

EFFECT OF INCUBATION BODY MASS ON REPRODUCTIVE SUCCESS AND SURVIVAL OF TWO EUROPEAN DIVING DUCKS: A TEST OF THE NUTRIENT LIMITATION HYPOTHESIS¹

PETER BLUMS² AND AIVARS MEDNIS

Institute of Biology, University of Latvia, Miera 3, LV-2169, Salaspils, Latvia

ROBERT G. CLARK

*Canadian Wildlife Service, Prairie and Northern Wildlife Research Centre,
115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada*

Abstract. The nutrient limitation hypothesis postulates that variation in nutrient reserves during egg laying and incubation are important predictors of future reproductive success of female waterfowl. We tested one component of this hypothesis in two European diving ducks, Common Pochard (*Aythya ferina*) and Tufted Duck (*Aythya fuligula*), relating body masses of incubating females to subsequent nest success, and to duckling and adult survival. We based our analyses on 3,224 Common Pochards and 1,812 Tufted Ducks captured and weighed during the last two weeks before ducklings hatched at Engure Marsh, Latvia, in 1978–1993. Adult (ASY) females from successful nests weighed significantly more than those from abandoned nests, but differences in body masses between two categories of nest fates were negligible for yearlings (SY). For both species, survival (measured as apparent return rate) of females (SY + ASY) was unrelated to their body masses. Duckling recruitment was independent of adult female body mass for both species, but yearling Common Pochards that provided recruits weighed more than those that produced none. Results of our study support the nutrient limitation hypothesis and we conclude that nutrient reserve levels may be important determinants of nest success in female ducks in general, especially for species that rely heavily on endogenous reserves during incubation.

Key words: *Aythya ferina*, *Aythya fuligula*, body mass, nest success, nutrient limitation hypothesis, recruitment, survival.

INTRODUCTION

To maximize fitness, benefits to female birds of producing eggs must outweigh potential costs of incubation, raising young, reduced survival, and lowered future reproduction. These trade-offs shape the evolution of life-histories and associated reproductive strategies (Williams 1966, Stearns 1992). Despite formidable difficulties in detecting costs of reproduction (Nur 1990), many clutch and brood manipulation studies have demonstrated the importance of maintaining parental body mass to successfully complete incubation or raise offspring without compromising parental survival (reviewed by Linden and Møller 1989, Jacobsen et al. 1995). In some species this pattern has not been found, however, so the nature and strength of presumed trade-offs are either absent or unknown.

Lack (1968) originally proposed that waterfowl clutch size was limited by the amount of stored nutrients available to females at the onset of laying, an idea that has empirical support (Alisauskas and Ankney 1992) but which remains controversial, especially as applied to ducks (Ankney et al. 1991, Arnold and Rohwer 1991). Until recently, however, nutrient limitation hypotheses focused primarily on egg production while failing to consider costs during incubation or thereafter. Several processes other than pre-laying nutrient acquisition, working singly or in concert, might limit clutch size in birds. For instance, restraint in use of reserves would be favored if females with greater nutrient stores after egg-laying had higher current reproductive success (Ankney and Alisauskas 1991). This hypothesis predicts that females withhold some nutrients that could be committed to egg formation to offset costs of incubation. In Snow Geese (*Chen caerulescens caerulescens*; Ankney and MacInnes 1978) and Common Eiders (*Somateria mollissima*; Korschgen 1977), reproductive failure was clearly linked with deteriorating fe-

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² Current address: Gaylord Memorial Laboratory, The School of Natural Resources, University of Missouri-Columbia, Puxico, MO 63960, e-mail: gaylord@sheltonbbs.com

male condition during incubation. Experienced, heavier female Canada Geese (*Branta canadensis*) were more attentive to nests than inexperienced females (Aldrich and Raveling 1983).

