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# THE EFFECTS OF LATE-INCUBATION BODY MASS ON REPRODUCTIVE SUCCESS AND SURVIVAL OF CANVASBACKS AND REDHEADS[1]

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*Abstract.* Intraspecific variation in nutrient reserves is believed to affect reproductive success of female waterfowl during egg laying and incubation (the nutrient-limitation hypothesis). We tested the nutrient-limitation hypothesis in Canvasbacks (*Aythya valisineria*) and Redheads (*A. americana*) by relating the body masses of incubating females with subsequent nest success, brood survival, and adult survival. Our analyses were based on 392 Canvasbacks and 76 Redheads captured and weighed during late incubation in southwestern Manitoba during 1983–1993. For Canvasbacks, there was a significant interaction between body mass and age; failed adults (ASY) weighed 3 g more than successful adults ($P = 0.65$), but failed yearlings (SY) weighed 37 g less than successful yearlings ($P = 0.03$). For Redheads, nest success was unrelated to body mass. For both species, brood survival and adult survival (i.e., return rates) were unrelated to female body mass. Thus, future reproductive success was correlated with body mass in only one out of seven test comparisons (i.e., nest success of yearling Canvasbacks). Although we had large sample sizes and used similar methods, our results were notably different from a previous study of prairie dabbling ducks (*Anas* spp.), where light-weight females were more likely to experience nest failure. For both studies, we believe that investigator-induced nest abandonment was an important cause of condition-dependent nest failure. We conclude that nutrient reserves were of minor importance in determining future reproductive success of adult Canvasbacks and Redheads, but may be important for yearlings.

*Key words: Body mass; Canvasback; incubation; nest success; nutrient reserves; Redhead; survival.*

## INTRODUCTION

Use of nutrient reserves during egg laying and incubation is common among North American waterfowl (Ankney and Alisauskas 1991, Alisauskas and Ankney 1992, Afton and Paulus 1992). The importance of nutrient reserves to breeding waterfowl was first demonstrated by Ankney and MacInnes (1978), who studied Lesser Snow Geese (*Chen caerulescens caerulescens*) at McConnell River, North West Territories. They showed that female body mass was positively correlated with potential clutch size and subsequent nesting success. Successful nesters collected late in incubation weighed more than failed nesters (geese with abandoned or destroyed nests), which in turn weighed more than geese that had starved to death on their nests. Lesser Snow Geese fed little between arrival on the breeding grounds and the end of incubation, and

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hence they were almost completely reliant on stored nutrients throughout laying and incubation (Ankney and McInnes 1978). However, such total reliance on stored nutrients is uncommon among waterfowl (Krapu and Reinecke 1992), even among other Arctic-nesting geese (Ankney 1984, Gauthier 1993). Thus, for temperate-nesting waterfowl that feed extensively during laying and incubation, nutrient reserves provide a smaller fraction of the energy and nutrients used during laying and incubation (Arnold and Rohwer 1991, Afton and Paulus 1992), and the extent to which these reserves limit reproduction remains controversial (Ankney et al. 1991, Arnold and Rohwer 1991).

Recently, Gloutney and Clark (1991) compared body masses of incubating female dabbling ducks (*Anas* spp.) with subsequent nesting success. For Mallards (*A. platyrhynchos*) and Northern Shovelers (*A. clypeata*), there were significant positive associations between late-incubation body mass and nesting success, whereas nesting success of Blue-winged Teal (*A. discors*) was unrelated to body mass. Gloutney and Clark (1991) speculated that this interspecific variation was related to body size and its effect on strategies of nutrient storage; body masses of Mallards and shovelers averaged 870 and 470 g during late incubation, whereas teal averaged only 325 g (Gloutney and Clark 1991). By virtue of their larger body sizes, Mallards and shovelers would be able to store greater absolute amounts of nutrient reserves before nesting, and they would also be able to use these reserves more efficiently due to lower mass-specific metabolic requirements (Afton and Paulus 1992). Blue-winged Teal, however, would have lower nutrient-storage capacity and relatively higher metabolic requirements which they would need to obtain from exogenous sources (i.e., by foraging during incubation recesses).

