

## THE PRELAYING INTERVAL OF EMPEROR GEESE ON THE YUKON-KUSKOKWIM DELTA, ALASKA

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**Abstract.** We marked 136 female Emperor Geese (*Chen canagica*) in western Alaska with VHF or satellite (PTT) transmitters from 1999 to 2003 to monitor their spring arrival and nest initiation dates on the Yukon Delta, and to estimate prelaying interval lengths once at the nesting area. Ninety-two females with functional transmitters returned to the Yukon Delta in the spring after they were marked, and we located the nests of 35 of these individuals. Prelaying intervals were influenced by when snow melted in the spring and individual arrival dates on the Yukon Delta. The median prelaying interval was 15 days (range = 12–19 days) in a year when snow melted relatively late, and 11 days (range = 4–16 days) in two warmer years when snow melted earlier. In years when snow melted earlier, prelaying intervals of <12 days for 11 of 15 females suggested they initiated rapid follicle development on spring staging areas. The prelaying interval declined by approximately 0.4 days and nest initiation date increased approximately 0.5 days for each day a female delayed her arrival. Thus, females that arrived first on the Yukon Delta had prelaying intervals up to four days longer, yet they nested up to five days earlier, than females that arrived last. The proximity of spring staging areas on the Alaska Peninsula to nesting areas on the Yukon Delta may enable Emperor Geese to alter timing of follicle development depending on annual conditions, and to invest nutrients acquired from both areas in eggs during their formation. Plasticity in timing of follicle development is likely advantageous in a variable environment where melting of snow cover in the spring can vary by 2–3 weeks annually.

**Key words:** arctic geese, *Chen canagica*, Emperor Goose, migration, nesting, rapid follicle growth, Yukon-Kuskokwim Delta.

### El Intervalo Previo a la Postura en *Chen canagica* en el Delta del Yukon-Kuskokwim, Alaska

**Resumen.** Entre 1999 y 2003, marcamos 136 hembras de *Chen canagica* en el oeste de Alaska con transmisores VHF o satelitales (PTT) para monitorear su arribo durante la primavera y las fechas de iniciación de nidos en el delta del Yukon, y para estimar la duración de los intervalos previos a la postura una vez que llegaron a las áreas de nidificación. Un total de 92 hembras con transmisores funcionales regresaron al delta del Yukon en la primavera posterior al momento en que fueron marcadas, y localizamos los nidos de 35 de esos individuos. Los intervalos previos a la postura fueron influenciados por el momento en que se derritió la nieve en la primavera y las fechas individuales de arribo al delta. La mediana del intervalo fue de 15 días (rango = 12–19 días) en un año en que la nieve se derritió relativamente tarde, y de 11 días (rango = 4–16 días) en dos años más cálidos en los que la nieve se derritió más temprano. En años en los que la nieve se derritió más temprano, los intervalos previos a la postura menores que 12 días para 11 de 15 hembras sugirieron que éstas iniciaron un desarrollo rápido de los folículos en las áreas de descanso durante la primavera. La duración del intervalo disminuyó en aproximadamente 0.4 días y la fecha de iniciación de los nidos incrementó en cerca de 0.5 días por cada día que una hembra retrasó su llegada. Así, las hembras que llegaron primero al delta del Yukon presentaron intervalos previos a la postura de hasta cuatro días más largos, pero anidaron hasta cinco días más temprano que las hembras que arribaron últimas. La proximidad de las áreas de escala de primavera en la Península de Alaska a las áreas de nidificación en el delta del Yukon podrían permitirle a estas aves alterar el desarrollo de los folículos dependiendo de las condiciones anuales, e invertir los nutrientes adquiridos en ambas áreas en la formación de huevos. La plasticidad en cuanto al momento en que se desarrollan los folículos probablemente resulta ventajosa en un ambiente variable en donde el momento en que se derrite la cobertura de nieve en la primavera puede variar anualmente entre 2 y 3 semanas.