Gloutney and Clark (1991) reported that heavier female Mallards (*Anas platyrhynchos*) and Northern Shovelers (*Anas clypeata*) had greater nest success than light-weight females, whereas no difference was discerned for Blue-winged Teal (*Anas discors*). Gloutney and Clark speculated that different interspecific patterns were related to lower nutrient storage capacity and therefore reduced reliance on reserves during incubation by teal. In a small sample ($n = 16$) of Common Goldeneye (*Bucephala clangula*), clutch abandonment was observed only in two females that lost most mass during incubation; these were among the lightest females before incubation was completed (Mallory and Weatherhead 1993). In contrast, Arnold et al. (1995) found no relationship between late incubation body mass and nest success of adult female Canvasbacks (*Aythya valisineria*) or Redheads (*A. americana*), although a weak correlation was found with yearling Canvasbacks. Because the latter two species are known to use stored nutrients for egg-laying and incubation (Noyes and Jarvis 1985, Barzen and Serie 1990), Arnold et al. (1995) concluded that nutrient reserves were only of minor importance during incubation. Further work is needed to resolve uncertainty over the role of nutrient reserves for successful nesting.

Over-investment in eggs also may be counterbalanced by lowered future adult survival or offspring recruitment, a central prediction of the cost of reproduction hypothesis (Stearns 1992). In Wood Ducks (*Aix sponsa*), Rohwer and Heusmann (1991) found no relationship between female return rates and clutch size. In their study, however, clutch size variation was induced by parasitic egg-dumping rather than by females laying larger-than-normal clutches. Energetic costs of incubating enlarged clutches may be trivial, especially under relatively benign climatic conditions (Gloutney et al. 1996). Furthermore, Rohwer and Heusmann did not evaluate return rate of female Wood Ducks in relation to body mass. In contrast, Hepp et al. (1990) found that light-weight female Wood Ducks at the end of incubation had lower survival rates than heavier females in one of three years. However, in Canvasbacks and Redheads, brood sur-

vival and adult female return rates were not related to late-incubation body mass (Arnold et al. 1995).

Thus, there are conflicting reports concerning the general significance of body reserves for successful incubation in ducks, as well as for subsequent effects on reproduction and survival. As part of a long-term study of European diving ducks (Blums et al. 1996), female Common Pochards (*Aythya ferina*, hereafter pochard) and Tufted Ducks (*Aythya fuligula*) were captured on nests during late incubation, banded, and their breeding performance and survival were monitored. Thus, we had an opportunity to re-evaluate one component of the nutrient reserve hypothesis, testing whether heavier females had greater nesting success than light-weight females. We also looked for a trade-off between current reproductive investment and future performance by determining whether lowered late-incubation body mass affected return rates of adult females or their offspring.

METHODS

This study was conducted on Engure Marsh (57°15'N, 23°07'E), Latvia, from 1978 to 1993. The study area, breeding populations of ducks, and general field procedures were described in detail by Blums et al. (1993, 1996). We captured females using drop-door traps (Blums et al. 1983) or dip nets; unmarked females were banded with conventional leg bands. Females were weighed using Pesola spring scales (± 10 g) and aged as yearlings (1-year-old) or adults (≥ 2 -year-old) based on wing feather criteria (Dane and Johnson 1975, Serie et al. 1982, Blums et al. 1996). A nest was successful if at least one duckling had hatched and left the nest. Failed nests were considered depredated or abandoned (see Arnold et al. 1995 for criteria). Abandoned nests were categorized as terminated due to human disturbance (female never returned to the nest after capture), or due to natural causes (the nest was attended by the female for one or more days following capture).

Information recorded for each nest included date, location, number of eggs in and out of the nest bowl, and incubation stage of eggs. To determine incubation stage, we initially used flotation of eggs (Westerskov 1950) calibrated for pochard and Tufted Duck (Mihelsons and Blums 1976), but gradually switched to candling (re-designed technique of Sobkowiak and Bird

