

THE INFLUENCE OF FEMALE AGE, BODY MASS, AND AMBIENT CONDITIONS ON REDHEAD INCUBATION CONSTANCY¹

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Abstract. Incubation constancy, i.e., the proportion of time on the nest, of female Redheads (*Aythya americana*) was examined during the summers of 1995 and 1996 in relation to female age, body mass, and ambient conditions. Redhead females exhibited one of the lowest incubation constancy (82%) among duck species (Anatidae), coupled with a comparatively high number of incubation recesses per day. Low constancy was not due to excessive disturbance at the nest or reduced maternal investment in the clutch, but was probably related to energetic constraints of the female imposed by laying parasitic eggs prior to nesting. As in most other duck species, incubation constancy decreased over the incubation period. Age, mass, and maximum daily temperature, and the interactions of initiation day \times age and mass \times date significantly influenced daily incubation constancy. Constancy was higher for older females and for females of lower body mass and was lower on days with higher maximum daily temperatures.

Key words: *Aythya americana*, body mass, incubation constancy, Redhead.

INTRODUCTION

Incubation patterns vary among North American waterfowl species and are influenced by several factors. Interspecific differences in body size are correlated with varying incubation patterns (Afton 1980, Afton and Paulus 1992). Large-bodied waterfowl, such as geese (Anserini), spend more time on the nest and rely heavily on endogenous reserves (Cooper 1978, Raveling 1979). In contrast, small-bodied species (Anatini, Aythyini) rely more on exogenous resources, therefore spending more time off the nest (Krapu 1981, Drobney 1982, Barzen and Serie 1990). Among small-bodied duck species, incubation constancy, defined as the percent of time per day spent on the nest, also varies by body size. Representatives of large-bodied divers (Aythyini) and dabblers (Anatini), such as Canvasbacks (*Aythya valisineria*) and Mallards (*Anas platyrhynchos*), exhibit incubation constancy of 87% and 89%, respectively (Gatti 1983, Meade 1996). In contrast, small-bodied representatives of divers and dabblers, such as Ring-necked Ducks (*Aythya collaris*) and Blue-winged Teal (*Anas discors*), maintain constancy of 82% and 80%, respectively (Harris 1970, Hohman 1986). Afton and Paulus (1992) determined that incubation constancy was positively related to body mass at the

beginning of incubation for all species they compared, although the relationship was strongest for geese and *Anas* species.

Ambient conditions, such as rainfall and temperature, also influence incubation patterns, particularly in small-bodied species. Large-bodied waterfowl have greater capacity for fat storage and thus rely on those reserves, whereas small-bodied species are unable to rely on endogenous reserves and must forage (Afton 1980, Afton and Paulus 1992). Caldwell and Cornell (1975) and Afton (1980) demonstrated an increase in constancy in dabbling ducks with a decrease in ambient temperature and during precipitation. Incubation constancy of Ring-necked Ducks, however, was not influenced by ambient temperature or precipitation (Hohman 1986). Ring-necked females took recesses from incubation both in the middle of the night when temperatures were lowest and in the middle of the day when temperatures were highest.

Intraspecific differences in age and body condition may further influence incubation patterns (Hepp et al. 1990). Constancy is influenced by age in Canada Geese (*Branta canadensis*) (Aldrich and Raveling 1983). Female geese nesting for the first time began incubation at a lower body mass and were less attentive than older, experienced hens. Furthermore, yearling Canvasbacks that were lighter had lower nest success, although body condition had no effect on

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hatchability of Redheads (*Aythya americana*) and adult Canvasbacks (Arnold et al. 1995). Lower incubation constancy may contribute to lower nest success of lighter, yearling Canvasbacks, but was not examined by Arnold et al. (1995). Arnold et al. (1995) may have failed to find a difference between age groups in Redheads due to few yearlings in the sample ($n = 5$).

Body condition, often measured as body mass, may account for observed intraspecific variation in constancy. Gatti (1983) demonstrated that female Mallards in poor condition were less attentive (lower constancy) during incubation as compared to those in better condition. Renesting ducks, whose reserves may be further depleted, incubate less attentively (Afton 1980). Additionally, Gloutney and Clark (1991) demonstrated that female Mallards and Northern Shovelers (*Anas clypeata*) that were lighter at the end of incubation had lower nest success, potentially due to lower incubation constancy.

