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CHANGE IN BODY MASS OF FEMALE COMMON GOLDENEYES DURING NESTING AND BROOD REARING

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ABSTRACT.—We measured body mass of female Common Goldeneyes (*Bucephala clangula*) during nesting on fish bearing lakes in northcentral Minnesota, in 1982–1985. Median body mass during egg laying was 775 g. Female mass during incubation varied among lakes and possibly years. Mass at the start of incubation (698–715 g) was 10.7–11.0% greater than that at hatching. Females regained most of the mass lost during incubation by the time they abandoned their class IIC or class III ducklings. Goldeneyes in Minnesota weighed less at the start of nesting than those studied on predominately fishless Ontario lakes; proportional mass loss during incubation was also substantially less than that reported in Ontario (approximately 20%). Differences in body mass dynamics may be related to the relative ease of food acquisition during nesting; foods might be acquired more easily in more productive wetlands despite the presence of fish. *Received 24 Feb. 1995, accepted 1 Sept. 1995.*

Relationships among incubation behavior, female body mass, and types of nutrients and energy sources used by temperate nesting waterfowl are understood reasonably well. In general, species that begin nesting earlier have greater body mass, forage relatively less while nesting, rely more on endogenous resources, and lose proportionately more mass during incubation than do later nesting species (see review in Afton and Paulus 1992). Common Goldeneyes (*Bucephala clangula*) deviate somewhat from this pattern. Although they are relatively small-bodied, females begin nesting soon after arrival when many wetlands are still ice-covered. Foraging territories also are defended vigorously during laying and early incubation (Savard 1984, Zicus and Hennes 1993). In addition, laying rates are low compared to other similar-sized waterfowl (cf Palmer 1976), and clutch mass can exceed female mass (Zicus, unpubl. data). These traits suggest that although females arrive with some stored reserves, exogenous nutrient sources may be important for clutch completion and female maintenance during incubation.

Mallory and Weatherhead (1993) recently predicted that female Common Goldeneyes lose approximately 18.5% of their body mass during incubation. Their prediction was based on relationships proposed by Afton and Paulus (1992) and appeared to be supported by data from an Ontario study where wetlands had been influenced extensively by acid

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deposition (Mallory et al. 1994). Harvey et al. (1989) concluded that Wood Duck (*Aix sponsa*) body mass dynamics during incubation varied substantially among and within individuals. They speculated that variability in Wood Duck incubation mass was related in part to fluctuating environmental conditions. Unfortunately, few published data relate local or regional environmental factors to body mass changes in other species of incubating waterfowl.

We describe body mass changes during nesting and brood rearing for female Common Goldeneyes in Minnesota. We examined the effects of different lakes and years and of changing reproductive stage on female body mass. Goldeneyes have been studied previously in areas where fish were absent or where goldeneyes appeared to favor fishless wetlands thereby avoiding dietary competition with fish during the reproductive period (Eriksson 1979, Eadie and Keast 1982, Blancher et al. 1992, and others). Whereas many lakes in Mallory and Weatherhead's 1993 study area were fishless (Mallory et al. 1994), each of our study lakes supported fish communities. Thus, our data should improve the understanding of goldeneye nesting biology where they commonly occupy fish-bearing lakes.

STUDY AREA AND METHODS

Female Common Goldeneyes were weighed during nesting on three lakes in Beltrami and Itasca counties of northcentral Minnesota. Refuge Pond, North Twin Lake, and Island Lake differed in size (46, 117, and 1250 ha, respectively), amount and type of public use, and use by goldeneyes (Zicus et al. 1995). The two larger lakes supported fish populations (dominated by Centrarchidae, Percidae and Esocidae) and were characterized by morphoedaphic indices (MEI) (Ryder 1965) of 6.75 and 18.01, respectively (Minn. Dept. Nat. Resour., Section of Fisheries, unpubl. data). These values are near optimum for highly productive fish communities (Ryder et al. 1974). The smallest lake supported only minnows. Females with hatched young were captured and weighed on Refuge Pond and Island and North Twin Lakes as well as on 10 additional lakes, each of which supported productive fish populations with species composition similar to those in the lakes where nesting ducks were weighed. These additional lakes had MEIs ranging from 4.52 to 21.78 (Minn. Dept. Nat. Resour., Section of Fisheries, unpubl. data).