1984), together with guides to aging embryos (Klett et al. 1986). Nest initiation date was estimated by back-dating the total number of eggs in the nest (1 egg laid day⁻¹), and by determining stage of incubation. Females of both species generally laid 1 egg day⁻¹ (42 and 29 confirmed cases for Tufted Duck and pochard, respectively), consistent with other findings (Bezzel 1969, Alisauskas and Ankney 1992). Twenty-one percent of nests were found during egg-laying; remaining nests were discovered after incubation had commenced. Hatching date was defined as the first date when at least several eggs in a clutch were externally pipped. Brood size was defined as the number of ducklings that left nests. We excluded from the analyses all females captured more than two weeks before nest exodus because mass loss rates appear to be higher during the first half of incubation (Kehoe 1989, Barzen and Serie 1990, Mallory and Weatherhead 1993). We regressed body masses of 3,572 female pochards and 2,096 Tufted Ducks against incubation stage and estimated the mean mass loss during the last 14 days of incubation (last day = ducklings in the nest). Pochards and Tufted Ducks lost on average 6 and 8%, respectively, of their body mass during this period. The greatest mass loss for both species occurred on the last day of incubation.

Two reproductive parameters were standardized to control for annual variation. Nest initiation and hatch dates were expressed as deviations from the yearly 10% quantile ($x - x_{10\%}$) of all nests (see Rohwer and Heusmann 1991 for similar approach). These are reasonably good indicators of annual nesting chronology because they are not overly influenced by the earliest nesting individuals and unknown renesters. Newly hatched ducklings were captured by hand at nests and banded with plasticine-filled oval aluminum bands (Blums et al. 1994).

Our approach was to follow the same statistical methods and procedures used by Arnold et al. (1995) in order to obtain comparable results with their and another (Gloutney and Clark 1991) study. We used logistic regression (PROC CATMOD, SAS Institute 1990) to compare subsequent nest success of nest-trapped females with the following six attributes: (1) body mass, (2) age (yearlings vs. adults), (3) year (1978–1993), (4) standardized nest initiation date, (5) incubation stage (days before the expected nest exodus) when the female was weighed, and (6)

number of host species' eggs. Variables 2 and 3 were categorical; the remaining were continuous. Nonsignificant two-way interactions involving body mass or age, and main effects were sequentially removed from the model until only significant predictors ($P < 0.05$) remained. When flattened wing length was included in these analyses, we obtained similar results for both species. Therefore, we are confident that patterns we detected were associated with differences in body mass, not variation in structural size as indexed by wing length.

We used general linear models (PROC GLM, SAS Institute 1990) to determine how body mass of incubating female pochard and Tufted Duck varied with nest fate, age, year, and nest initiation date. If overall models were significant, we removed nonsignificant two-way interactions and main effects ($P \geq 0.05$) from the model based on type III sums of squares. We used the Tukey-Kramer test for all multiple (> 2) comparisons of adjusted means.

We used logistic regression (PROC CATMOD) to analyze return rates of females. The response variable was return status of female (returned again in year $\geq [t + 1]$ vs. did not return), and predictor variables were female body mass and nest fate (measured in year t). Females captured outside permanent sampling areas and never seen again were excluded from analyses, because they may have returned to the marsh but were not recaptured.

We used logistic regression (PROC CATMOD) to analyze recruitment rates of ducklings produced by females that were weighed during late incubation. Analyses were similar to those described for nest fate, except that response variable was offspring recruitment status (one or more ducklings recruited in year $\geq [t + 1]$ vs. no ducklings recruited), and predictor variables were parent female body mass, year, parent female age, duckling hatching date, and brood size (all measured in year t). Females that hatched ducklings outside permanent sampling areas and whose offspring were never recaptured were excluded from analyses because ducklings may have survived and returned to the marsh but were not recaptured. For 2×2 contingency tables, we used likelihood ratio chi-square tests (SAS Institute 1990) unless specified otherwise. Least squares means are presented \pm SE.

TABLE 1. Sources of variation in nest success of Common Pochards and Tufted Ducks captured during late incubation at Engure Marsh, Latvia. Analyses were based on logistic regressions. Results are presented for female body mass and any significant covariates.