Redhead incubation patterns and variables that influence these patterns have not been adequately assessed. Low incubation constancy (73%) was attributed to high levels of disturbance at the nest and/or reduced maternal investment in the clutch (Low 1945). Saylor (1985) attributed increased recess time during drought years, as opposed to years in which water conditions were good, to a reduced food abundance and thus lower reserves of the female. Incubation patterns of Redhead hens may be further influenced by their reproductive strategy. Redheads are unusual in that they often lay parasitic eggs before initiating their own clutch of eggs (Saylor 1992). This behavior may result in reduced body condition that could influence subsequent incubation patterns. Although Redheads are a large-bodied diver species, their incubation constancy may be lower than expected due to a reduced body condition as a result of prior parasitic behaviors. If a reduced body condition affects constancy in Redheads, as it appears to do in Anatini, their incubation constancy patterns should be influenced by environmental variables much like small-bodied species. Additionally, age and experience of the hen could further affect constancy patterns and interact with reproductive strategy and body condition.

METHODS

Incubation data were collected in 1994 and 1995 near Minnedosa, Manitoba, Canada (50°10'N, 99°47'W). This area is characterized by numerous seasonally- to permanently-flooded wetlands, native aspen-parkland vegetation, and intensive agriculture. For a description of the study area see Stoudt (1982).

Redhead nests were located during daylight hours by searching emergent vegetation. Stage of incubation was determined by field candling (Weller 1956). At day 22–24 of incubation, hens were trapped on the nest to determine age and body mass. Age of hen was determined by plumage characteristics (Dane and Johnson 1975). Body mass to the nearest ± 5 g was determined with Pesola scales. Body mass is a good surrogate for condition in Redheads and was used as a comparative measure between females (Bailey 1979, Johnson et al. 1985; unpubl. data).

Weather data were recorded at Brandon Airport located 30 km southeast of the study site. Data included daily minimum and maximum temperature and daily precipitation.

Incubation constancy and attendance patterns were determined by the use of remote temperature sensors (Hobo Temp XT, Onset Computer Co., Pocasset, Massachusetts). When nests were located late in the laying stage (6 eggs) or during incubation, a “dummy” egg containing a temperature sensitive probe was situated in the middle of the nest. Probes were attached with silicon to the top of the egg, the location at which the closest contact between the probe and the hen’s brood patch would occur. Dummy eggs were constructed from hollowed out, large chicken eggs. Hollowed out eggs were reinforced internally with epoxy and attached to a rod stand, which extended perpendicular from the base of the egg. The rod stand secured the dummy egg in the nest, preventing the female from rolling the egg and ejecting it from the nest. Hobos were set to record temperature every 4.8 min, totaling 1,800 data points in 6 days. Data from recorders were down-loaded every six days, generally in the afternoon to reduce disturbance and maintain consistent set and down-load times.

Temperature data for each hen were visually scrutinized both as plotted data and on spreadsheets. A rise or drop in temperature of 3.0°C

was considered an "on" or "off" movement of the hen, respectively. If the drop in 3.0°C was not maintained for three time periods (14.4 min), the hen was scored as on the nest and considered involved in a comfort movement. An individual recess was calculated as the total time the hen was recorded off the nest to the next time she was recorded as on the nest. Average recess frequency and duration were calculated for each hen. Incubation constancy, defined as the percent of time the hen spent on the nest during a 24-hr period, was calculated for each hen. The relationship between daily average constancy, daily average recess number and duration was examined with Pearson's correlation analysis. The pattern of recess frequency was examined over a 24-hr period by dividing the day into 24 1-hr time periods and correlating frequency with time of day. The relationship between daily average constancy and Julian date was examined by correlation analysis.

To determine if daily constancy changed over the incubation period and the pattern of that change, individual hen daily constancy was examined with a mixed linear model with repeated measures and linear, quadratic, and cubic contrasts (PROC MIXED, SAS Institute 1996). The influence of all potential main effects (age, mass, initiation day, incubation day, Julian date, maximum temperature, minimum temperature, and precipitation) and significant two-way interactions on daily constancy were examined with a repeated measures, mixed linear model (PROC MIXED). Values presented are means \pm SE.

RESULTS

Data were collected from 71 hens in 1994 and 1995, totaling 446 incubation days. Days in which the hens were trapped or were disturbed by an investigator were excluded from analysis.