We tested Gloutney and Clark's (1991) hypothesis using data from two large-bodied species of prairie diving ducks: Canvasbacks (*Aythya valisineria*) and Redheads (*A. americana*). Mean late-incubation body masses of these two species averaged 1,000 and 860 g, respectively. Both species are known to utilize large amounts of nutrient reserves during egg formation and incubation (Noyes and Jarvis 1985, Barzen and Serie 1990, Afton and Paulus 1992), so we predicted that if nutrient reserves are important predictors of reproductive success, then both species should exhibit a positive relationship between body mass and nesting success.

## STUDY AREA AND METHODS

We studied the breeding ecology of Canvasbacks and Redheads near Minnedosa, Manitoba (50° 10′N, 99°47′W) during 1983–1990 and 1992–1993. Data were collected incidentally to other research objectives as part of three different studies: (1) Canvasback and Redhead population ecology (Anderson et al. in press a), (2) Canvasback and Redhead brood parasitism (Sorenson 1991, 1993), and (3) parental investment by brood-rearing Canvasbacks (de Sobrino 1995). The Anderson study area (1983–1990) consisted of two 15.8-km$^2$ study blocks. The Sorenson study area (1986–1988) was 10.4 km$^2$ in area and located immediately west of Anderson's north study block. The de Sobrino study area (1992–1993) was larger and included much of the area surrounding the Anderson study area. The Minnedosa area is characterized by numerous seasonally- to permanently-flooded wetlands, native aspen-parkland vegetation, and intensive agriculture (primarily small grains and oil seeds). The study region and general study procedures were described in greater detail by Stoudt (1982), Sorenson (1993), de Sobrino (1995), and Anderson et al. (in press a).

We attempted to trap all nesting female Canvasbacks that had not been marked previously. Redhead females were marked opportunistically, except by Sorenson (1991), who focused on them specifically. Our primary method of marking adult females was to capture them on nests during late incubation ($\bar{x}$ = 20.5, 90% range = 15–25 d incubated) using drop-door nest traps (Weller 1957, Blums et al. 1983). Traps generally were set during early afternoon in fair weather and checked one to two hours later; if empty, they were left set for another hour. If a first trapping attempt failed, we usually tried again after one or more days; however, we were unsuccessful in capturing approximately 12% of Canvasbacks and 19% of Redheads. We placed a USFWS aluminum leg-band and a nasal-marker (Doty and Greenwood 1974, Lokemoen and Sharp 1985) on each captured female. Females were weighed using Pesola spring scales (±10 g) and aged as yearlings (second-year; SY) or adults (after-second-year; ASY) based on wing-feather criteria (Dane and Johnson 1975, Serie et al. 1982). We recorded the number of Canvasback and Redhead eggs in each nest at the time of trapping. Due to interspecific nest parasitism, many Canvasback clutches also contained Redhead eggs, although the converse was rarely true (Sorenson 1991, 1993). The incubation stage of host eggs was determined by candling (Weller 1956) or flotation (Westerkov 1950; method calibrated for Canvasbacks by M. G. Anderson and B. D. Sullivan, unpubl. data). Females were released at the nest pond, usually within 15 min of removal from the trap.

We determined fates of nests by revisiting them approximately two days after their projected hatching dates. Nests were identified as hatched if one or more eggs had hatched. At hatched nests, we estimated the number of Canvasback and Redhead eggs that hatched based on the numbers of eggs known to be in the nest before hatch and the numbers of detached egg membranes, eggshell caps, and unhatched or destroyed eggs present in the nest after hatch (Anderson et al., in press a). For failed nests, we distinguished between destroyed nests (≥1 egg destroyed by a predator) and abandoned nests (eggs intact, but no longer attended by the hen). If a predator destroyed only part of a clutch and the hen then abandoned one or more intact eggs, we listed the nest as destroyed. For nests that hatched, we documented duckling survival based on observations of the marked hen with her brood. If a marked hen was observed two or more times unaccompanied by a brood, we assumed that the entire brood had died. Survival was estimated for each brood based on the number of surviving ducklings (of the host species) divided by the number of host ducklings that hatched. Canvasback broods commonly included parasitic Redhead ducklings (Stoudt 1982), but the number of parasitic ducklings had no discernable effect on host duckling survival (Anderson et al., in press b). We measured duckling survival at two age classes: Ib (approx. 10–18 days old) and IIb (33–42 days old, Dzubin 1959). Survival to age class IIb closely approximates fledging success (Stoudt 1982, Leonard 1990), but because we were unsuccessful at following all broods to this stage, we also measured survival to age class Ib. This provided us with larger sample sizes, and it also allowed us to focus directly on the first two weeks of brood-rearing when duckling mortality is most severe (Leonard 1990). We indexed adult survival based on resightings of nasal-marked females in future years (i.e., year $t + 1$ or later). Average annual resighting rates of adult female Canvasbacks and Redheads exceed 85 and 70%, respectively, and permanent emigration is rare (Anderson et al., in press a), so return rates represent a reasonable index of survival in these two species. Using mark-resighting estimates of adult survival and resighting probabilities (Anderson et al., in press a), we estimate that return rates underestimate adult female survival by about 2% for Canvasbacks and 7% for Redheads (corrections account for birds that survive without being resighted).