Female Common Goldeneyes were captured before incubation began with nest traps (Zicus 1989) and again when we inspected nest boxes for use. Females were leg banded with U.S. Fish and Wildlife Service bands. Incubating female mass was measured when possible during weekly nest checks, and females accompanying broods were weighed when they were caught nest prospecting (Zicus and Hennes 1989) and during annual leg banding (Johnson 1972). Mass was determined to the nearest 5 g using spring scales and was unadjusted for female structural size.

Reproductive stage for egg-laying females was defined relative to the start of incubation, and that of incubating and brood-rearing females was referenced to the departure of young from nests. This differs from the convention often used for incubating females. However, we believe it is preferable because it allows corresponding days to be compared more appropriately. Reproductive stage of females with young from unmonitored nests was estimated from the age of the majority of the ducklings in the brood. Duckling age was determined by comparison with known-age ducklings in various stages of plumage development. Plumage stages were assigned the following ages: IB—10 days, IC—18 days, IIA—27 days, IIB—35 days, and IIC—44 days.

We examined mass change of females before incubation using linear regression (PROC GLM; SAS Institute Inc. 1988). Year and location effects could not be examined because too few females were captured. Most females were weighed more than once during incubation, so we investigated their mass change using a generalized linear mixed model (GLMM) with maximum likelihood estimators (PROC MIXED; SAS Institute Inc. 1992). This approach allows measurements on subjects to be repeated within and across years. Dependencies among repeated measures are modelled explicitly and ensuing tests are adjusted for this dependence based on the underlying covariance structure (Laird and Ware 1982, Ware 1985). We determined (Jennrich and Schluchter 1986) that a compound symmetry covariance structure was optimal for our models. We modelled the effect of lake, year, linear, quadratic, and cubic effects of incubation day, and their interactions on female mass. When interactions were not significant ($\alpha = 0.05$), we used a reduced model. Log-likelihood ratio statistics were used to evaluate model goodness of fit, and simultaneous paired comparisons were made using a Bonferroni adjustment to pairwise differences in the time-adjusted means (Dobson 1990). Brood-rearing females were measured only once and their mass change was examined using linear regression (PROC GLM; SAS Institute Inc. 1988). We ignored possible lake and year effects because too few brood-rearing females were measured.

We further examined nonsignificant statistical results using post hoc power analyses (Anonymous 1995). Regression results were evaluated using a SAS MACRO (Latour 1992). Power calculations for the generalized linear mixed model were based on adjusted least squares effects estimated by PROC MIXED (SAS Institute Inc. 1992).

RESULTS

From 1982 to 1985, 45 females were weighed prior to or during egg-laying. In addition, 82 females were weighed repeatedly (1–5 times each year) for a total of 213 times at known points during incubation or with hatched young in the nest. One female was weighed in four years, five in three years, 25 in two years, and 51 in only one year for a total of 120 within-year time-series. During brood rearing, 63 females were weighed.

Prelaying and laying.—Reproductive status of females weighed before the start of incubation varied (Table 1). Those considered known nesters successfully incubated nests that we observed. Known nesters were weighed from one to 30 days before incubation (median = 15.5 days) and most likely represented females that were beginning to lay the clutch that they eventually incubated. In contrast, the sample of unknown status likely included females nesting elsewhere as well as those laying eggs parasitically when captured. We could not detect any linear trend in mass of known nesters during the laying period (mass change = 1.5 g/day, 95% confidence interval = −0.4 to 3.5).

Incubation.—We fit the GLMM to measurements of mass for females that successfully incubated a clutch. We detected no significant interac-

TABLE 1

MASS OF FEMALE COMMON GOLDENEYES CAPTURED DURING THE LAYING PERIOD IN NORTHCENTRAL MINNESOTA, 1982–85

	Mass (g)					Stage (days)[a]
Status	$\bar{x}$	SD	Median	Range	N	Median
Known nesters	768	34.0	775	685–810	16	15.5
Unknown	733	43.8	720	660–830	29	?

