was found. Nutrient reserves may influence successful incubation in some prairie-nesting ducks and the relationship may be stronger in larger species that are most capable of storing nutrients.

Key words: Blue-winged Teal; body mass; incubation; Mallard; Northern Shoveler; nutrient reserve hypothesis.

INTRODUCTION

Incubating birds must reconcile requirements of developing embryos with their own needs. In ducks, females incur most or all of the costs of incubation, and energy needed for incubation is obtained from both endogenous reserves and exogenous resources (Afton and Paulus, in press). Incubating females must maintain high levels of nest attentiveness to ensure proper embryonic development. Consequently, feeding time often is restricted, caloric intake usually falls below maintenance requirements (Drent et al. 1985), and this leads to declines in body mass during incubation (e.g., Ankney and Afton 1988, Gloutney 1989, Barzen and Serie 1990, Afton and Ankney 1991, Afton and Paulus, in press). Mass loss during reproduction is not necessarily detrimental (Sherry et al. 1980, Freed 1981, Gaston and Jones 1989), unless it affects current and future reproduction or survival (Moreno 1989).

Controversy over the importance of nutrient

reserves during reproduction to prairie-nesting ducks has focused mainly on egg production (e.g., Afton and Ankney 1991). However, excessive investment of nutrients in eggs may compromise successful incubation or brood-rearing (e.g., Ankney and MacInnes 1978, Thompson and Raveling 1987). Nutrient reserve levels influenced nest attentiveness and length of incubation in Canada Geese (*Branta canadensis*, Aldrich and Raveling 1983) and, for some species, lower attentiveness and longer incubation times lead to higher nest failure (Harvey 1971, Inglis 1977).

The relationship between incubation, body mass and nesting success has not been adequately examined in ground-nesting ducks (but see Hepp et al. 1990), where high levels of nest attentiveness may be expected to reduce predation risk (e.g., Erikstad et al. 1982) or minimize length of incubation (e.g., Arnold et al. 1987). Gatti (1983) suggested that excessive body mass loss in female Mallards (*Anas platyrhynchos*) might reduce their chances of surviving or nesting successfully, but he did not test this idea. We tested this hypothesis by asking the question: are females who successfully hatch eggs heavier than unsuccessful fe-

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TABLE 1. Mean body mass (g) ($\bar{x} \pm 1$ SD) of female Mallards, Northern Shovelers, and Blue-winged Teal that hatched eggs and those that failed.

Species	Nest fate		<i>t</i> ^a	<i>P</i>
	Hatched	Failed		
Mallard	874.6 \pm 52.7 (45)	837.9 \pm 58.2 (12)	2.09	*
Shoveler	474.3 \pm 29.0 (30)	442.5 \pm 39.2 (6)	2.31	*
Teal	325.2 \pm 21.1 (41)	324.4 \pm 19.6 (11)	0.13	ns

^a 1-tailed *t*-test where * is $P < 0.05$ and ns is not significant.

males? Comparisons of Mallard, Northern Shoveler (*A. clypeata*; hereafter shoveler) and Blue-winged Teal (*A. discors*; hereafter teal) females enabled us to determine whether interspecific differences existed in this relationship (Moreno 1989).

STUDY AREA AND METHODS

From 1983 to 1990, we captured female Mallards, shovelers and teal on their nests during the last eight days of incubation at the St. Denis National Wildlife Area in southcentral Saskatchewan (see Sugden and Beyersbergen (1985) for a description of the area). Stage of incubation was estimated using a field candler, or egg floatation, together with guides to aging embryos (see Klett et al. 1986). Birds were weighed to the nearest 5 g with a Pesola scale, and shovelers (Palmer 1976) and Mallards (Krapu et al. 1979) were aged (yearling or adult) using feather characteristics. We were unable to age most teal. Nests were checked near the expected hatch date to determine whether eggs had hatched (Klett et al. 1986). If one or more eggs hatched, then the nest was considered successful; nests that were depredated or abandoned were considered unsuccessful.

From 1986 to 1990, predator numbers were artificially reduced on the study area. Therefore, we compared body mass data collected in this period with data collected earlier, to ensure that their inclusion did not affect results. However, there were no differences between body masses of females captured in the two periods (2-tailed *t*-tests: Mallards, $t = 0.4138$, $df = 43$, $P > 0.7$; shovelers, $t = 0.5344$, $df = 28$, $P > 0.5$; teal, $t = -0.2750$, $df = 39$, $P > 0.7$). Similarly, there were no differences in variances (2-tailed *F*-test: Mallards, $F = 1.048$, $df = 21, 36$, $P > 0.05$; shovelers, $F = 1.527$, $df = 11, 25$, $P > 0.05$; teal, $F = 1.378$, $df = 26, 25$, $P > 0.05$).