We used logistic regression (PROC CATMOD, SAS Institute Inc. 1985) to compare subsequent nest success (hatched vs. failed) of nest-trapped female Canvasbacks with the following nine attributes: (1) body mass, (2) age (SY vs. ASY), (3) year (1983–1990, 1992–1993), (4) nest initiation date (Julian), (5) number of Canvasback eggs, (6) number of Redhead eggs (for both 5 and 6, eggs submerged outside the nest bowl were excluded), (7) incubation stage of the host's eggs, (8) whether or not the nest was fenced, and (9) whether or not clutch size was manipulated. Variables 1, 4, 5, 6, and 7 were continuous; the remaining variables were categorical. We included variables 2–9 in our analyses because we wanted to control for any suspected sources of extraneous variation in nesting success in order to obtain a more powerful test of the main effect of body mass. We predicted that nest losses would be higher for yearlings than for adults (Serie et al. 1992), higher during drought years (Serie et al. 1992, Sorenson 1993), and higher for late nesting attempts (Sorenson 1991). For clutch size, we predicted that Canvasbacks would be less likely to abandon large clutches of Canvasback eggs (Forbes et al. 1994), but more likely to abandon clutches containing large numbers of parasitic Redhead eggs (Weller 1959). We did not determine numbers of parasitically laid Canvasback eggs on the Anderson and de Sobrino study areas, so our prediction for Canvasback eggs was confounded somewhat by intraspecific nest parasitism (see Sorenson 1993). We predicted that loss rates would be higher for birds trapped early in the nesting cycle because these nests would be exposed to predators for a longer period (Johnson 1979), and because ducks are more prone to abandon nests during early nesting stages (Forbes et al. 1994). We fenced nests and manipulated clutches on one study block of the Anderson study area (Anderson et al., in press b) and on the de

TABLE 1. Annual variation in numbers of hatched (H), abandoned (A), and destroyed (D) nests of adult Canvasbacks, yearling Canvasbacks, and Redheads nest-trapped during late incubation.

| Year | Adult Canvasbacks | | | Yearling Canvasbacks | | | Redheads[a] | | |
|---|---|---|---|---|---|---|---|---|---|
| | H | A | D | H | A | D | H | A | D |
| 1983 | 24 | 2 | 3 | 9 | 2 | 1 | 0 | 0 | 0 |
| 1984 | 19 | 4 | 3 | 1 | 0 | 1 | 3 | 0 | 2 |
| 1985 | 21 | 0 | 6 | 0 | 0 | 0 | 4 | 3 | 2 |
| 1986 | 57 | 1 | 11 | 7 | 0 | 2 | 21 | 2 | 2 |
| 1987 | 70 | 3 | 3 | 8 | 0 | 1 | 18 | 0 | 4 |
| 1988 | 28 | 5 | 10 | 2 | 4 | 1 | 2 | 3 | 2 |
| 1989 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1990 | 8 | 1 | 6 | 0 | 0 | 0 | 1 | 0 | 1 |
| 1992 | 7 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1993 | 32 | 10 | 8 | 0 | 0 | 0 | 2 | 0 | 0 |
| Total | 267 | 33 | 53 | 27 | 6 | 6 | 51 | 8 | 13 |

[a] In 1987 there were four yearling Redheads (1 H, 3 A); all others were adults.

Sobrino study area (de Sobrino 1995, fences were used only in 1992). From previous analyses, we know that these treatments did not affect clutch abandonment, but may have reduced predation losses in some years (Anderson et al., in press b). Thus, we controlled for these manipulations in our analyses. We included all nine predictor variables in our initial model, plus all two-way interactions involving body mass or age (attempts to fit models with greater numbers of interactions resulted in inestimable parameters). We sequentially deleted nonsignificant variables (beginning with the largest *P* value) until only significant predictors ($P < 0.05$) remained. If the body mass variable was deleted at an early stage of analysis, we tested it again after all remaining nonsignificant variables had been removed.