Incubation constancy was calculated from 29 hens, each with at least 8 days of incubation data totaling 348 days, ranging from 8 to 20 days per hen. Constancy was 0.819 ± 0.007 (range 0.751–0.897). Incubation constancy was not different between females that initiated nests early vs. late in the season ($t_{27} = 1.06$, $P = 0.30$). Redhead hens took an average of 7.2 ± 0.4 recesses per day for an average of 46.8 ± 2.3 min. Average incubation constancy was negatively correlated with average recess number ($r = -0.57$, $n = 29$, $P < 0.001$), whereas average recess number was negatively correlated with

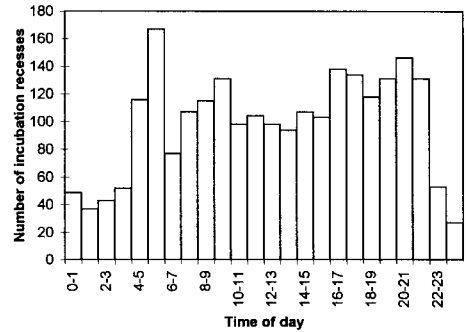


FIGURE 1. Initiation timing of Redhead incubation recesses. Time of day is represented as 24 1-hr time blocks, beginning at midnight (0).

average recess duration ($r = -0.57$, $n = 29$, $P < 0.001$). Recess frequency was not correlated with time of day ($r = 0.29$, $n = 24$, $P = 0.17$) (Fig. 1).

The analysis of the pattern of incubation constancy over the 24-day incubation period indicated a daily decrease in constancy with increasing incubation day. A mixed, linear model with repeated measures ($t_{316} = 38.2$, $P < 0.00$) revealed significant linear ($t_{316} = 2.13$, $P = 0.03$) and quadratic ($t_{316} = -2.16$, $P = 0.03$) trends and a marginally significant cubic fit ($t_{316} = 1.86$, $P = 0.06$) of constancy with incubation day (Fig. 2). This indicates that constancy increased from day 1 to day 8, decreased between day 9 and 21, and increased slightly at the end of the incubation period.

In a mixed linear model, the main effects of age, mass, and maximum daily temperature, and two-way interactions of initiation day \times age, and mass \times Julian date significantly influenced daily incubation constancy (Table 1). Older hens exhibited higher average constancy (0.831 ± 0.009 , $n = 12$) than yearlings (0.811 ± 0.016 , $n = 8$). Lower constancy of yearlings was associated with more daily recesses (8.2 ± 0.9) of shorter duration (42.9 ± 5.1 min) than adults (6.2 ± 0.5 ; 49.1 ± 3.0 min, respectively). The interaction between initiation day and age indicated that yearling females tend to increase constancy late in the season compared to adults whose constancy tends to decrease with time.

Females that ended incubation with a lower body mass maintained higher incubation constancy over the incubation period as compared to heavier females at the end of incubation (Table 1, Fig. 3). Mass and Julian date also inter-

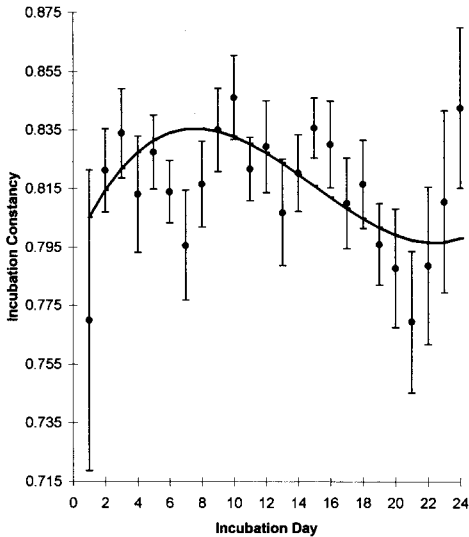


FIGURE 2. Curve fit of Redhead predicted daily incubation constancy over the incubation period and raw average constancy with standard error bars. Predicted constancy = $0.793866 + [(incubation\ day)(0.012357)] + [(incubation\ day^2)(-0.00109)] + [(incubation\ day^3)(0.0000243)]$.

acted to influence incubation constancy: females incubating early in the season exhibited decreased constancy with an increase in end-of-incubation body mass vs. females incubating later in the season, which exhibited an incubation constancy that is fairly consistent over the range of end-of-incubation body masses (Fig. 4).

