NEST AND BROOD ATTENTIVENESS IN FEMALE BLACK DUCKS

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ABSTRACT.—Incubation rhythms and brood attentiveness of radio-marked Black Ducks (*Anas rubripes*) were studied in southcentral Maine during 1977–1980. Recess duration and frequency differed between three females nesting near wetlands ($\bar{x}$ = 82 min, 2.3 recesses/day) and two nesting at upland sites ($\bar{x}$ = 183 min, 1.1 recesses/day), but incubation constancy was similar for all birds ($\bar{x}$ = 86.7%). A fourth wetland-nesting female apparently responded to the absence of down and concealing cover at the nest site by taking shorter and fewer recesses ($\bar{x}$ = 34 min, 1.0 recesses/day) than did other wetland-nesters with typical nests. Wetland-nesters took longer recesses with increasing air temperature and following long incubation sessions. After their ducklings were two weeks old, two brood-rearing females began leaving their broods to forage on nearby wetlands. Duration of rearing recess ($\bar{x}$ = 56 min) and total recess time ($\bar{x}$ = 94 min/day) were less during this mid-rearing stage than during the latter part of rearing ($\bar{x}$ = 265 min, 488 min/day). The two hen-brood bonds terminated at 43 and 48 days. We suggest that small endogenous nutrient reserves and the low density of invertebrate foods, typical of Black Duck breeding habitat, were critical factors affecting the evolution of Black Duck incubation behavior. Bouts of inattention during brood rearing may have also evolved in relation to food requirements; by foraging on wetlands away from their broods, females avoid competing with offspring for common food resources.

The behavior of female anatids during incubation and brood-rearing reflects the energetic demands of the reproductive season. High incubation constancy is typical of geese (Ryder 1970, MacInnes et al. 1974, Ankney and MacInnes 1978) and Common Eiders (*Somateria mollissima*; Korschgen 1977), which depend on stored nutrient reserves during this period. The females of smaller anatids are unable to store large endogenous reserves and, therefore, depend on environmental food resources to meet most of their metabolic requirements during incubation (Afton 1979). Because food is obtained during incubation recesses, recess duration and frequency may be related to metabolic reserves (Afton 1978), feeding efficiency (McKinney 1970), and density and availability of food resources.

Incubation rhythms and brood attentiveness of female Black Ducks (*Anas rubripes*) have not been quantified. Mendall (1958:96) stated that "Black Ducks normally have only two rest periods per day, one in the early morning and another in late afternoon." He estimated the duration of incubation recesses at 60 min. Coulter and Miller (1968:20) concluded that "there was no period of the day when the majority of hens were off their nests." After hatching, female dabbling ducks usually remain with their broods until the ducklings are seven to eight weeks old (Munro 1949, Evans et al. 1952), although the duration of the hen-brood bond differs among species (Beard 1964, Ball et al. 1975). Before this time, hens leave their ducklings for periods ranging from 15–75 min (Beard 1964) to several hours or all day (Mendall 1958:126, Ball et al. 1975). We describe here the schedule of nest and brood attentiveness of radio-marked Black Ducks and relate the timing and duration of incubation recesses to weather and nest location.

STUDY AREA AND METHODS

Our study was conducted during 1977–1980 in the mixed hardwoods-spruce habitat of southcentral Maine described in detail by Ringelman (1980). The 151-km² study area averaged 0.74 ponds/km², most of which were classified as (1) persistent emergent, (2) broad-leaved deciduous and evergreen shrub, or (3) broad-leaved deciduous forested, palustrine wetlands (Cowardin et al. 1979). Black Ducks nested in low densities characteristic of most breeding habitat, averaging 19 resident pairs/100 km². Aquatic macroinvertebrates, the primary food source for breeding Black Ducks and ducklings (Reinecke 1979, Reinecke and

Owen 1980), occurred in densities ranging from 288 (deciduous shrub habitat) to 1,953 (floating-leaved vegetation) mg dry weight/m³ (Ringelman 1980).