A similar analysis was conducted for Redhead nests, but we deleted variables 5, 8, and 9 because only three clutches contained Canvasback eggs, no nests were fenced, and only two clutches were manipulated. In addition, too few Redhead females were trapped in most years to test for annual effects.

We used general linear models (PROC GLM, SAS Institute 1985) to determine how body masses of incubating female Canvasbacks and Redheads varied with year, age, nest fate, initiation date, and incubation stage. For these analyses, we started with full models including the main effects plus all two-way interactions. Nonsignificant effects ($P \geq 0.05$) were sequentially deleted based on *F*-tests calculated from type III sums of squares.

We compared brood survival to female body mass, female age, year, hatch date, and hatched brood size using a general linear model (PROC GLM, SAS Institute 1985). Significance was inferred based on type III sums of squares, using procedures described above. We conducted separate analyses for each species and for each duckling age class (i.e., Ib and IIb).

We used logistic regression to analyze return rates of Canvasback and Redhead females. Analyses were similar to those described for nest fate, except that the response variable was return status (i.e., seen again in year $\geq t + 1$ vs. not seen again) and the predictor variables were body mass, year, nest fate, age, and nest initiation date (all measured in year *t*). For $2 \times 2$ contingency tables we used continuity-adjusted $\chi^2$ tests (SAS Institute 1985). Means are presented ±1 SE.

## RESULTS

We trapped and weighed 393 Canvasbacks and 76 Redheads during late incubation. We excluded one Canvasback that died during handling; it weighed 1,200 g and was the heaviest female that we handled. Of the remaining 392 Canvasback nests, 294 hatched (75.0%), 39 were abandoned (10.0%), and 59 were destroyed by predators (15.0%) (Table 1). For Redheads, 52 nests hatched (68.4%), 11 were abandoned (14.5%), and 13 were destroyed (17.1%). Proportions of successful, abandoned, and depredated nests did not differ between species ($G = 1.67$, 2 df $P = 0.43$). Female body mass did not differ between abandoned and destroyed nests for Canvasbacks (990 ± 8 vs. 1,004 ± 7; $F = 1.78$, $P = 0.18$) or Redheads (856 ± 9 vs. 849 ± 10; $F = 0.25$, $P = 0.62$), so we pooled abandoned and destroyed nests (i.e., failed nesters) for subsequent analyses.

Nest success of Canvasbacks was influenced by a significant interaction between age and body mass ($\chi^2 = 7.95$, 1 df, $P = 0.005$), so we conducted separate analyses for adults ($n = 353$) and yearlings ($n = 39$). Nest fates of adults (ASY) were affected by year and clutch manipulation (Table 2), but were unaffected by body mass ($\chi^2 = 0.14$, 1 df, $P = 0.71$), with failed adults weighing nonsignificantly more than successful adults (1,006 ± 5 g [$n = 86$] vs. 1,003 ± 3 g [$n = 267$]; $P = 0.65$). Year effects were likely related to fluctuating water levels; about 50% of the total deviance explained by the test statistic for annual

TABLE 2. Sources of variation in nest success of Canvasbacks and Redheads nest-trapped during late incubation. Analyses were based on logistic regressions. Results are presented for body mass and any significant covariates.

| Group | Model GOF[a] | | | Predictor | Predictor(s) | | |
|---|---|---|---|---|---|---|---|
| | $\chi^2$ | df | $P$ | | $\chi^2$ | df | $P$ |
| Canvasbacks[b] | 363.15 | 369 | 0.58 | Body mass | 7.59 | 1 | 0.006 |
| | | | | Age | 8.19 | 1 | 0.004 |
| | | | | Year | 32.65 | 9 | 0.0002 |
| | | | | Clutch manip. | 7.02 | 1 | 0.008 |
| | | | | Age × body mass | 7.95 | 1 | 0.005 |
| Adults | 5.27 | 7 | 0.63 | Body mass | 0.14 | 1 | 0.71 |
| | | | | Year | 30.04 | 9 | 0.0004 |
| | | | | Clutch manip. | 4.59 | 1 | 0.03 |
| Yearlings | 11.15 | 12 | 0.52 | Body mass | 8.83 | 1 | 0.003 |
| Redheads | 38.64 | 34 | 0.27 | Body mass | 0.06 | 1 | 0.81 |
| | | | | Age | 4.09 | 1 | 0.04 |

