FEMALE HOODED MERGANSER BODY MASS DURING NESTING[1]

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Abstract: Body mass of female Hooded Mergansers (*Lophodytes cucullatus*) nesting in widely dispersed and newly erected wooden nest boxes in northcentral Minnesota was measured in 1982–1985. Median body mass during egg-laying was 635 g. Female mass during incubation varied significantly among years, but decreased monotonically at the same rate (1.0 g day^{-1}) each year. Mass at the end of incubation (519–494 g) was 5.7 to 6.0% less than when incubation began. There was no indication that females having the greatest body mass began nesting earliest. However, females with the greatest body mass incubated the largest clutches and hatched the most young. Comparison of the observed body mass-clutch size relationship with one assumed to exist in the absence of intraspecific brood parasitism indicated that more parasitic eggs were laid in nests incubated by heavier females.

Key words: Hooded Mergansers, Lophodytes cucullatus, *incubation body mass, brood parasitism.*

INTRODUCTION

Changes in the body mass of females during incubation have been studied for many waterfowl (see review in Afton and Paulus 1992). However, within-species variability of body mass change during incubation is still poorly understood for most species, particularly the degree to which body mass responds to varying environmental conditions. Mass change of incubating Common Goldeneyes (*Bucephala clangula*) differed substantially from Ontario to Minnesota (Mallory and Weatherhead 1993, Zicus and Riggs 1996) and even among lakes and years in the same locality (Zicus and Riggs 1996). Similar comparative studies are needed for other species. Hooded Mergansers (*Lophodytes cucullatus*) nest from northern Florida and New Mexico northward to at least southern Canada (Dugger et al. 1994). Thus, they are likely to encounter a wide range of environmental conditions that could influence foraging patterns, nutrient acquisition, and ultimately incubation body mass change and reproduction.

Body mass change was measured during nesting for female Hooded Mergansers in Minnesota. Yearly differences and the effect of incubation stage on female body mass were examined. Body mass of fe-

males in relation to the date incubation started, size of the incubated clutch, and number of young hatched also was assessed.

METHODS

STUDY AREA

The study was conducted in northcentral Minnesota. The area contained lakes and wetlands in an east-west morainic ridge with a narrow sandy plain extending to the north (see Zicus 1990 for a more detailed description). Open-water ponds supporting little emergent shoreline vegetation were the predominate wetland type. Wetland densities in the moraine averaged 7–8 basins km^{-2}. The hilly moraine was almost entirely forested by aspen (*Populus* spp.) with lesser amounts of birch (*Betula* spp.) and basswood (*Tilia americana*). Pines (*Pinus* spp.), particularly jack pine (*P. banksiana*), dominated the sand plain.

PROCEDURE

Twice-weekly checks of wooden nest boxes began in mid- to late March each year. When an egg was found, nests were reexamined weekly. At each visit, clutch size was noted and several eggs were candled (Weller 1956). As hatch day approached, nests were visited more frequently to determine exact hatch dates. Females, when present during a nest-box check, were captured, weighed, and leg-banded. Body mass was determined to the nearest 5 g and was not scaled to account for variable female skeletal size.

A variety of information was used to determine nesting chronology. For nests that were visited more than once during laying, the dates the first and last eggs were laid were estimated by assuming an average laying rate of 1 egg every 2 days (Dugger et al. 1994). Intraspecific brood parasitism was common (Zicus 1990), and nests often received > 1 Hooded Merganser egg in 2 days. For these nests and those that were examined once during laying, incubation starts were estimated by backdating from known hatching dates. I assumed a 32-day incubation period (Zicus 1990, Dugger et al. 1994) when candling eggs and backdating nests. Clutch size included parasitic and nonparasitic merganser eggs as there was no reliable way to distinguish the two. Eggs laid as a result of brood parasitism by Wood Ducks (*Aix sponsa*) and Common Goldeneyes were not included in the analysis. Reproductive stage for egg-laying females was defined relative to the start of incubation, and that of incubating females was referenced to the departure of young from nests. This differs from the convention often

used for incubating females, but it is preferable because it allows more meaningful comparison among corresponding days (Zicus et al. 1995).

Many females were weighed more than once during incubation, so their mass change was investigated 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 modeled explicitly and ensuing tests are adjusted for this dependence based on the underlying covariance structure (Laird and Ware 1982, Ware 1985). A first-order autoregressive covariance structure was determined to be optimal for the models (Jennrich and Schluchter 1986). I modeled the effect of year, linear, quadratic, and cubic effects of incubation day, and day of incubation interactions with year on female mass. When interactions were not significant (α = 0.05), a reduced model was used. Simultaneous paired comparisons were made using a Bonferroni adjustment to pairwise differences in the time-adjusted means (Dobson 1990).