Ducks were captured with rocket nets or nest traps (Coulter 1958) before or during incubation and fitted with adjustable (Dwyer 1972), back-mounted radio transmitters (Cedar Creek Bioelectronics Laboratory). Transmitter packages weighed 25–30 g and had an effective range of 1.5–3.0 km with a mean life of 80 days. Rustrak recorders (model 228), coupled to receivers (AVM model LA12) and three-element yagi antennas, continuously monitored incubating and brood-rearing females. When placed near the nest or rearing wetland, this system detected changes in signal attenuation caused by bird movement, as well as the presence or absence of the bird.

Average percent of the time the hen spent on the nest per day is termed "incubation constancy" (Skutch 1962), whereas "recesses" are periods when the hen is away from the nest. Periods spent on the nest are "incubation sessions." Simple and multiple correlation analyses were used to determine which of nine independent variables were related to the (1) start of incubation recesses, (2) recess duration, (3) total daily recess time, and (4) recess frequency per day. Weather variables, measured at a base station 0.1–5.0 km from a nest, included air temperature at the time of recess, temperature at sunrise and sunset, daily high temperature, relative humidity at the start of recess, lowest humidity during the 24-h period, and the presence or absence of rain during the recess. Biological and temporal parameters included the stage of incubation and number of minutes elapsed since the end of the previous recess. Some dependent variables were used as independent variables in the appropriate model. Multiple correlation analysis identified the combination of independent variables that maximized the overall R-square of the regression function. Significance was judged by F values for the entire function as well as by the individual contribution of each variable.

RESULTS

NEST ATTENTIVENESS

Nest attentiveness of five radio-marked females was monitored by recorder over a 64-day period during 1977–1980. Three hens (field numbers 04, 28, 30) occupied nests in vegetation next to wetlands, and two hens (02, 45) nested in upland sites >1 km from the pond used during incubation recesses. Nests near wetlands were usually constructed in herbaceous (*Carex* spp., *Typha* spp., *Calama-*

grostis canadensis) or shrub (*Myrica gale, Chamaedaphne calyculata*) vegetation, whereas upland nests were beneath conifers (*Abies balsamea, Thuja occidentalis, Tsuga canadensis*) or slash. Incubation constancy ($\bar{x}$ = 86.7%, SD = 1.21) did not differ among these birds ($P > 0.10$), but recess duration, timing, and frequency differed widely between wetland-nesting and upland-nesting hens ($P < 0.001$). These differences are presumed to reflect important behavioral adaptations related to nest location; we therefore treated each group separately for statistical comparisons.

Wetland-nesters averaged 2.3 recesses/day (range = 1–4) with a mean recess duration of 82 min, whereas upland-nesters took less frequent ($\bar{x}$ = 1.1 recesses/day, range = 0–2) but longer ($\bar{x}$ = 183 min) recesses (Table 1). Time of recess initiation was more consistent within than among hens (Fig. 1). Wetland-nesting females usually started a recess shortly after sunrise, but upland-nesters almost always took their recesses in late afternoon. With only one exception, which probably resulted from disturbance at the nest, all recesses after day one of incubation occurred during daylight. This overnight absence was not included in analyses of incubation rhythms.

Incubation rhythm components of upland-nesting females were not influenced by weather variables or stage of incubation ($P > 0.10$). However, the behavior of wetland-nesting hens as a group was affected by weather and the duration and timing of prior recesses. Long recesses were associated with a combination of high air temperatures and long incubation sessions preceding the recess ($R^2 = 0.13$, $P < 0.01$), but recess duration was not related to relative humidity or rain. On days when several recesses were taken, the first recess occurred early in the day ($R^2 = 0.33$, $P < 0.05$). Total recess time per day was not correlated with measured weather variables or with incubation chronology of any hens ($P > 0.05$).