Species and age	Model GOF			Predictor	Predictors	
	χ^2	df	<i>P</i>		χ^2_1	<i>P</i>
Common Pochard	785.6	2,842	1.0	Body mass	15.8	<0.001
				Age	4.5	<0.05
				Date	15.2	<0.001
				Clutch size	7.5	<0.01
				Age × body mass	4.3	<0.05
adults	538.4	2,055	1.0	Body mass	30.5	<0.001
				Date	9.4	<0.01
				Clutch size	4.1	<0.05
yearlings	246.4	785	1.0	Body mass	1.5	ns
				Date	6.6	=0.01
				Clutch size	4.1	<0.05
Tufted Duck	413.5	1,630	1.0	Body mass	7.2	<0.01
				Date	16.2	<0.001
				Clutch size	9.2	<0.01

RESULTS

We captured and weighed 3,224 pochards and 1,812 Tufted Ducks during the last two weeks of incubation. Most of these females nested successfully: for pochard, 3,066 (95%) nests hatched, 59 (2%) were depredated, and 99 (3%) were abandoned; for Tufted Ducks, 1,753 (97%) nests hatched, 9 (0.5%) were depredated, and 50 (3%) were abandoned. There was no difference in body mass between females that abandoned nests because of human interference (e.g., capture) and those that abandoned due to natural causes (pochard, 756 ± 5 g, $n = 77$ vs. 766 ± 10 g, $n = 22$, $F_{1,97} = 0.8$, $P > 0.3$; Tufted Duck, 623 ± 6 g, $n = 31$ vs. 614 ± 8 g, $n = 18$, $F_{2,46} = 0.7$, $P = 0.4$). Near hatch, incubating females from successful nests were heavier than those from abandoned nests (multiple comparisons: pochard, $P < 0.001$; Tufted Duck, $P = 0.04$). Females from depredated nests were lighter than those from successful nests and heavier than those from abandoned nests, but differences were not significant (multiple comparisons: Tufted Duck, $P > 0.6$; pochard, $P > 0.1$). There were similar proportions of yearlings and adults within groups of all females from successful and abandoned nests for both species (Tufted Duck, $G_1 = 3.5$, $P = 0.06$; pochard, $G_1 = 0.6$, $P > 0.4$).

Nest success of pochards was influenced by female age, nest initiation date, clutch size, and a significant interaction between age and body mass (Table 1). The interaction of age and body

mass was significant ($P < 0.05$), so we conducted separate analyses for adults ($n = 2,313$) and yearlings ($n = 852$). Nest fates of adult pochards were affected by body mass and nest initiation date (Table 1); successful females weighed more than those that abandoned nests (788 ± 1 g, $n = 2,208$ vs. 762 ± 5 g, $n = 68$, $P < 0.001$). Nest fates of yearlings were unaffected by body mass ($P > 0.2$), but were influenced by nest initiation date and clutch size (Table 1). Yearling pochards from successful nests weighed no more than those from abandoned nests (761 ± 2 g, $n = 783$ vs. 756 ± 7 g, $n = 31$, $P > 0.4$), but there were more eggs in abandoned (9.0 ± 0.3) than successful nests (7.9 ± 0.1) when controlled for nest initiation date ($P = 0.001$). Within each age group successful nesters initiated nests 3 days earlier than females from abandoned nests ($P < 0.02$).

For pochards, we checked if nest success was still influenced by female body mass when females from abandoned and depredated nests were combined in one category of failed nesters. Success was influenced by female body mass (logistic regression, $\chi^2 = 33.1$, $P < 0.001$) and incubation stage ($\chi^2 = 5.1$, $P = 0.02$); successful females of pooled age groups were heavier (ANCOVA, $P < 0.001$) than those that failed (774 ± 1 g, $n = 2,988$ vs. 759 ± 3 g, $n = 159$).

Nest success of Tufted Ducks was influenced by female body mass, nest initiation date, and clutch size (Table 1). There was some evidence that nest success was affected by the interaction

TABLE 2. Sources of variation in body mass of female Common Pochards and Tufted Ducks during late incubation.