[a] A non-significant goodness-of-fit (GOF) test indicates that the model adequately describes the data.
[b] The age × body mass interaction was significant for Canvasbacks, therefore we provided separate analyses for each age class.

effects (i.e., $\chi^2 = 31.82$ with 9 df) could be accounted for by replacing the nine parameter estimates for year effects with a single parameter describing annual variation in May water levels (Fig. 1; $\chi^2 = 16.05$ with 1 df). Nests with manipulated clutches were more successful than unmanipulated clutches, probably because the host's clutch was usually replaced with eggs that were further along in incubation, and average exposure to nest predation was therefore shortened by about five days at manipulated nests (Anderson et al., in press b). Adult body mass tended to vary among years (Table 3; $P = 0.07$), but was not affected by any other variable ($P > 0.37$).

Among yearling (SY) Canvasbacks, failed nesters weighed 37 g less than successful nesters (946 ± 14 g [$n = 12$] vs. 983 ± 9 g [$n = 27$]; $P = 0.03$). No other variables influenced nest success of yearlings ($P > 0.37$). Body mass of yearlings varied with nest fate, year, and the interaction between year and nest fate (Table 3). During 1986–1988, failed yearlings weighed significantly less (or nearly so) than successful yearlings, but in 1983 no difference was detected (Table 4).

Nest fates of Redheads were affected only by female age (Table 2, $P = 0.04$); 20 of 71 adult nests failed (28.2%), versus 4 of 5 yearling nests (80%). Body mass of successful nesters was 859 ± 9 g, versus 853 ± 7 g for unsuccessful nesters ($\chi^2 = 0.06$, $P = 0.81$). Redhead body mass was not related to any other variable that we analyzed ($P > 0.47$).

Duckling survival was independent of female body mass for both species (Fig. 2). Correlations between body mass and duckling survival were −0.03 and 0.05 for Ib and IIb Canvasback broods ($P = 0.71$ and 0.64, $n = 139$ and 107, respectively), and 0.08 and 0.26 for Ib and IIb Redhead broods ($P = 0.69$ and 0.37, $n = 24$ and 14, respectively). No other variables (i.e., year, hatch date, or initial brood size) were significant ($P > 0.30$).

TABLE 3. Sources of variation in body mass of female Canvasbacks and Redheads during late incubation.

| Group | Model | | | Predictor[a] | Predictor(s) | |
|---|---|---|---|---|---|---|
| | $F$ | $P$ | $R^2$ | | $F$ | $P$ |
| Canvasbacks | 6.81 | 0.0002 | 0.05 | Fate | 3.69 | 0.06 |
| | | | | Age | 19.95 | 0.0001 |
| | | | | Fate × age | 4.97 | 0.03 |
| Adults | 0.04 | 0.84 | 0.00 | Fate | 0.04 | 0.84 |
| Yearlings | 7.10 | 0.0001 | 0.62 | Fate | 28.08 | 0.0001 |
| | | | | Year | 0.46 | 0.71 |
| | | | | Fate × year[b] | 7.59 | 0.0006 |
| Redheads | 0.07 | 0.80 | 0.00 | Fate | 0.07 | 0.80 |

[a] See text for presentation and discussion of effect sizes.
[b] See Table 4 for analysis of Fate × year interaction effect.

TABLE 4. Annual variation in body mass of successful and unsuccessful yearling Canvasbacks.

| Year | Successful nesters $\bar{x}$ ± SE ($n$) | Unsuccessful nesters $\bar{x}$ ± SE ($n$) | $P$ |
|---|---|---|---|
| 1983–1984[a] | 968 ± 7 (10) | 975 ± 10 (4) | 0.57 |
| 1986 | 995 ± 8 (7) | 930 ± 15 (2) | 0.0005 |
| 1987 | 984 ± 7 (8) | 940 ± 21 (1) | 0.06 |
| 1988 | 1,015 ± 15 (2) | 931 ± 9 (5) | 0.0001 |

[a] Only one successful and one unsuccessful nester were trapped in 1984; data from these two birds were therefore combined with 1983 data for analysis.