The extent to which normal incubation rhythms may be altered by unusual circumstances was illustrated by the behavior of a fourth wetland-nesting female. This hen (29) nested in the center of a 0.5-ha wetland in a stand of moderately dense narrow-leaved cattails (*Typha angustifolia*). Shortly after the clutch was laid, rain raised the water level in the pond. The hen responded by incorporating all vegetation within a 0.5-m radius into her nest, leaving the nest platform completely exposed. This response to rising water is common in duck species that nest over water, but it is rare in the Black Duck, occurring less than 5% of the time (Mendall 1958:83). All down
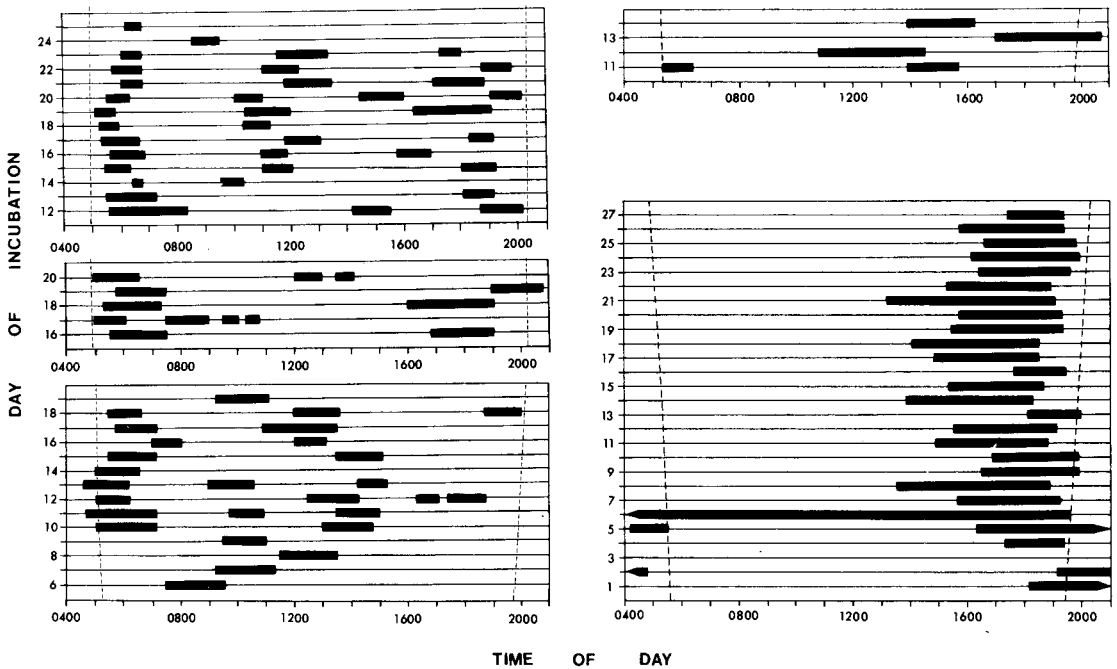
FIGURE 1. Nest attentiveness of wetland-nesting (left) and upland-nesting (right) Black Ducks. Horizontal bars represent incubation recesses, dashed vertical lines indicate sunrise and sunset, and pointed bars signify overnight recesses.

was buried beneath 30 cm of the new nest material, and only three to four dead leaves of cattail were pulled over the remaining clutch of three eggs during recesses. At least two eggs rolled out of the nest during the building process and were recovered in the water beside the nest.

Recess duration and frequency for this hen ($\bar{x} = 34$ min, 1.0 recesses/day) differed from those previously described for wetland-nesters ($P < 0.001$). Furthermore, mean time of recess initiation was much earlier ($P < 0.001$), with recesses frequently beginning before sunrise (Fig. 2). Recess duration was positively correlated with the air temperature at time of recess ($R^2 = 0.25$, $P < 0.01$) but not with the length of the preceding attentive period, as had been observed for other wetland-nesting females. Two embryos in this clutch died during the latter stages of development, and one egg hatched.