[a] Days prior to the start of incubation.

tions among the main effects (lake and year) and linear, quadratic, or cubic measures of incubation day (all *P*s > 0.46) that affected mass loss. Two models, one linear and one cubic with incubation day, indicated mass was influenced by stage of incubation. The cubic model fit the data best ($G^2 = 16.48$, df = 2, $P < 0.001$) and indicated a curvilinear effect of stage on female mass (Table 2 and Fig. 1).

Body mass also was influenced by conditions related to specific lakes ($F = 2.72$; df = 2, 79; $P = 0.072$). Female body mass was greater throughout incubation on Island Lake than on North Twin Lake ($F = 4.29$; df = 1, 79; $P = 0.041$), but mass did not differ between Refuge Pond and either North Twin ($F = 0.00$; df = 1, 79; $P = 0.980$) or Island Lake ($F = 1.94$; df = 1, 79; $P = 0.167$) (Fig. 1).

We detected no effect due to different years with the GLMM ($F = 0.75$; df = 3, 125; $P = 0.523$), but graphical comparison of body mass of females for whom we had measurements in 1982 and 1983 suggested year might have an effect. Each of the four females was weighed at similar points during incubation both years, and each was 20–40 g lighter in 1983 than 1982 (Fig. 2).

Four of eight females that abandoned their nests during incubation had

TABLE 2

ESTIMATED COEFFICIENTS FOR POLYNOMIAL MEASURES OF INCUBATION DAY ON MASS CHANGE IN FEMALE COMMON GOLDENEYES FROM THREE NORTHCENTAL MINNESOTA LAKES, 1982–1985

Measure	$\hat{\beta}$	SE ($\hat{\beta}$)	P[a]
Day	6.3027	1.1799	<0.001
Day^2	−0.4127	0.0995	<0.001
Day^3	0.0083	0.0023	<0.001

[a] Two-sided test H_0: $\beta = 0$.

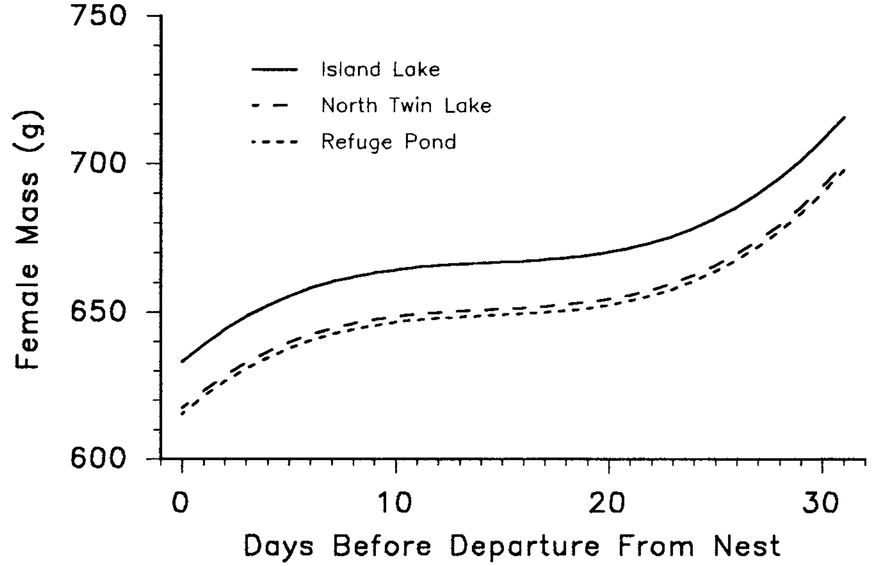

FIG. 1. Maximum likelihood estimates of cubic temporal trend in female Common Goldeneye body mass during incubation on three northcentral Minnesota lakes, 1982–1985.

a body mass greater than that predicted for successful females at the comparable point in incubation, and four were less than predicted.

Brood rearing.—Females in the composite sample regained body mass at approximately 2 grams/day ($F = 51.7$; df = 1, 62; $P < 0.001$) from the low they had reached when the young departed the nest (Fig. 3). Females apparently regained most of the body mass lost during incubation by the time they left their broods of class IIC or class III ducklings to molt.