Body mass of returning female Canvasbacks averaged 5 g less than for nonreturning females (998 ± 3 g vs. 1,003 ± 6 g; $n$ = 255 and 69, respectively), but this slight difference was not significant ($\chi^2 = 0.41$, 1 df, $P = 0.39$). However, early nesting Canvasbacks had a higher probability of being seen in a future year ($\chi^2 = 8.87$, 1 df, $P = 0.003$). Mean Julian nest initiation dates were 139.5 ± 0.8 (20 May) for females that were seen again ($n$ = 261) and 144.7 ± 1.7 for (25 May) females that were not seen again ($n$ = 70). For Redheads, return rates were unrelated to any measured variable ($P \geq 0.26$). Females that were seen again weighed 859 ± 8 ($n$ = 50), whereas females that were not seen again weighed 845 ± 13 ($n$ = 24; $\chi^2 = 0.98$, 1 df, $P = 0.32$).

## DISCUSSION

Body mass did not affect subsequent nesting success of Redheads. For Canvasbacks, body mass had no effect on nesting success of adults (ASY), but was related to nesting success among yearlings (SY). The differences in body mass between successful and unsuccessful Redheads and adult Canvasbacks averaged 6 and −3 g, respectively, and we dismiss them as inconsequential (i.e., <1% of mean body mass). However, the 37 g difference between successful and unsuccessful yearling Canvasbacks represents about 4% of average late-incubation body mass. If this latter difference represents variation in body fat, then successful females would have had about 333 additional kcal of reserve energy (assuming 9.0 kcal/g fat), which would have allowed them to incubate approximately 2.6 additional days without food (calculations follow Afton and Paulus 1992: Table 3–13). Alternatively, if the difference reflected variation in reserve protein, then successful females would have had about 40 additional kcal of reserve energy (assuming 75% water content of muscle tissue and 4.3 kcal/g lean dry muscle mass), which would have allowed

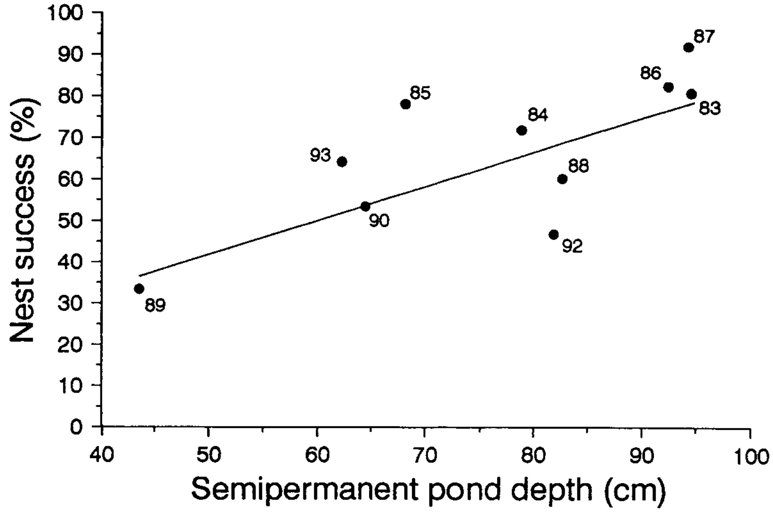

FIGURE 1. Annual variation in nest success of nest-trapped female Canvasbacks in relation to maximum depth of semipermanent ponds in early May ($\chi^2 = 31.82$, $P < 0.0001$; see text). Pond data are from Anderson et al. (In press a).