BROOD ATTENTIVENESS

Continuous data on brood attentiveness were obtained for two females (Fig. 3). Both hens remained with their ducklings constantly during the early stages of rearing, although the duration of this attentive stage differed between birds (hen 02, 19 days; hen 49, 14 days). In the first eight days following this stage, rearing recess duration ($\bar{x} = 56$ min, SD = 30.0) and total recess time ($\bar{x} = 94$ min/day, SD = 78.9) were much less ($P < 0.001$) than during the final rearing stage ($\bar{x} = 265$ min, SD = 297.8, 488 min/day, SD = 322.1). Recess frequency did not differ ($P > 0.10$) between mid-rearing ($\bar{x} = 1.5$ recesses/day) and late-rearing ($\bar{x} = 1.8$ recesses/day). Immediately before dissolution of the hen-brood bond, the duration of rearing recesses increased substantially, occasionally lasting the entire daylight period. Hens fed and loafed on four to

TABLE 1. Components of the incubation rhythm ($\bar{x} \pm$ SD) for five radio-marked Black Ducks.

| Bird number | Nest location | Days monitored | Recess | | Session duration (min) | Incubation constancy % |
			Duration (min)	Frequency (no./day)		
04	Wetland	14	71 ± 31.2	2.6 ± 0.85	463 ± 287.4	87.3
28	Wetland	5	86 ± 47.3	2.4 ± 1.14	414 ± 349.8	85.7
30	Wetland	14	89 ± 27.8	2.0 ± 1.00	636 ± 445.2	87.9
45	Upland	27	214 ± 114.0	1.0 ± 0.29	1,210 ± 188.6	85.1
02	Upland	4	151 ± 70.5	1.2 ± 0.45	1,056 ± 467.6	87.4

six wetlands 1.3–3.5 km from the rearing pond during recesses, but usually returned to their ducklings at night following daylong absences.

The time of complete dissolution of the hen-brood bond differed between females. Bird 02 increased the duration of rearing recesses abruptly following day 39, and left the rearing wetland permanently on day 48. Visual observations on the behavior of female 49 and her brood on days 43 and 44 of rearing indicated that ducklings failed to respond to her vocalizations and foraged long distances from her, suggesting that the bond had been terminated. This hen continued to use the rearing pond at irregular intervals for the following 16 days; on nine of these days she did not leave the rearing wetland, but on three other days she was absent overnight for periods up to 11.5 h.

DISCUSSION

For single-sex, intermittent incubators such as the Black Duck, incubation rhythms have evolved in such a way as to maintain optimum egg temperatures while assuring sufficient time for foraging and non-foraging activities. Caldwell and Cornwell (1975) reported that captive Mallards (*Anas platyrhynchos*) spent 94.6% of the day on the nest, whereas the incubation constancy of other anatids ranges from 72.6–98.5% (see review in Afton 1980). Because the period an individual can survive on stored nutrients decreases with body size (Calder 1974:114), Afton (1978) hypothesized that small anatid species are more dependent on environmental food resources to fulfill energy requirements (reflected in a lower incubation constancy) than are larger species. The Black Duck, however, has an incubation constancy (86.7%) similar to that of smaller species such as the Northern Shoveler (*A. clypeata*, 84.6%; Afton 1980) and European Green-winged Teal (*A. crecca crecca*, 85.1%; cited in Afton 1980).

Black Ducks obtain energy for reproduction by relying on foods procured on the breeding grounds supplemented by a small endogenous energy reserve accumulated in migrational or wintering habitats (Owen and Reinecke 1979). Recent evidence (Krapu 1981) indicates that endogenous reserves are important for providing energy used to obtain high protein foods in the breeding habitat. Nevertheless, the limited quantity of stored energy dictates a heavy reliance on exogenous sources. This dependence on high-protein invertebrates, coupled with the relatively low density of aquatic invertebrates in northeastern U.S. wetlands (Reinecke 1977, Ringelman 1980), suggests that Black Ducks may require additional for-
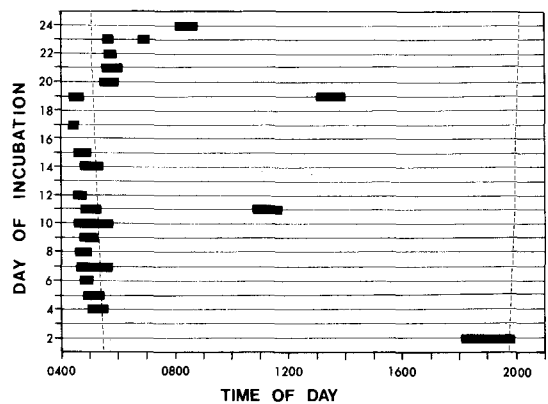

