

mum one-day spring counts at Attu over the past 20 years include 150 in 1980 and 122 in 1988 (American Birds and National Audubon Society Field Notes reports; unpubl. data).

These are the first breeding records of *C. cygnus* and *F. montifringilla* for Alaska and North America. Previous nesting by Palearctic species on Attu include White-tailed Eagle (*Haliaeetus albicilla*) in 1982–1983 (Tobish and Balch 1987), Wood Sandpiper (*Tringa glaveola*) in 1973 (Gibson and Byrd 1973), and Black-backed Wagtail (*Motacilla lugens*) in 1983 (Wagner 1991).

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FACTORS AFFECTING DURATION OF INCUBATION IN BLACK BRANT¹

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Abstract. We investigated factors affecting duration of incubation in Black Brant (*Branta bernicla*) during 1992 and 1993 on the Yukon-Kuskokwim Delta, Alaska. Duration of incubation varied with clutch size and decreased with later nest initiation. In contrast to other studies, we found no relationship between incubation period and ambient temperature, mean egg size, or nest attentiveness. We hypothesize that a decrease in incubation length with later first egg date is an adaptation by females to reduce disadvantages of hatching late. We suggest that potential costs of reduced embryonic development time outweigh benefits for females that are able to initiate nesting early because their eggs hatch early enough to maximize recruitment of hatched young. For females that nest late, however, advantages to reproductive success of hatching earlier may outweigh costs of reduced development time.

Key words: Black Brant, *Branta bernicla*, first egg date, incubation period, nest attentiveness.

Duration of incubation varies greatly among species; part of this variation is attributable to differences in egg mass because length of incubation is positively correlated with egg mass (Rahn and Ar 1974, Martin and Arnold 1991, Arnold 1993). Nevertheless, some species have much longer incubation periods than predicted by egg size alone. Boersma (1982) proposed that longer than expected incubation in Fork-tailed Storm-Petrels resulted from frequent parental neglect of eggs and concomitant low mean incubation temperatures. Egg temperature must be maintained above 26°C for development of avian embryos to occur, and embryos develop faster when maintained closer to their optimum developmental temperature of 32–36°C (Webb 1987). Thus, the greater proportion of time an embryo is maintained near its optimum developmental temperature, the shorter its incubation period.

Factors that affect female quality, such as body size,

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are associated with female nest attentiveness (Afton 1980, Aldrich and Raveling 1983, Eichholz 1996), which in turn may affect length of incubation period in waterfowl (Aldrich and Raveling 1983, Wilson and Verbeek 1995). Aldrich and Raveling (1983) noted that more attentive females in a captive flock of Canada Geese (*Branta canadensis*) had shorter incubation periods, whereas Wilson and Verbeek (1995) reported Wood Ducks (*Aix sponsa*) that kept eggs at a more constant temperature had shorter incubation periods. Variation in date of clutch initiation is greater than variation in hatching date for Lesser Snow Geese (*Chen caerulescens*) (Finney and Cooke 1978, Findlay and Cooke 1982) and Black Brant (*Branta bernicla*) (Sedinger, unpubl. data), as well as most other waterfowl (reviewed by Rohwer 1992). This pattern has been attributed to a decrease in clutch size as date of nest initiation increases in these species (Findlay and Cooke 1982, Hamann and Cooke 1989, Rohwer 1992), but it also could be influenced by a decrease in duration of the incubation period of later initiating females.

Hatching dates of geese nesting in the Arctic and sub-Arctic strongly influence gosling fitness. Sedinger and Flint (1991), Cooch et al. (1991), and Lindholm et al. (1994) reported that pre-fledging goslings hatched later in the nesting season grew more slowly, which they attributed to a decrease in nutrient availability as the brood-rearing season progresses. Cooke et al. (1984) and Sedinger et al. (1995) observed lower survival for later-hatching or smaller goslings through the first year of life. Sedinger et al. (1995) also reported that small goslings became small adults, which in turn influenced lifetime reproductive success. Because $\geq 70\%$ of brant nests are initiated within a 7-day period (M. Lindberg, pers. comm.), changes in hatching date of only a few days can affect available forage, thus, significantly influencing fitness.

We investigated factors influencing duration of incubation periods of Black Brant (hereafter brant). Because of fitness costs of hatching late, we expected females to be selected to hatch their eggs as early as possible. We examined effects of year, clutch size, clutch volume, mean egg volume, nest attentiveness, body size, and first egg date on incubation period. We predicted that incubation period would increase with clutch size, clutch volume, and mean egg volume because larger clutches and eggs require more time to complete development. We also predicted that incubation period would decrease for females that were more attentive to their nests, and decrease for females that initiated clutches later in the nesting season, because of fitness advantages of hatching early.