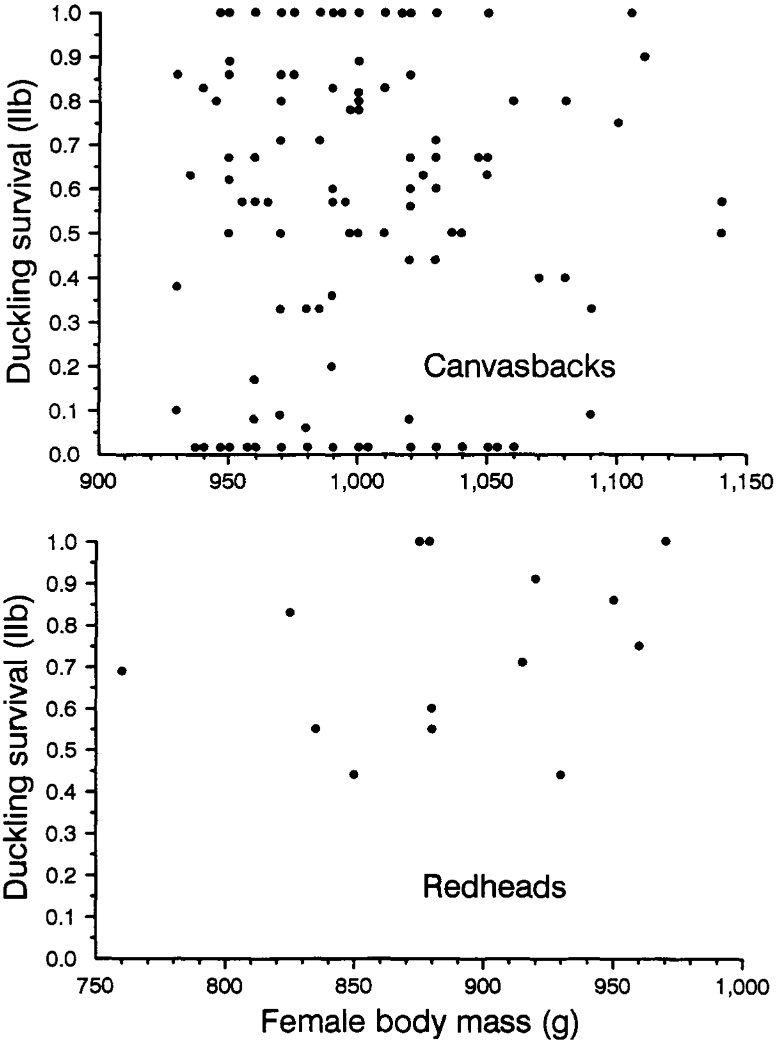

FIGURE 2. Proportions of Canvasback and Redhead ducklings surviving to age-class IIb (ca. 33–42 days old) in relation to female body mass during late incubation. Each datum represents one brood. Neither correlation was signification (see text).

them to incubate only 0.3 additional days. We conclude that if the relationship between body mass and nest success in yearling Canvasbacks is causal, then it is probably related to variation in body fat, because the energy that would be available from catabolizing 37 g of muscle tissue appears to be trivial.

Gloutney and Clark (1991) observed significant ($P = 0.02$, 1-tailed) differences in body mass of 37 and 32 g between successful and unsuccessful Mallards and Northern Shovelers, respectively, but not between successful and unsuccessful Blue-winged Teal ($P = 0.44$). Their samples included 57 Mallards, 36 Northern Shovelers, and 52 Blue-winged Teal, which were roughly equivalent to our samples of 76 Redheads and 39 yearling Canvasbacks, but much smaller than our sample of 353 adult Canvasbacks. Our samples of adult Canvasbacks and Redheads were large enough to have detected significant differences ($P \leq 0.05$, 1-tailed) in body mass of 9 and 21 g with 80% power, and Gloutney and Clark's sample of Blue-winged Teal was sufficient to detect a difference of about 14 g (Steel and Torrie 1980:118–119). Thus, if Blue-winged Teal, Redheads, and adult Canvasbacks had exhibited 30 to 40 g differences in body mass between successful and failed nesters (as did Mallards, shovelers, and yearling Canvasbacks), it almost surely would have been significant. Hence, we conclude that the different responses of these species to variation in body mass are not artifacts of sample size variation.

Gloutney and Clark (1991) attributed the absence of a significant relationship between body mass and nest success in Blue-winged Teal to their small body size and concomitant inability to store large amounts of nutrient reserves. Nevertheless, teal lose proportionately as much body mass during incubation as do Mallards and Northern Shovelers (Afton and Paulus 1992, Table 3–13), so this explanation may not be appropriate. Furthermore, this explanation clearly cannot apply to adult Canvasbacks, which outweigh all these species, or to Redheads, which are similar in mass to Mallards, but outweigh shovelers and teal.