DISCUSSION

Our results differed markedly from previous measurements of Common Goldeneye mass. Minnesota goldeneyes appear to weigh less at the onset of nesting than do Ontario birds. Mallory (1991:17) reported that prelaying females averaged 875 g at his Wanapitei study site and 842 g at a site farther east. These values are 67–100 g more than our median at the start of laying and 12–45 g more than our heaviest females. Whether females truly differ to this extent is unclear. Our sample of prelaying females was small, and we weighed females at various times during prelaying and laying. Furthermore, the Wanapitei values are estimates obtained by adjusting female mass determined during incubation to account

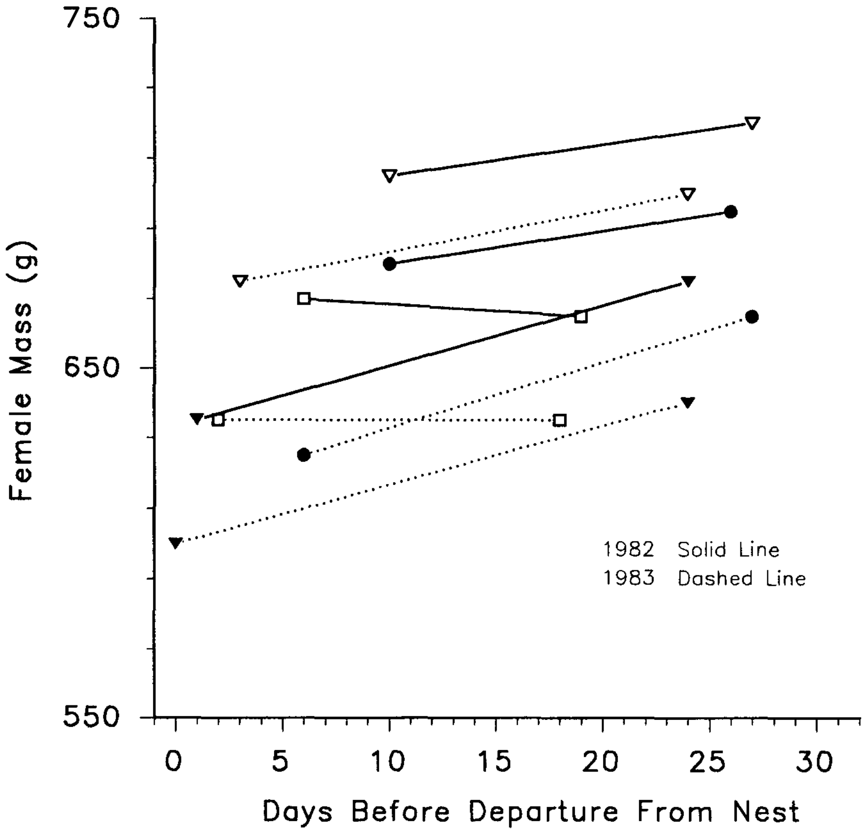

FIG. 2. Body mass of individual female Common Goldeneyes measured during incubation while nesting on three northcentral Minnesota lakes, 1982 and 1983. Individual females are identified by unique symbols.

for incubation mass loss and that assumed lost in the course of laying a clutch (Mallory 1991:16–17). Goldeneye females have been reported to lose approximately 22 g/egg (i.e., approximately 11 g/day) during egg laying (H. G. Lumsden, unpubl. data cited in Mallory 1991). We did not detect this sort of change in Minnesota, and there was sufficient power (>0.99) to detect a change of as little as 6 g/day. Projected mass of Wanapitei females may be biased high because mass loss per egg in Ontario is now believed to be <22 g (M. L. Mallory, Environ. Can., pers. comm.). Nonetheless, model predictions of mass for Minnesota females at the start of incubation ranged from 698–715 g depending on factors associated with the nesting lake. In contrast, Ontario goldeneyes appear