FIGURE 2.   Nest attentiveness of Black Duck 29, which built up her nest in response to flooding. Horizontal bars represent incubation recesses, and dashed vertical lines indicate sunrise and sunset.

aging time, manifested by longer or more frequent incubation recesses, to acquire sufficient food. Thus, we believe the reason Black Ducks do not fit the general pattern of increasing attentiveness with body weight, as propsed by Afton (1978), is because this relationship is modified by the overriding effects of low food density and small endogenous energy reserves. These factors were probably of critical importance in the evolution of Black Duck incubation behavior. Incubation constancies derived from pen studies in which food was readily available (e.g., Caldwell and Cornwell 1975), as well as for species that forage on highly productive prairie wetlands, might be expected to differ from those obtained for the Black Duck.

Waterfowl, like most bird species, are believed to select their nesting sites primarily by an innate reaction released by certain environmental stimuli (Hildén 1965). Nest locations may affect both nesting success and duckling survival. Females who nest close to water avoid the long overland brood movements, and resultant high duckling mortality (Ball et al. 1975), associated with remote nests. The disadvantages associated with upland nesting may in turn be offset by a reduction in predation within spatially heterogeneous upland sites (Bowman and Harris 1980) or avoidance of flooding during spring rains, a frequent cause of nest failure in the Northeast (Mendall 1958). These proximate factors may be important in the evolution of nest site preference. Once a site is selected, different attentiveness rhythms may be advantageous for reducing energy costs during incubation.

The cost of an incubation recess includes the energy needed to fly to and from the feeding area, the energy used in foraging and other
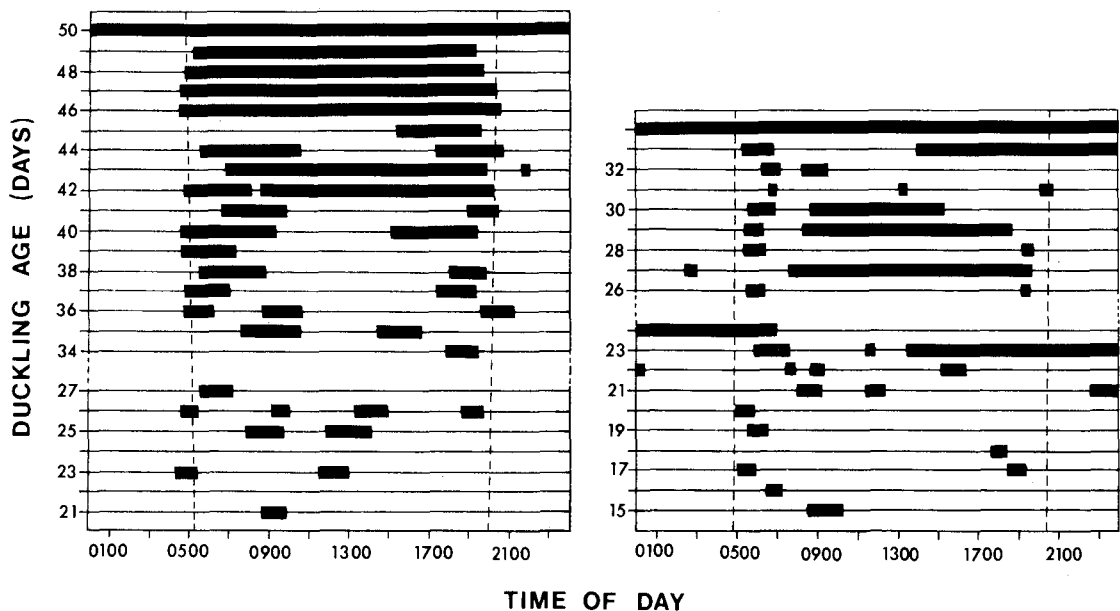
FIGURE 3.   Brood attentiveness of Black Duck 02 (left) and 49. Horizontal bars represent rearing recesses, and dashed vertical lines indicate sunrise and sunset.