We examined whether successful females in our study were representative of females with "superior" condition or mass reported in other studies. This was justified for shoveler and teal

because annual mixing of their populations often occurs in response to variations in the distribution of precipitation and wetlands across the prairies (Johnson and Grier 1988) and, compared with Mallard, they exhibit lower levels of philopatry (e.g., Lokemoen et al. 1990, R. G. Clark, unpubl. data). For direct comparison with our data, body mass was regressed on day of incubation for the last 18 days of incubation with shoveler (A. D. Afton, pers. comm.) and teal data (Harris 1970). Residual body mass was calculated by subtracting the mass of females *observed* in our study from the mass *predicted* from the regression equations based on the independent samples of shovelers and teal.

We used analysis of covariance (ANCOVA; Proc. GLM, SAS 1985) to compare body mass of successful and unsuccessful females, adjusting for possible effects on body mass of year, laying date and stage of incubation. Statistical methods followed Zar (1984), with significance set at the 0.05 level. We used methods described by Endler (1986:171–172) to calculate directional (*i*) and variance (*j*) selection differentials; *i* measures the proportional change in the mean and *j* measures the proportional change in variance. The significance of *i* and *j* is tested with *t* and *F*-tests, respectively.

RESULTS

At the end of incubation successful Mallards and shovelers were heavier than unsuccessful females, but the pattern was not observed in teal (Table 1). There were similar proportions of adults and yearling females within each of the hatched and failed groups. Furthermore, with Mallards and shovelers, there were no differences (both *t*-tests, $P > 0.25$) in the masses of adults and yearlings weighed during the last 8 days of incubation. When the effects of year, laying date, and stage of incubation were controlled statistically (ANCOVA), differences in body mass of successful and unsuccessful females remained significant (Table 2). Body mass of teal varied

TABLE 2. Sources of variation in body mass of incubating Mallards, Northern Shovelers, and Blue-winged Teal. Shown are significance levels (*P*)^a based on analysis of covariance conducted separately for each species.

Source of variance	Teal <i>P</i>	Shoveler <i>P</i>	Mallard <i>P</i>
Model	0.010	0.083	0.042
Stage of incubation	0.596	0.083	0.254
Year	0.005	0.430	0.068
Initiation date	0.002	0.369	0.086
Fate	0.437	0.024	0.018

^a Based on Type III Sum of Squares.

with year and laying date (Table 2). Significant directional selection on body mass was found with Mallards and shovelers (Table 3) when successful and unsuccessful females were compared. No selection occurred with teal.

When matched for overlap in stage of incubation (last 18 days of incubation), the body masses of shovelers in our study did not differ (2-tailed *t*-test on means: $t = -0.3395$, $df = 50$, $P > 0.7$; 2-tailed *F*-test on variances: $F = 1.25$, $df = 15,35$, $P > 0.6$) from those recorded in Manitoba (A. D. Afton, pers. comm., Ankney and Afton 1988). Female shovelers which successfully hatched eggs had significantly (1-tailed Mann-Whitney test: $U = 267$, $n_1 = 12$, $n_2 = 32$, $P < 0.05$) higher residual values of body mass ($\bar{x} = -1.58$, $SD = 25.8$, $n = 32$) than unsuccessful females ($\bar{x} = -39.7$, $SD = 46.2$, $n = 12$). Residual body masses of successful ($\bar{x} = 1.26$, $SD = 21.2$, $n = 42$) and unsuccessful female teal ($\bar{x} = 2.65$, $SD = 20.2$, $n = 10$) did not differ (1-tailed Mann-Whitney test: $U = 211.5$; $n_1 = 10$, $n_2 = 42$; $P > 0.05$).

DISCUSSION

Our results for Mallards and shovelers are consistent with the hypothesis that nutrient reserves are needed to complete incubation successfully. This hypothesis is also supported by work with

Lesser Snow Geese (*Chen caerulescens caerulescens*) and Common Eiders (*Somateria mollissima*). Snow Geese are known to die at the end of incubation as a result of depleted energy reserves (Ankney and MacInnes 1978). Korschgen (1977) found a relationship between mass and nest abandonment in Common Eiders; relatively heavy females were less prone to abandon their nests than light females.