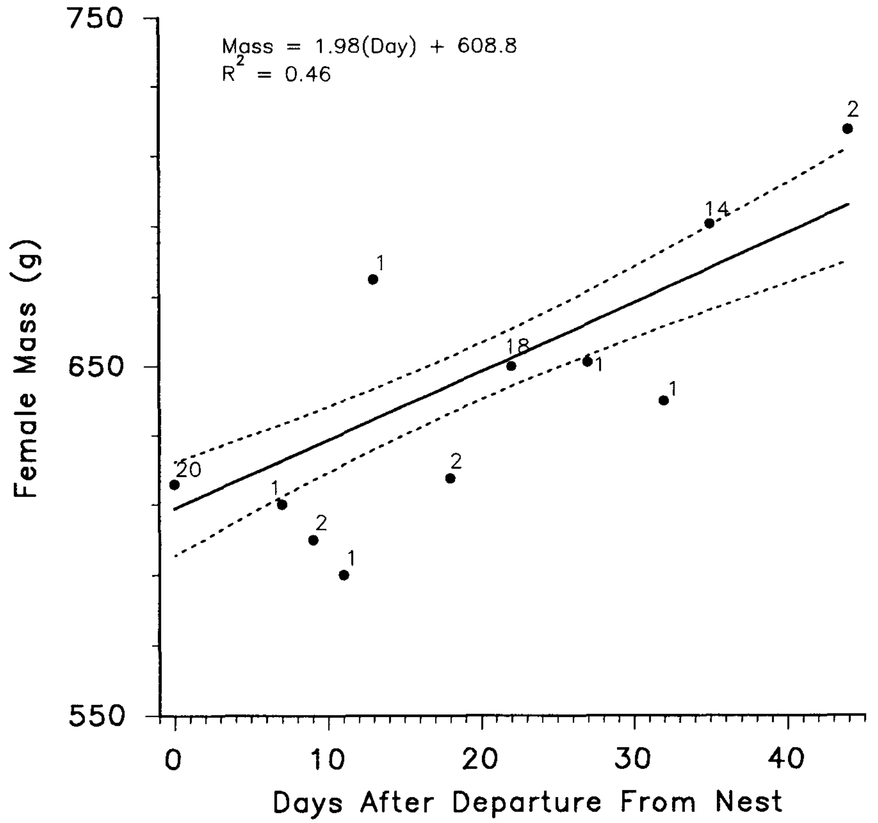

FIG. 3. Linear regression predictions (±95% confidence limits) and observed mean body mass (sample sizes) for female Common Goldeneyes with hatched young on 12 northcentral Minnesota lakes, 1982–1985.

to begin incubation at 752–829 g (calculated from Mallory and Weatherhead 1993).

Minnesota goldeneye females lost proportionately less mass during incubation than Ontario birds. Rate of mass change did not differ among nesting lakes or years, although our analysis indicated location and possibly year affected overall incubation mass. The proportionate mass loss by goldeneyes from the start of incubation until broods departed the nest (31 days) was 10.7–11.0% depending on the nesting lake. In comparison, Mallory and Weatherhead (1993) estimated mean mass loss variously and reported changes for Ontario goldeneyes of 16.7% (page 853), 17.8% (page 856), and 24.5% (calculated from equation page 853 using 31 days of incubation).

Incubating Common Goldeneyes apparently lose body mass in a nonlinear fashion (Mallory and Weatherhead 1993, this study). However, our analysis suggested a different pattern than that described for birds in Ontario. Minnesota goldeneyes experienced a rapid initial decline during early incubation, reduced rate of loss in mid-incubation, and an increased rate of loss again prior to hatching and duckling departure. Mass loss during incubation for Ontario females has been modelled as decreasing monotonically with the lowest mass occurring on the last day of incubation (Mallory and Weatherhead 1993:equation p. 853). However, Mallory and Weatherhead (1993:853) also indicated that some females reached their lowest mass as early as day 18 of incubation, after which some mass was regained.