Nest initiation date, date incubation started, incubated clutch size, and number of hatched young were regressed on female body mass residuals (PROC REG; SAS Institute Inc. 1990). In this analysis, only the residual from the first measurement of a female's body mass in each year was included. Females whose weights were associated with positive residuals were assumed to be heavier than the typical female and those with a negative residual were assumed to be lighter. Years were pooled in the analysis because yearly nesting chronology was similar (Zicus 1990).

Confidence intervals (95%) for the percent of all incubated eggs and hatched ducklings that occurred in nests incubated by females with positive body mass residuals were computed using the normal approximation for binomial proportions (Steel and Torrie 1980).

I also compared the relationship between body mass residuals and total clutch size with a presumed relationship that might have existed in the absence of brood parasitism. Clutch size, in the absence of brood parasitism, might be related to female mass in three ways: (1) number of eggs could be related positively to mass, (2) number of eggs could be independent of mass, or (3) number of eggs could be related inversely to mass. Egg-laying potential in Mallards (*Anas platyrhynchos*) is positively related to spring body mass (Johnson et al. 1987); thus, I assumed a positive linear relationship between merganser clutch size and female mass. The slope of the presumed relationship was established by further assuming that females with the smallest observed body-mass residuals laid the smallest clutches (5 eggs) and that those with the largest residuals laid the largest clutches (13 eggs). Five-egg clutches were the smallest incubated in the population and 13 eggs is likely near the maximum that a female can lay in one clutch (Zicus 1990).

RESULTS

Ten females were weighed during egg-laying, 42 during incubation, and seven with hatched young in the
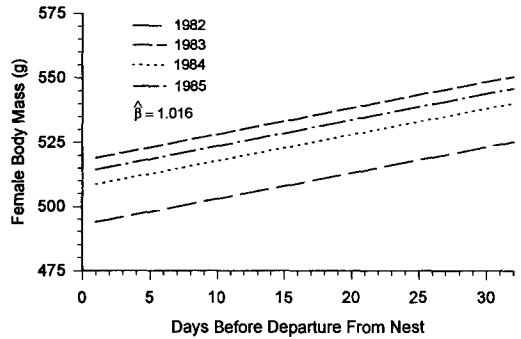

FIGURE. 1. Maximum likelihood estimates of linear trend in female Hooded Merganser body mass during incubation in northcentral Minnesota, 1982–1985. $\hat{\beta}$ is the common slope for all years.

nest. Females were weighed repeatedly during nesting from one to five times each year. This resulted in 100 weights at known points during incubation. Two females were weighed in four years, one in three years, eight in two years, and 30 in only one year. As a result, the analysis included 57 within-year time-series from 1982 to 1985. During the study, 13, 13, 24, and 7 females were weighed each year, respectively.

FEMALE BODY MASS

Egg-laying females were weighed from 1 to 20 days before they started incubating (median = 3 days). Weights ranged from 570 to 720 g (median = 635 g).

The GLMM was fit to measurements of mass for incubating females that successfully incubated clutches or had their nests destroyed during incubation by predators. Neither the cubic nor the quadratic model fit the data. For the linear model, there was no day of incubation $\times$ year interaction ($F_{3,51}$ = 0.43, P = 0.74) indicating slopes were similar in all years. However, both day of incubation ($F_{1,54}$ = 36.68, $P < 0.001$) and year ($F_{3,54}$ = 4.53, P = 0.007) influenced body mass significantly (Fig. 1). The model indicated that females lost approximately 5.7 to 6.0 percent of their body mass during incubation (day 32 to day 1).

The GLMM also estimated that females weighed from 493 to 518 g when they departed the nest with the brood (model intercepts) depending on the year. Unadjusted median body mass for females ready to leave the nest with hatched young was 480 g (range = 470–540).