However, the relationship may be species-specific because the prediction was not supported with teal. We suspect that absolute body size is an important factor underlying the relationship between body mass at the end of incubation and nesting success because it likely reflects inter-specific differences in lipid storage capability. At the start of incubation, large-bodied species may have both proportionately and absolutely greater reserves than small-bodied species. Consequently, large-bodied species can place more reliance on reserves during incubation than small-bodied species (Ankney 1984, Afton and Paulus, in press). For example, Mallards and shovelers may use endogenous reserves to adopt incubation strategies which reduce predation risk or decrease incubation periods. In teal and other small ducks, other factors such as heat loading or egg cooling, may be important in determining incubation strategies (Gloutney 1989) and, ultimately, reproductive success. The annual variation in body mass that we observed in teal and, to a lesser extent, Mallards (Table 2) may have been related to yearly differences in food availability and weather conditions. In short, how endogenous and environmental constraints interact to mediate the relationship between body mass of incubating waterfowl and nest success requires further study.

Directional selection on body mass of female Mallards and shovelers was related to nest success. Although this process favored ducks that had greater body mass at the end of incubation, the heritabilities of both body mass and pattern

TABLE 3. Standardized directional (*i*) and stabilizing (*j*) selection differentials for body mass of successful and unsuccessful female ducks (data in Table 1).

Species	Successful females compared with			
	Unsuccessful females		Pooled sample ^a	
	<i>i</i>	<i>j</i>	<i>i</i>	<i>j</i>
Mallard	0.64 ^b	-0.22	0.14	-0.09
Northern Shoveler	0.82 ^b	-0.45	0.15	-0.21
Blue-winged teal	-0.13	0.16	-0.02	0.06

^a Successful and unsuccessful females combined.

^b $P < 0.05$.

of nutrient allocation to reproduction are unknown. Boag and van Noordwijk (1987) suggested that morphological characteristics, including mass, have relatively low heritabilities. Also, we assumed that the intraspecific differences in body mass between successful and unsuccessful females were not driven solely by morphological differences in body size. Structurally small ducks do not necessarily have proportionately smaller nutrient reserves, but they may be more susceptible to thermal stress when nesting. We are unaware of any *a priori* reason to suspect that predation acts selectively on structurally small female ducks; however, until it is examined directly, we cannot rule out this possibility.

Inter- and intraspecific analyses of incubating ducks demonstrate a positive relationship between nest attentiveness and body mass (Gloutney 1989, Afton and Paulus, in press). There is considerable intraspecific variability in the use of endogenous reserves to balance energy requirements of females during reproduction (Ankney and MacInnes 1978; Krapu 1981; Drobney 1982; Gatti 1983; Ankney 1984; Tome 1984; Alisauskas and Ankney 1985, in press; Martin 1987; Afton and Paulus, in press). However, lipids contribute a relatively small proportion of the total energy required for incubation in most anatids (Afton and Paulus, in press). For example, based on body mass at the start of incubation (Mallards = 964 g [Gatti 1983], shovelers = 569 g [Afton 1980], teal = 387 g [Harris 1970]), endogenous reserves accounted for 24.7, 15.6, and 11.4%, respectively, of the energy needed for incubation (See Afton and Paulus, in press: 40, for methods). Relatively heavy females may be more attentive to their eggs than lighter females, and this may become increasingly important at lower ambient temperatures (Gloutney 1989, Hepp et al. 1990). Hepp et al. (1990) found that heavier female Wood Ducks (*Aix sponsa*) lost mass at a greater rate than did lighter females during incubation, but they did not measure incubation behavior. Furthermore, factors regulating breeding effort in hole-nesting Wood Ducks may be very different from those important to ground-nesting ducks.

The controversy over clutch size limitation in waterfowl has focused on the protein limitation (Drobney and Frederickson 1985), lipid limitation (Ankney and Afton 1988), and migrational uncertainty (Rohwer, in press) hypotheses. How-

ever, endogenous reserves are used throughout reproduction and nutrient and energetic constraints on egg production are governed by the need to maintain reserves for use later in the reproductive cycle (Martin 1987). Some duck species inhabiting unpredictable prairie habitats (Krapu et al. 1983, Eldridge and Krapu 1988) may employ strategies similar to arctic-nesting geese and eiders, in maintaining a critical amount of endogenous reserves to help meet the costs of incubation. Hepp et al. (1990) found a positive relationship between body mass of females at the end of incubation and survival to the next breeding season, suggesting that incubation can be an important cost of reproduction in some years. Our findings, together with those of Hepp et al. (1990), amplify the need to examine how investment in eggs and incubation interact to influence short and long-term fitness in waterfowl. Long-term studies of individuals will best resolve these questions.

Finally, it is clear that broad extrapolation of results from single species studies perhaps is premature. For example, Rohwer (1985) rejected Lack's (1947) hypothesis that incubation ability sets the adaptive limit to clutch size in teal, and suggested that adaptive limits to clutch size in most waterfowl are set by processes occurring in the laying stage, for instance, during egg production (Lack 1968). Our results demonstrate that teal may not be representative of all ducks and, in fact, are different from Mallard and shovelers in terms of incubation mass loss and its relationship to nest success.

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