Finally, as daily maximum temperature increased, daily constancy decreased. Daily constancy was not affected by minimum daily temperature, daily precipitation, initiation day, incubation day, or Julian date (Table 1).

DISCUSSION

Female Redheads exhibit unusual incubation patterns both interspecifically and intraspecifically. Both for their size and in absolute terms, Redhead females maintain an average incubation constancy that is among the lowest of all waterfowl species and is the lowest reported for diver species. The relationship between body size and incubation constancy in ducks, proposed by Afton (1980) and Afton and Paulus (1992), does not apply without modification to female Redheads. Furthermore, high recess frequency and timing of recess initiations adds to this unique pattern. Whereas most North American ducks exhibit either a uni- or bimodal re-

cess pattern during daylight hours, Redheads initiate recesses with equal frequency during all daylight hours and occasionally initiate at night. Nocturnal recesses of significant duration are uncommon for ducks (Ringelman et al. 1982).

Incubation constancy decreased over the incubation period, a pattern that is observed in many duck species (Afton 1980, Brown and Fredrickson 1987, Mallory and Weatherhead 1993). This pattern often has been attributed to increasing ambient temperature with increasing incubation period (Mallory and Weatherhead 1993), an increase in embryonic heat production (Drent 1970), and/or energetic constraints on the female (Afton and Paulus 1992). Although increased ambient temperatures were proposed to explain decreased constancy in Goldeneyes (*Bucephala clangula*) (Mallory and Weatherhead 1993), temperature did not influence Redhead patterns because Julian date and daily constancy were not related. Redhead females may be responding to an increase in embryonic heat production as proposed by Drent (1970); however, this effect was not assessed in the present study. Energetic constraints, in the form of declining endogenous reserves as incubation progresses, may force females to acquire more exogenous nutrient sources thus resulting in decreased attendance at the nest (Afton and Paulus 1992). Canada Geese exhibit a decreased constancy and an increased reliance on exogenous food supplies as incubation progresses (Murphy and Boag 1989) and, in captivity, take longer recesses as they approach their lowest body masses at the end of incubation.

Ambient conditions also may account for interspecific variation in incubation constancy. Large-bodied waterfowl are relatively unaffected

TABLE 1. The influence of the main effects and significant two-way interactions on Redhead incubation constancy.

Variable	t_{234}	P
Age	-2.60	0.01
Mass	-2.29	0.02
Initiation day	-0.18	0.98
Incubation day	-0.03	0.98
Julian date	-1.53	0.13
Maximum daily temperature	-2.55	0.01
Minimum daily temperature	0.38	0.70
Precipitation	0.82	0.41
Initiation day \times age	2.51	0.01
Mass \times Julian date	2.25	0.03

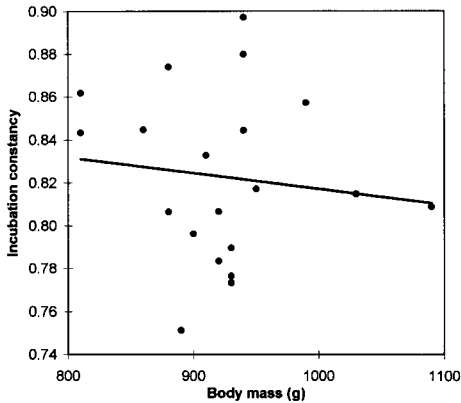


FIGURE 3. Relationship between Redhead body mass (raw data) taken at the end of incubation and incubation constancy.

ed by weather extremes because they rely heavily on endogenous reserves (Cooper 1978, Raveling 1979), whereas small-bodied females often modify incubation behavior in relation to varying ambient conditions. Constancy often increases during rain, and as ambient temperatures decrease (Caldwell and Cornell 1975, Afton 1980). Some species, however, do not respond to either temperature or precipitation (Ringelman et al. 1982, Hohman 1986). Redhead females apparently respond only to maximum daily temperature, like Goldeneyes (Mallory and Weatherhead 1993), decreasing daily constancy on days with higher maximum temperatures.