Species and age	Model			Predictor	Predictors					
	F	P	R ²		F	P				
Common Pochard	19.9	<0.001	0.21	Fate	13.1	<0.001				
				Age	35.2	<0.001				
				Year	10.4	<0.001				
				Date	4.2	<0.05				
				Clutch size	12.3	<0.001				
				Fate × age ^a	6.6	<0.01				
				adults	13.2	<0.001	0.17	Fate	28.3	<0.001
								Year	9.6	<0.001
								Clutch size	4.4	<0.05
								Date × year	3.2	<0.001
yearlings	7.4	<0.001	0.14	Stage × clutch size	6.1	<0.01				
				Fate	0.5	ns				
				Year	7.9	<0.001				
				Date	11.6	<0.001				
Tufted Duck	15.6	<0.001	0.15	Clutch size	13.4	<0.001				
				Fate	1.9	ns				
				Age	4.8	<0.05				
				Year	3.1	<0.001				
				Date	17.5	<0.001				
				Stage	84.1	<0.001				
				Fate × age	4.5	<0.05				
				adults	8.2	<0.001	0.10	Fate	9.7	<0.01
								Year	3.1	<0.001
								Date	18.6	<0.001
Stage	71.5	<0.001								
yearlings	6.0	<0.01	0.03	Fate	0.1	ns				
				Stage	11.8	<0.001				

^a Six more interaction terms for Common Pochard were significant ($P < 0.01$).

of age and body mass ($P = 0.07$), so we checked for possible age-related differences in body mass between females from successful and abandoned nests using analysis of covariance. There was no difference for yearlings (the trend was opposite to that of adults, $P > 0.7$), but adult females from successful nests weighed significantly more than those from abandoned nests (644 ± 1 g, $n = 1,389$ vs. 623 ± 7 g, $n = 34$, $P = 0.002$).

Body masses of both species were affected by the interaction of age and nest fate, therefore we conducted separate analyses for yearlings and adults (Table 2). Body mass varied with nest fate only for adults, the difference between successful and abandoned nests being larger for pochard than for Tufted Duck (see above). Body mass of both species was influenced also by age and year, but these relationships will be addressed elsewhere (Blums et al., unpubl. data).

Logistic regression analyses revealed age-related variation in nest fates only for pochard (Table 1); however, nest success was independent of female age ($P > 0.3$) for this species when

the interaction term between age and body mass was removed from the model (the data still fit the model perfectly, $P = 1.0$). For both species, we tested for this relationship with a much larger data set using a G -test and by adding the time period (1958–1977) when incubating females were not weighed. This additional analysis confirmed our findings: for pochard, 133 (4.4%) of 3,018 adult nests were abandoned versus 56 (5.0%) of 1,132 yearling nests ($P > 0.4$); for Tufted Duck, 119 (4.8%) of 2,485 adult nests were abandoned versus 40 (6.8%) of 592 yearling nests ($P = 0.06$).

Although results of GOF tests for analyses of return rates (PROC CATMOD) were highly significant, indicating that the data did not fit models, we checked for differences in body mass using analysis of covariance. Body mass of returning and nonreturning females (SY + ASY) was similar ($P > 0.4$) for both species (Tufted Duck, 638 ± 1 g, $n = 1,140$ vs. 636 ± 2 g, $n = 452$; pochard, 782 ± 1 g, $n = 1,581$ vs. 782 ± 1 g, $n = 754$).

Duckling recruitment was independent of par-

ent female body mass for Tufted Duck ($\chi^2_1 = 1.6$, $P > 0.2$) but not pochard ($\chi^2_1 = 9.6$, $P = 0.002$). Data were well suited for these models (GOF tests, $P = 1.0$). Major sources of variation for both species were hatching time and year (P s < 0.001). Because the interaction term between age and body mass was significant ($P = 0.01$) for pochard, we conducted separate analyses for adults and yearlings. Recruitment rates of adults were unaffected by body mass ($P > 0.4$), but yearlings that produced recruits had significantly higher body mass than those that did not (784 ± 7 g, $n = 40$ vs. 762 ± 2 g, $n = 394$, $P = 0.001$). Regardless of species and parent female age, broods that produced recruits hatched at least 3.4–6.5 days earlier than those that did not (P s < 0.001); the difference (6.5 days) being the largest for yearling pochards when controlled for other significant effects.