METHODS

We conducted our study during summers of 1992 and 1993 at the Tutakoke River brant colony, located at the mouth of the Tutakoke River (61°15'N, 165°37'W) on the Yukon-Kuskokwim Delta NWR, Alaska. Nesting habitat is dominated by wet sedge (*Carex ramenskii*) meadows, but brant feed mostly on patches of *C. subspathacea* and the grass *Puccinellia phryganodes* on edges of ponds, rivers, and coastal mud flats. Beginning in 1985, adults and goslings were captured and banded with individually coded leg bands to allow in-

dividual identification. Of the approximately 10,000 nesting individuals at the colony (Anthony et al. 1995), about 30% were banded. Females of known age were originally banded as goslings or in their second summer, as determined by plumage characteristics (Bellrose 1980).

We randomly established 48 circular, 50-m radius plots before initiation of nests to record nesting chronology of brant on the colony. Each plot was visited every four days until egg laying was complete to record number of nests on each plot, first egg date, number of eggs laid, and clutch completion date. To estimate egg and clutch volume, length (L) and width (W) of eggs were measured to the nearest 0.1 mm using dial calipers, and external egg volume was estimated from the equation $V = 8.22 + (0.4636LW^2)/1,000$ (Flint and Sedinger 1992). First egg dates were calculated for nests located before the last egg was laid by subtracting number of eggs in the nest from dates that nests were located, assuming brant lay one egg every 30–36 hr (D. Person, pers. comm.). Eggs were classified as hatched when goslings pipped shells. Incubation period was calculated from dates second eggs were laid, when incubation begins in brant (Flint et al. 1994, Eichholz, unpubl. data), to the date the first egg pipped.

Nests on plots provided a large sample of nests for which we did not monitor behavior but for which we knew incubation period, first egg date, egg size, and clutch volume. We recorded daily high temperatures using a maximum-minimum thermometer attached to a board and placed on the shaded north side of a Weatherport wall tent. We calculated mean daily high ambient temperatures for each female during incubation by summing the daily high ambient temperatures for each female, then dividing by the number of days the female incubated. Daily high temperature was used because females were least attentive to nests during the warmest portion of the day (Eichholz 1996), and ambient temperature should have the greatest effect on incubation behavior.

We measured nest attentiveness by observing females from three towers that supported observation blinds 3–6 m above the ground. A predetermined sample of nests, selected for visibility from the tower, was chosen at each tower location. We began observations by randomly selecting a sample nest, then rotating 360°, noting whether each female was on or off the nest at the instant the nest was first observed. We then took a short 3 to 5 min break and repeated the procedure. This procedure was continued until the observer left the tower. The proportion of point samples in which a female was on her nest during a sampling period was calculated as her nest attentiveness for that sampling period. Number of sampling periods ranged from 4–15 per nest and we only used sampling periods in analyses if they were at least 1.5 hr long and at least 4 point samples were obtained for every nest.

To prevent artificially reducing variation from pseudoreplication, we used each female's mean nest attentiveness. Means were adjusted for factors found to significantly affect within-female variation by the following coefficients: time period + 0.005 to 0.072, depending upon time of day observation was taken;

TABLE 1. Means \pm SD for variables in model incubation period = nest attentiveness + first egg (Julian) date + mean egg volume + clutch size + mean daily high ambient temperature + year ($n = 42$). In 1992 peak first egg date was 8 days later than in 1993, so 8 days were subtracted from 1992 first egg dates to standardize first egg dates across years.

Variable	Mean	SD
Incubation period (days) 1992	25.2	1.3
1993	25.1	1.2
Nest attentiveness (%)	86.0	9.6
First egg date (Julian)	145.5	1.8
Mean egg volume (cc)	75.6	4.5
Clutch size	4.3	0.7
Mean daily high temp. ($^{\circ}$ C)	14.7	0.8

precipitation category -0.034 , if it rained during the sampling period; high ambient temperature of date observation was taken multiplied by -0.0047 , day of incubation observation was taken multiplied by -0.012 , and (day of incubation observation was taken)² multiplied by 0.0033 (Eichholz 1996). A squared term of day of incubation was included in the analysis to allow a quadratic equation to explain more of the variation. These adjusted means then were used for all analyses. We were able to examine relationships between incubation length and first egg date, mean daily high ambient temperature, clutch size, mean egg volume, and year for a larger sample of females for which nest attentiveness data were not collected.