Female mass when broods departed the nest was similar in Ontario and Minnesota, but again measurements are not directly comparable. Mallory and Weatherhead (1993:856) reported that mean body mass of 10 females at the end of incubation was 626 g. However, two of the females included in their sample had deserted their nests after 18 and 24 days of incubation, respectively. By comparison, Minnesota females were predicted to weigh 615–633 g on the departure day (model intercepts) depending on the lake. Unadjusted arithmetic mean mass on the day broods departed the nest was 616 g (N = 20).

Mallory and Weatherhead (1993) speculated that female goldeneyes that lost too large a proportion of their initial incubation weight or dropped below approximately 600 g might be more prone to nest abandonment than others. We observed no indication that mass of females deserting their nests differed from that of successful females, but more data are needed. Furthermore, seven of 20 successful females weighed the day ducklings departed the nest were less than 600 g and five were ≤580 g. Some females remained below 600 g well into brood rearing.

Methodology alone does not explain the marked differences in incubation mass and proportional mass change during incubation in our study versus those reported for Ontario goldeneyes. At least two explanations are tenable. In addition to the well known difference existing in geese, body size has been shown to vary geographically in some passerines (Aldrich and James 1991, Twedt et al. 1994). Ontario females may be structurally larger than those nesting in Minnesota and thus able to return to breeding areas with more stored reserves. Alternatively, Ontario females may be similar in size but may return with proportionately more stored resources (i.e., better condition). Several studies (e.g., Gatti 1983, Harvey et al. 1989, Aldrich and Raveling 1983) have reported that heavier individuals lost a greater proportion of their body mass in incubation than lighter conspecifics. Gatti (1983) reasoned that heavier Mallards (*Anas* *platyrhynchos*) could afford to lose more mass than those in poorer condition. In contrast, Kennamer and Hepp (1987) reported that double-brooded Wood Duck females lost a smaller proportion of their body mass after their first nesting than single-brooded females and may have been in better condition as a result.

Whether Ontario females are structurally larger than those in Minnesota or just begin incubation in better condition, incubation constancy was similar in the two locations (Mallory and Weatherhead 1993, Zicus et al. 1995). Together with the disparate mass loss and comparable weights at the end of incubation, these results indicate that either differences in foraging time during incubation recesses exist or else Ontario females consume less food or food of lower quality during incubation than do Minnesota females. Most resident nesting goldeneyes from Island Lake and Refuge Pond appeared to forage exclusively on their respective lakes, whereas most females nesting on North Twin Lake foraged elsewhere. Zicus and Hennes (1993) observed nesting female goldeneyes feeding at least as much as most small-bodied waterfowl which rely extensively on exogenous resources. They also reported that time devoted to foraging during nesting varied among years and concluded that females foraged less when food was most available. Harvey et al. (1989) likewise believed that reduced food availability in some years contributed to a greater relative mass loss during incubation in Wood Ducks. Furthermore, incubation mass was lowest on Refuge Pond, the location among our three study sites where Zicus et al. (1995) reported low incubation constancy in a concurrent study. They speculated that low constancy was a consequence of increased foraging time because of more difficult food acquisition.

Goldeneye mass during incubation varied among the lakes that we studied. Although we detected no differences among years with the GLMM, measurement of a small sample of the same females in two consecutive years suggested that yearly differences of at least 20 g might exist in some years. The GLMM analysis had low power (0.46) at $\alpha = 0.05$ to detect such a difference. Nonetheless, the among lake and year mass differences we measured were less than differences between Minnesota and Ontario. Mann and Sedinger (1993) suggested that Northern Pintail (*Anas acuta*) females nesting in Alaska relied more on endogenous resources than temperate nesting congeners because of less productive high latitude wetlands. Goldeneyes might use different nesting strategies depending on average environmental conditions and food availability in the regions they occupy. In some regions, wetland productivity may be sufficient to provide adequate goldeneye food availability even in the presence of fish (DesGranges and Gagnon 1994:220). Resource acquisition would then be less constrained by female foraging time because food could be acquired easily. Patterns of body mass change before and during incubation indicate this situation is likely in Minnesota. Alternatively, females might rely more on resources acquired before arrival to nesting areas where wetland productivity is low. If nesting strategy within the species is flexible, relationships among habitat quality, female mass, and reproductive effort and success (Mallory et al. 1994) may need to be reexamined.

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