DISCUSSION

Two recent studies of the importance of body mass during late incubation to nesting success in female prairie-nesting ducks produced conflicting results. Gloutney and Clark (1991) found a positive association between body mass and nest success for Mallards and Northern Shovelers, but not for Blue-winged Teal, whereas Arnold et al. (1995), investigating two species of diving ducks, found such an association only for yearling Canvasbacks. Both studies pooled abandoned and depredated nests in a single category of failed breeders.

Our analyses were restricted primarily to females from successful and abandoned nests because we did not find significant differences in body masses between females of depredated and successful (or abandoned) nests. Moreover, the difference was smaller between successful and depredated nests (9 g) than between depredated and abandoned nests (12 g) for pochard (for Tufted Duck, sample size of destroyed nests was too small to make valid comparisons). Furthermore, in our study, body mass in both species was not different between females that abandoned nests because of natural causes and those that deserted because of human interference. This justified pooling all abandoned nests in one category and our findings cannot easily be dismissed simply as being an artifact of human interference. Arnold et al. (1995) suggested that investigator-induced nest abandonment is an important cause of condition-dependent nest failure

and that light-weight birds may have greater nest abandonment even in the absence of investigator disturbance. Body condition (measured as incubation body mass) of Magellanic Penguin (*Spheniscus magellanicus*) interacted with human disturbance to cause nest desertion (Yorio and Boersma 1994), but few other studies have investigated the sensitivity of light-weight birds to disturbance.

We were able to detect significant differences in body mass that were smaller than those for Mallards and Northern Shovelers (Gloutney and Clark 1991) and yearling Canvasbacks (Arnold et al. 1995) because our sample sizes were much larger (5,036 females over 16 years), especially for successful nesters. Body mass did not differ between successful and failed adult Canvasbacks (Arnold et al. 1995), but we suspect this resulted because depredated and abandoned nests were pooled in one category of failed breeders (females from abandoned nests were on average 14 g lighter than females from depredated nests).

We conducted additional analyses including a measure of structural size (flattened wing length) in the model but none of the original results changed. There also was no difference in wing length between females from successful and abandoned nests both for adults and yearlings.

Results of our study are consistent with the nutrient limitation hypothesis. Body mass (a measure of reserve levels) during incubation was an important predictor of nest success in female pochard and Tufted Duck, a pattern reported for other ducks (Korschgen 1977, Gloutney and Clark 1991, Mallory and Weatherhead 1993) and Lesser Snow Geese (Ankney and MacInnes 1978). The difference in body mass between adult females from successful and abandoned nests averaged 27 and 21 g, for pochards and Tufted Ducks, respectively. Body mass was not associated with nest success in yearling pochards and yearling Tufted Ducks.

Some studies have revealed age-specific differences in how females store and use nutrients during reproduction. For example, yearling female Gadwalls (*Anas strepera*) relied less on reserves for egg production and apparently were less efficient in storing nutrient reserves than were adults (Ankney and Alisauskas 1991). In Ruddy Ducks (*Oxyura jamaicensis*), adult females had more lipid and protein than yearlings at all stages of egg formation, and were more

likely to breed than yearlings (Alisauskas and Ankeny 1994). First-time breeding captive Canada Geese with low initial body mass consumed more food when they reached low critical weight; in contrast, experienced breeders relied on endogenous reserves until goslings hatched (Aldrich and Raveling 1983). Whether yearling ducks use nutrient reserves differently than adults during incubation is poorly known, and well-designed experimentation is required to clarify this issue.

Females decrease incubation constancy as nutrient reserves are depleted and body condition deteriorates, thereby increasing exposure of eggs to predation (Aldrich and Raveling 1983, Afton and Paulus 1992, Bromley and Jarvis 1993), an idea that requires further evaluation with ducks. Mammals are the major predators of duck nests across North America (Sargeant et al. 1993, Baldassarre and Bolen 1994), especially in prairie-parkland habitats where two opposing studies (Gloutney and Clark 1991, Arnold et al. 1995) were conducted. Most mammals would not be deterred by the presence of the female on the nest (Thompson and Raveling 1987, Owen and Black 1990), but increased recess frequency might enhance nest detection. We believe that many predators find nests by chance and eat eggs opportunistically (Clark and Nudds 1991); thus, many depredated breeding females should have relatively good body condition. Selective predation on unattended nests (presumed light weight females) may be more important for species subjected to extensive avian predation throughout their breeding range. However, such waterfowl (e.g., Common Eider) have evolved reproductive patterns such as high incubation constancy that minimize this threat (Milne 1976, Korschgen 1977, Thompson and Raveling 1987).