Analysis of covariance (ANCOVA) was used to test for factors that influence incubation period with year and clutch size as class variables, mean egg volume, adjusted nest attentiveness, mean ambient high temperature, and first egg date as covariates, and all two-way interactions (PROC GLM, SAS Institute 1990). The model then was systematically reduced by removing nonsignificant ($P > 0.05$) interactions followed by independent variables sequentially, beginning with the variable that explained the least amount of variation. Values presented are means \pm SD.

RESULTS

Incubation varied from 23 to 29 days ($\bar{x} = 25.1 \pm 1.2$, $n = 88$) over the 2-yr study. For the sample of females ($n = 42$) for which we had the most complete data, we did not detect associations between incubation period and the following variables: nest attentiveness, first egg (Julian) date, mean egg volume, clutch size, mean daily high ambient temperature, or year ($F_{6,35} < 0.5$, $P > 0.49$ for all variables; Table 1). For the larger sample of females for which nest attentiveness was not measured ($n = 88$), length of incubation decreased with first egg date and varied with clutch size (Fig. 1), whereas mean daily high ambient temperature, year, and mean egg volume had no significant affect ($F_{6,81} < 0.4$, $P > 0.5$ for all interactions and variables). Similar results were obtained (clutch size $F_{4,83} = 29.3$, $P < 0.001$; first egg date $F_{4,83} = 8.0$, $P < 0.01$) when using the more traditional definition of incubation pe-

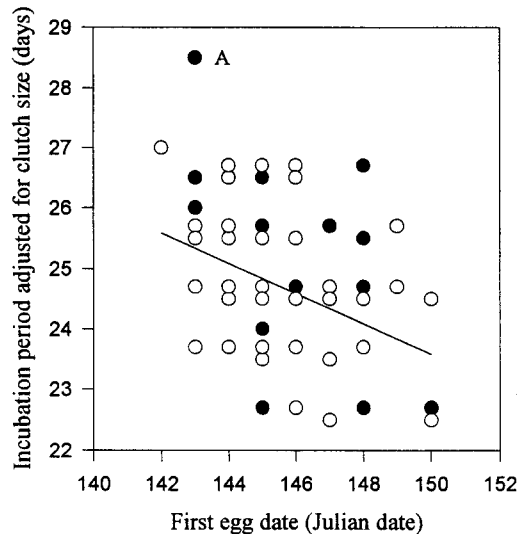


FIGURE 1. Duration of incubation period as a function of first egg date for 88 female brant in 1992 (filled circles) and in 1993 (open circles) ($F_{4,83} = 8.02$, $P < 0.01$). Incubation period is adjusted for effect of clutch size ($F_{4,83} = 4.01$, $P < 0.05$) and some circles represent multiple data points. In 1992, peak initiation was 8 days later than in 1993, so 8 days were subtracted from first egg dates in 1992. We ran analyses both including the point labeled A and without it. For both data sets, date explained a significant proportion of the length of incubation data.

riod from date last egg was laid to date first egg hatched.

DISCUSSION

IMPLICATIONS OF SHORTER INCUBATION PERIODS

A female may influence hatching date in two ways: initiate her clutch early and/or decrease the time from clutch initiation to hatching. Brant clutch initiation extends over a 14–20 ($\bar{x} = 15.8$) day period (M. Lindberg, pers. comm.), indicating that not all females begin nesting when nest sites first become available. Regardless of factors regulating timing of clutch initiation, reduction of incubation length by late-initiating females may reduce costs of nesting late. Decreasing incubation length could increase female fitness in two ways: (1) eggs of females with shorter incubation are exposed to predation for shorter periods, and (2) goslings from eggs requiring shorter development times hatch earlier relative to eggs laid on the same date but requiring longer incubation periods, thereby accruing advantages of early hatching such as faster growth, higher survival, and larger adult size (Cooch et al. 1991, Lindholm et al. 1994, Sedinger et al. 1995).

FACTORS AFFECTING DURATION OF INCUBATION

Even though smaller females that initiate nesting later have smaller mean egg size (Eichholz 1996) and later-initiating females have shorter incubation periods (this

study), we were unable to detect a relationship between egg size (Rahn and Ar 1974, Arnold 1993) or nest attentiveness (Aldrich and Raveling 1983) and incubation length. Because females with larger clutch volumes initiated clutches earlier and were more attentive than those nesting later (Eichholz 1996), we expected females initiating early to have shorter incubation periods based upon Aldrich and Raveling (1983) and Wilson and Verbeek (1995). Nonetheless, in brant, later nesting females had shorter incubation periods, even after controlling for clutch size. These females must use mechanisms other than increased nest attentiveness to reduce length of incubation period. Such mechanisms might include faster developing embryos or goslings that hatch with less mature tissue (Alisauskas 1986, Slattery and Alisauskas 1995), decreasing time required for development in the egg. Given advantages of early hatching, use of mechanisms that decrease length of incubation by later initiating females, but not early initiating females, implies that there is a cost to reducing embryonic development time.