Although Gloutney and Clark (1991) did not identify causes of nest failure in their study, we suspect that their results (particularly for Mallards) may have been due to investigator-induced nest abandonment. Mallards are well known for their tendency to abandon nests in response to investigator disturbance (Rohwer 1984, Forbes et al. 1994), especially from nest trapping (Hunt and Anderson 1966, Coulter and Miller 1968). Investigator-induced nest abandonment in Mallards can be largely eliminated if hens are anesthetized during handling (Rotella and Ratti 1990; D. W. Howerter, pers. comm.), but this technique was not widely known when Gloutney and Clark (1991) conducted their study. Nest trapping also may have increased abandonment by Canvasbacks in our study (see also Serie et al. 1992). On the Anderson study area, 21 of 250 (8.4%) Canvasbacks abandoned their nests after trapping, whereas 0 of 59 nests were abandoned if the female was not trapped ($G_{adj}$ = 4.07, $P = 0.04$; this analysis was restricted to untrapped nests that had been discovered at similar stages of incubation [15–25 days]). Investigator disturbance might also have contributed to the age-related variation that we observed in nest fates of Canvasbacks. During 1983–1984 and 1986–1988 (the only five years in which yearlings were known to have nested), 6 of 39 yearlings (15.4%) abandoned following nest trapping, whereas only 16 of 246 adults (6.5%) abandoned during these years ($\chi^2_{adj} = 2.58$, $P = 0.11$). Nevertheless, if we excluded nests that were abandoned, we still observed a significant relationship between nest success and body mass in yearling Canvasbacks ($\chi^2 = 6.22$, $P = 0.01$). Thus, variation in sensitivity to investigator disturbance may have affected our results for yearling Canvasbacks, as well as Gloutney and Clark's (1991) results for Mallards and Northern Shovelers, but such results still indicate that this source of nest failure was condition dependent. Such a response might be indicative of a natural tendency for light-weight birds to have greater nest abandonment in the absence of investigator disturbance, but we suggest that such a natural response would be weaker than an investigator-induced response.

Critics could argue that many light-weight Canvasbacks and Redheads may have lost their nests before we were able to trap them during the last 10 days of incubation, but this criticism would also apply to Gloutney and Clark's (1991) study. Although we did not measure body mass during early incubation, Hepp et al. (1990) were able to weigh female Wood Ducks (*Aix sponsa*) during both early (< 15 days) and late (> 15 days) incubation; however, they observed no effects of early-incubation body mass on hatching success ($P > 0.55$) or length of incubation ($P > 0.15$), despite impressive sample sizes ($n$ = 152 birds over three years).

For temperate-nesting waterfowl, we suspect that nutrient reserves are more likely to affect incubation behavior, rather than likelihood of nest abandonment. Incubating ducks that find themselves low on reserves should be able to increase their foraging time (i.e., they obtain > 70% of their energy requirements exogenously; see Afton and Paulus 1992, Table 3–13). Increasing the amount of time spent foraging would lead to reduced incubation constancy, which might result in lower hatchability or longer incubation time (and hence, longer exposure to nest predators), but both of these costs would be lower than that incurred by outright abandonment of a nesting attempt.

Although we did not measure behavioral tradeoffs during incubation, we were able to assess potential trade-offs after incubation was completed. However, late-incubation body mass did not affect subsequent reproductive success during brood-rearing, or the likelihood that adults would survive to breed again. For Canvasbacks, our sample of monitored broods was large enough to have provided significant results ($P < 0.05$, 2-tailed), even for relatively weak relationships ($r^2 > 0.025$); nevertheless, we did not detect an effect of adult female body mass on duckling survival ($r^2 < 0.003$, $P > 0.64$). With respect to adult survival, we would have had an 80% chance (1-tailed test, $P < 0.05$) of detecting a difference as small as 9 g between returning and non-returning female Canvasbacks, but the observed difference was only 5 g, and it was in the wrong direction. For Redheads, our tests had less power to detect significant differences (brood survival: $r^2 > 0.23$; adult survival: effect size > 21 g), so it was not surprising that we observed none. Thus, at least for Canvasbacks, we conclude that variation in adult female body mass had no future effects on brood survival or adult return rates.

Body mass was associated with future reproductive success in only one analysis involving nest success of yearling Canvasbacks. Although it was tempting to dismiss this single significant result as an artifact of small sample size ($n = 39$), the small sample was attributable to lower reproductive effort and success among yearlings (Serie et al. 1992), and not to insufficient sampling effort. Our results suggest that yearling Canvasbacks may also have more difficulty meeting the energetic demands of incubation. Further studies of the effects of age on the energetics of laying and incubation in Canvasbacks would be enlightening.

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