behaviors, and the cost of rewarming the eggs following a recess (recovery energy). The rate of energy expenditure by Black Ducks in flight (42.7 kcal/h; Wooley and Owen 1978) is much greater than the estimated cost of incubating (3.8 kcal/h, resting activity; Wooley and Owen 1978) and rewarming (Vleck 1981) a clutch, but whereas the amount of flight energy used is nearly a direct function of flight distance, the rate of egg cooling decreases with recess duration. Thus, the recovery energy per minute of recess is lower among hens who take long recesses, with a single daily recess being the most efficient incubation rhythm (Drent 1973). Upland-nesting Black Ducks travel farther to feeding areas, and therefore incur generally higher flight costs, than do wetland-nesting birds (Ringelman 1980). That increased flight time may substantially alter the energy budget of breeding Black Ducks was demonstrated by Owen and Reinecke (1979). We hypothesize that upland-nesting birds compensate for increased flight costs by making only one round-trip a day and acquiring all food during the single, long recess. Recesses taken during the afternoon may further reduce energy costs by minimizing cooling rates and therefore recovery energy. In contrast, wetland-nesting hens usually forage on wetlands close to the nest (Ringelman 1980). The proximity of feeding areas may allow these birds to adopt an incubation rhythm of several short recesses per day.

Nest attentiveness is known to be influenced by feedback from cold eggs acting on sensory receptors in the skin of the brood patch (White and Kinney 1974). Long attentiveness sessions and short, infrequent recesses of female 29 possibly resulted from the poor insulation qualities of the nest acting through this feedback mechanism, since the density of invertebrate foods at this hen's foraging site was similar to that at feeding sites used by other incubating birds (Ringelman 1980). The fact that recesses occurred during the pre-dawn hours when the thermal environment was least favorable implies that other considerations, such as the avoidance of egg overheating or concealment from predators, may have been important in determining the timing of recesses. Direct insolation can raise egg temperature to lethal limits in a brief period (Snart 1970); by remaining on the nest during midday, a female can shade the eggs or carry off excess heat during high temperatures (Howell and Bartholomew 1962, Maclean 1967). Eggs unconcealed during daylight would be susceptible to avian predators, particularly the Common Crow (*Corvus brachyrhynchos*), a known predator of Black Duck eggs (Stotts and Davis 1960).

Rearing recesses and eventual dissolution of the bond between a hen and her brood presumably have evolved to maximize genetic fitness of the hen by increasing the likelihood of offspring and hen survival. During early and mid-rearing, ducklings must be brooded by the hen to maintain homeostasis when ambient air temperatures drop below 10°C (Koskimies and Lahti 1964); hence close attentiveness by

the hen is critical during this period. Brood-rearing females also alert their offspring to predators, select the rearing wetland, and may direct the brood to the best foraging patches. Young Black Ducks approach adult size by 50–60 days of age, with a concomitant increase in food consumption. Brood-rearing females continue to rely on invertebrate food during the late-rearing period (Reinecke and Owen 1980) while storing endogenous nutrient reserves preparatory to molt. Concurrently, aquatic invertebrates in northeastern U.S. wetlands generally become less abundant in late summer (Whitman 1974, Reinecke 1977, Ringelman 1980). Because the demand for invertebrate foods by both hen and ducklings remains high even while the supply is declining, we hypothesize that female Black Ducks may avoid competing with their offspring for food by foraging in adjacent wetlands during rearing recesses. Thus, food availability, modified by endogenous energy reserves, may play a critical role in the incubation and brood attentiveness rhythms of Black Ducks nesting in south-central Maine.

ACKNOWLEDGMENTS

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