Several hypotheses have been offered to explain the low incubation constancy and unique incubation patterns exhibited by Redheads: (1) excessive disturbance at the nest (Low 1945), (2) reduced maternal investment (Low 1945), and (3) energetic constraints on the female. If excessive disturbance at the nest due to parasitic behaviors of other hens significantly reduces constancy, one would expect early nesters, those nesting during peak parasitic events, to exhibit lower constancy than later nesters. In this study, constancy of early and late nesters was not significantly different. Reduced maternal investment in the clutch seemingly would not account for lower constancy of Redheads because hatch success of Redheads is not significantly lower than other diver species. However, the relative reproductive effort of Redheads is unknown. Furthermore, other duck species that experience parasitism, such as Canvasbacks, Wood Ducks

(*Aix sponsa*), and Goldeneyes, do not exhibit reduced constancy or investment.

Finally, energetic constraints imposed by prior parasitic behaviors of the incubating female may account for the low constancy exhibited by a relatively large-bodied species. Redhead body condition may indeed override the relationship between body mass and incubation constancy, much like that proposed for Black Ducks (*Anas rubripes*), which face energetic constraints due to low densities of aquatic invertebrate prey (Ringelman et al. 1982). Additionally, Noyes and Jarvis (1985) demonstrated that female Redheads used most of their stored lipids during laying (46%) and continued to deplete lipid reserves during incubation, investing 30% of their remaining reserves. They attributed the large amount of lipid reserves lost during the laying period by females to both parasitic laying and the laying of a nested clutch. They concluded that many, if not all, females in their study laid parasitic eggs because parasitic rates were 65%. Although prior parasitic behaviors of hens in my study were not known, Redheads parasitized 85% of Canvasbacks nests in 1995, which may indicate that many Redheads parasitized prior to nesting.

Energetic constraints, coupled with age/experience, may further account for intraspecific differences observed in female Redheads. Captive Canada Geese exhibited different incubation

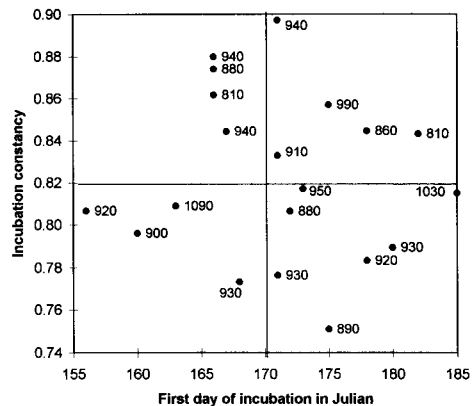


FIGURE 4. The interaction between Julian date and mass on incubation constancy in Redheads. Females incubating early in the season exhibit higher incubation constancy and lower end-of-incubation body mass vs. females incubating later in the season, which exhibit lower incubation constancy with higher end-of-incubation body mass.

patterns between young and older experienced females (Aldrich and Raveling 1983), such that during the fourth week of incubation, young females were off the nest three times more often than older females. Adult female Redheads exhibited higher constancy with fewer recesses of longer duration; however, prior experience of those hens is unknown. Adult females may be more efficient competitors and foragers, thus more capable of maintaining sufficient nutrient reserves allowing a higher incubation constancy. Higher constancy may increase nest success, given that nest success has been shown to be influenced by age in Redheads (Arnold et al. 1995).

Body mass may further explain intraspecific variation in incubation patterns. Canada Geese that were heavier at the beginning of incubation exhibited higher nest attentiveness (Aldrich and Raveling 1983). In another study, a single female Ringed-neck Duck observed over a 3-yr period exhibited the lowest incubation constancy during a year in which she entered reproduction in a reduced body condition and when invertebrate numbers were depressed (Hohman 1986). In my study, heavier female Redheads that were weighed at the end of incubation, maintained lower incubation constancy than lighter hens. Mass taken at the end of incubation may obscure the comparison between body mass and constancy because in other species heavier hens at the beginning of incubation lose more mass over the incubation period than lighter hens (Harvey et al. 1989, Hepp et al. 1990). In captivity, heavier female Redheads at the beginning of incubation lost significantly more mass than lighter females (unpubl. data). Therefore, I suggest that mass taken at the end of incubation is a poor predictor of initial body mass for individual Redheads and that heavier hens entering incubation maintain a higher incubation constancy and lose more mass than lighter hens.

I propose that female Redhead incubation constancy is lower than predicted given their body size due to the energetic constraints imposed by parasitic behaviors of nesting hens, and intraspecific differences can be attributed to energetic constraints and hen age or experience.

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