REPRODUCTIVE ATTRIBUTES

Model residuals for female body mass were not correlated with the date nest initiation began (r = 0.11, n = 20, P = 0.65) and were only weakly and negatively correlated with the date that a female started incubating a nest (r = -0.29, n = 58, P = 0.03). In addition, incubated clutch size was not correlated with nest initiation date (r = -0.29, n = 20, P = 0.22) and only weakly and negatively correlated with the date incubation started (r = -0.29, n = 58, P = 0.03). Apparently, egg-laying did not begin earlier in
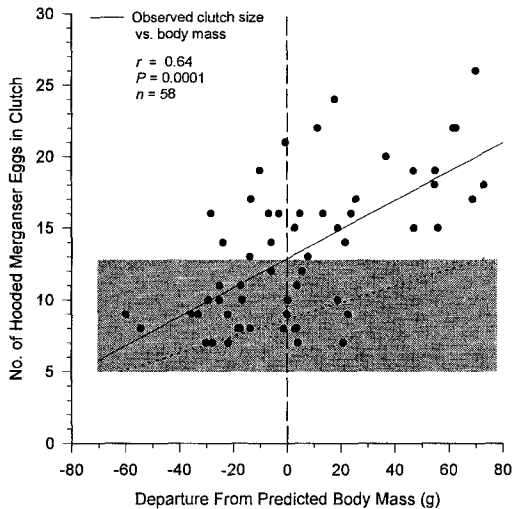
FIGURE. 2. Correlation of linear model residuals for body mass with number of Hooded Merganser eggs in the clutch in northcentral Minnesota, 1982–1985. Shaded area represents the presumed range in unparasitized clutch size. Dotted line represents the relationship between body mass and clutch size that was assumed to exist in the absence of brood parasitism.

FIGURE. 3. Correlation of linear model residuals for body mass with number of hatched Hooded Merganser eggs in the clutch in northcentral Minnesota, 1982–1985.

nests incubated by heavier females than it did in nests incubated by lighter females; however, heavier females may have begun incubation earlier. Further, there was no compelling evidence that nests with larger clutches were established earlier in the season than those with smaller clutches.

Body mass residuals of incubating females were correlated ($r = 0.64$, $n = 58$, $P < 0.001$) with the total number of Hooded Merganser eggs in the clutch (Fig. 2) and the number of hatched merganser ducklings ($r = 0.60$, $n = 48$, $P < 0.001$) (Fig. 3). These positive correlations suggested that heavier females incubated larger clutches and hatched more young than lighter females. When nests were pooled across all years, females with positive residuals incubated 60.5 percent (95% confidence interval = 57.1 to 63.9%) of all incubated merganser eggs and hatched 64.5 percent (95% confidence interval = 60.7 to 68.3%) of all ducklings.

The observed relationship between body mass residuals and incubated clutch size (Fig. 2) had an estimated slope of 0.10 (95% confidence interval = 0.07 to 0.13). This was significantly greater than the slope (0.06) of the relationship between female body mass and the number of eggs laid in a clutch that was assumed to exist in the absence of brood parasitism. This indicated that more intraspecific brood parasitism occurred in nests incubated by heavier females than in those incubated by lighter birds.

DISCUSSION

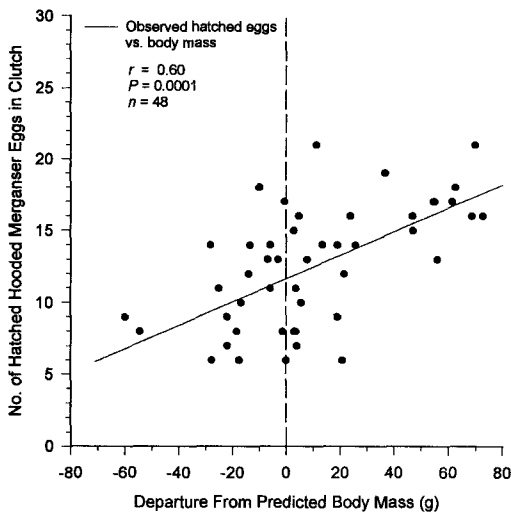Female Hooded Mergansers lost little body mass in the course of incubation. Considering their small body size, this was expected. Afton and Paulus (1992) predicted that females of small-bodied species would rely more on exogenous nutrient sources, exhibit lower incubation constancy, and lose proportionately less mass than would larger-bodied females. Although they are small-bodied, Hooded Mergansers may still rely, at least partially, on stored nutrients to initiate nesting. Nesting starts in Minnesota at a time when wetlands and small lakes are just beginning to become ice-free (Zicus 1990). This chronology differs from other small-bodied ducks such as Blue-winged Teal (*Anas discors*) and Northern Shovelers (*A. clypeata*) that forage intensively after arrival on the nesting grounds before egg-laying begins. Low egg-laying rates by Hooded Mergansers (Zicus 1990, Dugger et al. 1994) may be one factor that allows females to complete a clutch early in the season while relying on primarily exogenous nutrient sources.

Hooded Merganser mass loss during incubation might be greater in other locations although there are too few data to know. Mallory et al. (1993) estimated that nine females lost >3 g day^{-1} in Ontario based on single measurements taken during incubation and pooled over a number of years. This rate suggests a loss of about 17 percent of female body mass during incubation, assuming an incubation period of 32 days. Kennamer et al. (1988) reported on two South Carolina females which were measured once in early incubation and again at hatching; mass change averaged about 13 percent assuming a 32-day incubation period (calculated from Kennamer et al. 1988).