Thus we believe that late incubation body mass of females from abandoned nests (including those abandoned due to investigator influence) may be a more reliable predictor of poor female condition and subsequent nest success than is body mass of females from depredated nests. Pooling depredated and abandoned nests into one category of failed breeders produced similar results, likely because some portion of depredated nests may have been abandoned before predation occurred, and there may be proportionally more light-weight females among depredated than among successful nesters. How-

ever, large sample sizes often would be required to detect a significant relationship between female body mass and nest success.

Late nests had a higher probability of abandonment. If low levels of nutrient reserves cause nest abandonment by late breeders, then early breeders should have greater incubation body mass. Covariance analysis revealed a strong association between nest initiation date and body mass during late incubation for the Tufted Duck but only a slight trend for pochard when effects of age, incubation stage, and nest fate were controlled (Blums et al., unpubl. data). This suggests that female condition may be partially responsible for increased nest abandonment by late breeders. Lowered propensity to continue incubation and brood care (see below) late in the breeding season may be governed endocrinologically and may be prevalent in temperate-nesting ducks that need sufficient time for completion of molt and deposition of fat reserves before fall migration commences. We suggest that human-induced nest abandonment may be enhanced near the end of breeding season regardless of incubation stage.

There was weak evidence that yearling Tufted Ducks were more likely to abandon nests than adults, but nest abandonment was not related to female age for pochards. This is consistent with nest defense theory which predicts greater nest abandonment in cohorts or species that have greater likelihood of future reproduction (Forbes et al. 1994). Yearling Tufted Ducks have a high likelihood of breeding again because survival is similar to ASY females (Blums et al. 1996). For pochards, survival of SY birds was lower than that of ASY females (Blums et al. 1996), and likelihood of breeding might be similar for these two age groups. Yearling Canvasbacks abandoned nests more often than adults in Manitoba, Canada ($P = 0.05$; our two-tailed Fisher's exact test, based on five year data reported by Arnold et al. 1995:Table 1). Thus, Canvasback seem to have similar patterns of nest abandonment with respect to age, as we identified in Tufted Ducks. Unfortunately, adequate survival data for yearling and adult Canvasbacks are not available.

We suggest that temperate-nesting duck species that rely almost entirely on stored nutrient reserves during incubation (Common Eiders; Korschgen 1977, Parker and Holm 1990) should show a stronger relationship between incubation body mass and nest success than species that

rely less on stored reserves. This association should be weak (possibly undetectable, unless sample sizes are large) or nonexistent for species that rely heavily on exogenous energy (Wood Ducks in southern breeding areas; Kennamer and Hepp 1987). Thus, the strength of the relationship between body mass and nest success could exhibit much interspecific variation. Unfortunately, it is difficult to test this hypothesis because little published information is available on species-specific rates of body mass loss during incubation (reviewed by Afton and Paulus 1992) and on the relationship between incubation body mass and nest success (Gloutney and Clark 1991, Arnold et al. 1995). Fewer heavy female Common Eiders abandoned nests than lighter females (Korschgen 1977). Mallory and Weatherhead (1993) found that two of 16 females deserted nests on day 18 and 24 after incubation started because of high loss rates of body mass and poor physical condition. Among five other North American duck species, female body mass affected nest success in Mallards and Northern Shovelers (Gloutney and Clark 1991), and yearling Canvasbacks (Arnold et al. 1995).