Slattery and Alisauskas (1995) reported goslings of Ross' Geese (*Chen rossii*) hatch at relatively larger size compared to adult size, had heavier gizzards for their body size, and more functionally mature skeletal muscle tissue than Lesser Snow Geese. Slattery and Alisauskas (1995) hypothesized that the relatively more advanced development of Ross' Geese compared to Lesser Snow Geese at hatch is due to longer incubation period relative to egg size for Ross' Geese. We hypothesize that for brant, costs of reducing development time outweigh the benefits for females that are able to initiate nesting early, because their eggs hatch early enough to ensure high reproductive success. However, for females that initiate nesting late, advantages of hatching early may outweigh costs of reducing development time, therefore, late initiating females invoke a mechanism to shorten their incubation period.

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NOCTURNAL VARIATION IN BODY TEMPERATURE OF GRIFFON VULTURES¹

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Abstract. The variation in body temperature over 24 hr was measured by implanting temperature measuring radio transmitters in the abdominal cavity of six captive Griffon Vultures (*Gyps fulvus*). Body temperature was measured when the birds were under three different feeding regimes: within 24 hr of feeding (while digesting), 2–3 days after feeding (post-absorptive state), and 9.5–10.5 days after feeding (food deprived). For all birds, nocturnal body temperature was significantly lower than diurnal body temperature. The decline in body temperature at night was significantly greater in food deprived birds, which at 10.5 days post-feeding had dropped by 4–6°C. We suggest that this is an adaptation to reduce energy requirements of Griffon Vultures during periods of food shortage.

Key words: ambient temperature, body core temperature, daily temperature variation, food deprivation, Griffon Vulture, *Gyps fulvus*.

Birds usually show a daily variation in body core temperature (T_b), with maximum temperatures occurring during the period of activity and minimum temperatures occurring during the period of inactivity (Calder and King 1974, Aschoff 1982). In small diurnal birds, the nocturnal drop in T_b is known to be greater in periods of food shortage (Stuebe and Ketterson 1982, Hohtola et al. 1991, Waite 1991) or exposure to cold stress conditions (Saarela et al. 1989, 1991). In these situations, nocturnal drop in T_b is commonly used to conserve energy (Reinertsen 1983). Nocturnal drop in T_b also has been demonstrated in several species of birds of prey, which are often exposed to extensive

periods of food deprivation as a result of irregular feeding or food shortage (Hatch 1970, Larochele et al. 1982, Chaplin et al. 1984).

Griffon Vultures (of the genus *Gyps*) are a group of large birds which might be particularly expected to have developed adaptations for conserving energy. Being obligatory scavengers, they are totally dependent on finding dead animals, which are an unpredictable and irregular food supply (Houston 1974). Radio telemetry tracking in Israel has shown that Eurasian Griffon Vultures (*Gyps fulvus*) regularly withstand periods of 7 to 10 days between successive feedings (Bahat et al. 1993). We examined the hypothesis that in order to decrease the metabolism needed for maintenance during a prolonged fast, the Eurasian Griffon Vulture reduces the gradient between ambient temperature (T_a) and T_b by decreasing its T_b . We also investigated the daily T_b variation of Griffon Vultures and considered whether the extent of nocturnal drop in T_b is influenced by their plane of nutrition.

METHODS

Four immature (between 2 and 4 years old) and two adult birds (over 6 years old) were used in this study. All were hatched in captivity or had been in captivity for over 3 years and were accustomed to handling. Birds were kept in individual outdoor cages (2 × 4 × 2 m) at the Zoological Garden, Tel-Aviv University. Experiments were done between 29 July and 13 September 1993 (summer), when ambient temperature (T_a) ranged from 18.7°C to 35.2°C. Average (\pm SD) T_a during the experiments was 21.0 \pm 3.3°C. The birds were not exposed to T_a exceeding the limits of their thermoneutral zone (Bahat 1995), therefore exposure to heat or cold stress was avoided. All birds were exposed to natural light/dark cycles.

T_b was measured by implanted transmitters (model TM-Disc, Mini-Mitter, Sunriver, Oregon). Each transmitter weighed 13.5 g, measured 34 mm in length and 18 mm in diameter, and had a 6 month battery life.

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