Many factors, including nesting chronology, female age, body condition, and access to food, have been related to the reproductive output of waterfowl. For cavity nesting species, the extent and magnitude of intraspecific brood parasitism also can be important (Jones and Leopold 1967, Morse and Wight

1969, Heusmann et al. 1980, Semel et al. 1988). Various hypotheses about the significance of intraspecific brood parasitism have been proposed (see review in Sayler 1992), but reasons why specific nests are parasitized remain poorly understood.

Several mechanisms consistent with a number of hypotheses have been used to explain the selection of specific nests by females laying eggs parasitically. Semel et al. (1988) suggested that highly visible nest structures erected in high densities were parasitized more by Wood Ducks. During this study, nest structures available to Hooded Mergansers were newly erected and widely spaced in the landscape (Zicus 1990), likely minimizing the effects of structure placement on intraspecific brood parasitism. Nonetheless, brood parasitism was prevalent in all years. Both Redheads (*Aythya americana*) (Weller 1959, Sayler 1985) and Wood Ducks (Grice and Rogers 1965, Clawson et al. 1979) have been reported to lay more parasitic eggs early in the nesting season. As a result, nests established earlier would be parasitized more and would likely have the largest clutch sizes. In my study, size of the incubated clutch was most strongly correlated with the body mass of the incubating female and proportionately more parasitic eggs occurred in nests incubated by the heavy females. I observed no compelling evidence that nests with more eggs or those incubated by the heaviest females were initiated earlier in the season than other nests.

The extent to which heavier females incubated proportionately more parasitic eggs was estimated conservatively. The other two assumptions regarding the relationship between female body mass and clutch size in the absence of brood parasitism that could have been considered would have increased the difference between the slopes of the observed and assumed relationships. This also would be true if the minimum clutch produced by a single female was >5 eggs or the maximum clutch that a single female can lay was <13 eggs. The observation that females with the greatest body mass tended to incubate proportionately more parasitic eggs is consistent with at least two hypotheses proposed to explain brood parasitism (Sayler 1992). Perhaps two or more females begin laying eggs in the same nest, and the heaviest female displaces other females and incubates the clutch. Female mass and the ability to displace other females could be related to age, reproductive experience, physical condition, or some combination. Alternatively, this could represent a situation wherein heavier females (i.e., mothers) were parasitized by lighter daughters. Clearly, much remains to be learned about brood parasitism in Hooded Mergansers.

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VARIATION IN INCUBATION PERIODS AND EGG METABOLISM IN MALLARDS: INTRINSIC MECHANISMS TO PROMOTE HATCH SYNCHRONY[1]

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Abstract: We investigated factors affecting incubation time and metabolic rates of Mallard (Anas platyrhynchos) eggs incubated under constant environmental conditions. Time required to reach the star-pipped stage of hatch varied significantly among females, but not with laying sequence or egg size. Metabolic rate of eggs varied positively with position in the laying sequence and tended to vary among females. Metabolic rate did not vary with egg volume or incubation length. Our results indicate metabolic rate may act as one synchronization mechanism for hatch. The role of maternal effects in development time should be considered in subsequent studies of incubation time in ducks.

Key words: Mallard, Anas platyrhynchos, metabolism, egg, incubation, incubation length.

INTRODUCTION

Waterfowl typically begin incubation before the clutch is complete (Caldwell and Cornwell 1975, Cooper 1978, Afton and Paulus 1992), which results in developmental asynchrony of eggs within clutches at the end of laying (Caldwell and Cornwell 1975, Afton 1979, Kennamer et al. 1990). However, asynchrony at hatching is less than that observed at the end of laying (Caldwell and Cornwell 1975, Afton 1979, Cargill and Cooke 1981), suggesting that some mechanisms exist to synchronize hatch (Afton 1979, Davies and Cooke 1983). Such mechanisms could include developmental retardation of eggs laid early in the laying sequence or developmental acceleration of eggs laid after the onset of incubation (Davies and Cooke 1983). Regardless of how such mechanisms work, eggs within clutches must have variable incubation lengths.

Synchronization mechanisms could be either extrinsic to the egg or intrinsic to the egg. Extrinsic mechanisms could include behavior of the parent. For example, eggs in the center of the nest have higher temperatures (Caldwell and Cornwell 1975), thus females may alter development time of specific eggs by regulating egg position in the nest. Also, vocal stimulation decreases time to hatching (Vince 1966, Orcutt and Orcutt 1976) and may accelerate development of later laid eggs (Davies and Cooke 1983). Intrinsic factors include inherent properties of the egg, such as egg composition, egg size, or physiology. Smaller eggs require less incubation, both among and within species (Worth 1940, Rahn and Ar 1974, Arnold 1993). Martin and Arnold (1991) found