Reliance on endogenous reserves during incubation might be more important in northernmost breeding areas because of lower ambient temperatures. If this relationship exists, there should be latitudinal variation in strategies governing how females store and use nutrient reserves during incubation and how nutrient reserves during incubation affect nest success. Testing these predictions with widespread species, such as Wood Ducks or other species, would be enlightening. Although factors regulating breeding effort in cavity-nesting ducks may be different from those important to ground-nesting anatids (Gloutney and Clark 1991), cavity nesters can lose a proportionally large amount of body mass in northern breeding areas. For example, female Common Goldeneyes (Mallory and Weatherhead 1993) and Hooded Mergansers (*Lophodytes cucullatus*; Mallory et al. 1993) lost more body mass (20 and 16%, respectively) during incubation in Ontario, Canada than Wood Ducks in South Carolina (9%; Kennamer and Hepp 1987). Unfortunately, we are unaware of comparative data for Wood Ducks nesting near the northern limit of their breeding distribution. Interesting comparable data exist for Common Eiders breeding at 79°N latitude in Spitsbergen, Norway (Parker

and Holm 1990) and at 44°N in Maine (Korschgen 1977). Patterns of nutrient use and weight change were similar at both locations, even though there was a 35° difference in latitude between breeding sites. Eiders saved energy by laying smaller eggs and had shorter incubation periods in Spitsbergen, thereby possibly adjusting to High Arctic conditions (Parker and Holm 1990).

Body mass of returning and nonreturning females were similar in our study. Variation in incubation body mass had no effect on survival of female Canvasbacks and Redheads in Canada (Arnold et al. 1995). Thus, neither study provides evidence that late incubation body mass affects female survival in over-water-nesting diving ducks. A positive relationship between late incubation body mass and survival in female box-nesting Wood Ducks occurred in one of three years (Hepp et al. 1990).

A positive association between female body mass and offspring recruitment was detected only in yearling pochards. The difference in mass between yearling pochards that produced recruits and those that did not was 22 g; perhaps light-weight females abandoned broods shortly after hatching. It is not clear why we did not find this trend for yearling Tufted Ducks, although it may be due to smaller sample size. In both species, ducklings that hatched early had a higher recruitment rate than those hatching late, a relationship that will be addressed in greater detail elsewhere.

Duckling survival was independent of parent female body mass for Canvasback and Redhead during two posthatch periods of approximately 14 and 38 days in Canada (Arnold et al. 1995). We found that female body mass influenced duckling recruitment only for yearling pochards; perhaps it is generally unwise to expect a difference in ducks. First, unlike during nesting, female survival may be very high during brood-rearing. Furthermore, body mass is very dynamic and adult females may easily regain mass after ducklings hatch. However, inexperienced yearlings may have difficulties in doing so or they may be more prone to abandon their broods. It appears that pochards reach maturity later than Tufted Ducks as indicated by lower breeding propensity of yearlings on the Engure Marsh (0.70 vs. 0.89 in pochard and Tufted Duck, respectively; Blums et al. 1996:Table 8). Possibly, a considerable proportion of yearling

pochards that attempted to nest were in poor physical condition, hatched ducklings very late in the season, and produced no recruits (there was a 6.5 day difference in hatching dates between broods that produced recruits and those that did not). Although nest success of yearling and older females appears to be similar (Hepp and Kenamer 1993, Blums et al. 1997), reproductive success of yearlings (in terms of recruits produced) is perhaps negligible in diving ducks. At this point we know nothing about age-specific costs of first breeding and their fitness consequences (for individuals and the population, *sensu* Cooke et al. 1995) in ducks, but we intend to address these questions in the future.

Arnold et al. (1995) investigated two North American diving ducks and suggested that, for temperate-nesting waterfowl, nutrient reserves are more likely to affect incubation behavior rather than likelihood of nest abandonment. The results of our long-term study provide good evidence for a relationship between late incubation body mass and probability of nest abandonment. To better understand the relationship between female body mass and nest success, well-designed studies with known age individuals are necessary. If our predictions are correct, then one of the most appropriate duck species to study is the Common Eider because of its heavy reliance on stored nutrient reserves during incubation (Korschgen 1977, Parker and Holm 1990).

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