## INTRODUCTION

Arctic geese initiate nesting following lengthy migrations to seasonal environments where snow cover can melt at different times among years. The timing of migration and nest initiation are important to reproductive success of geese because late-nesting females typically lay fewer eggs (Rohwer 1992, Dalhaug et al. 1996, Lepage et al. 2000), and late-hatched goslings encounter lower quality forage and have slower growth rates (Sedinger and Raveling 1986, Lindholm et al. 1994). Small, late-hatched goslings have a lower likelihood of survival (Cooch 2002). Date of nest initiation is a function of when the female initiates rapid follicle growth (Alisauskas and Ankney 1992). Geese require 11–14 days between the onset of rapid follicle growth and initiation of egg-laying (Raveling 1978, Ely and Raveling 1984), and during that period must meet the high nutritional costs of egg development (Alisauskas and Ankney 1992). By initiating rapid follicle growth during migration, some geese can begin to lay eggs within five days of their arrival at the nesting area, but must rely more heavily on nutrients acquired during migration stopovers to fulfill the nutritional demands of egg formation (Ryder 1970, Ankney and MacInnes 1978, Ebbinge and Spaans 1995). They may suffer reduced reproductive success if the melting of snow is delayed and limited nest site availability or access to forage causes females to resorb mature follicles (Barry 1962, Raveling 1978). Conversely, other geese initiate nests  $\geq 12$  days after their arrival at nesting areas because they delay onset of rapid follicle growth until migration is complete (Raveling 1978). During egg development they can secure local nutrients at the nesting area (Fox and Madsen 1981, Budeau et al. 1991, Bromley and Jarvis 1993), but may also rely on endogenous reserves acquired during migration to some degree (Gauthier et al. 2003). Geese that delay follicle growth until arrival at the nesting area are less prone to reproductive failure resulting from delayed melting of snow (Raveling 1978, Ely and Raveling 1984).

Measuring the interval between a female's arrival at the nesting area and nest initiation (hereafter "prelaying interval") improves understanding of the timing of egg development relative to arrival at the nesting area, where

a female likely acquires nutrients for follicle growth, and how reproductive effort can be affected by annual variation in when snow melts. Most studies have considered the prelaying interval as the period between peak arrival and peak nest initiation for a local nesting population. These estimates may be biased if the presence of transient birds obscures peak arrival of local nesting adults, or if geese spend part of the prelaying interval beyond the boundaries of an observer's study area. Furthermore, estimates of the prelaying interval based on peak arrival and nest initiation dates do not provide information on individual variation, which may arise if females in good physiological condition initiate nests sooner than geese in poor condition (Drent and Daan 1980, Rowe et al. 1994). Females that delay nest initiation due to poor body condition may lay fewer eggs (Bêty et al. 2003).

We estimated prelaying intervals of Emperor Geese that nested in western Alaska to determine when females initiated rapid follicle growth relative to their arrival at the nesting area and to understand how length of the prelaying interval varied in response to spring conditions. By monitoring geese marked with radio or satellite transmitters we were able to observe temporal relationships between arrival and nest initiation date at the individual level. We also examined whether Emperor Geese that migrated different distances arrived at the nesting area on different dates and if migration distance affected nest initiation date or clutch size. We examined these relationships because some Emperor Geese migrate only 650 km from wintering areas on the Alaska Peninsula whereas others migrate  $>2500$  km from wintering areas in the Commander or western Aleutian Islands. Finally, we measured how far female Emperor Geese remained from the nest site during the prelaying interval to better understand where females likely obtained nutrients after their arrival at the nesting area.

## METHODS

We captured adult female Emperor Geese along with their mates and broods in corral traps during their flightless period in late July and early August in 1999, 2002, and 2003 at 10 sites in two approximately 100 km<sup>2</sup> regions near the Kashunuk and Manokinak Rivers on the

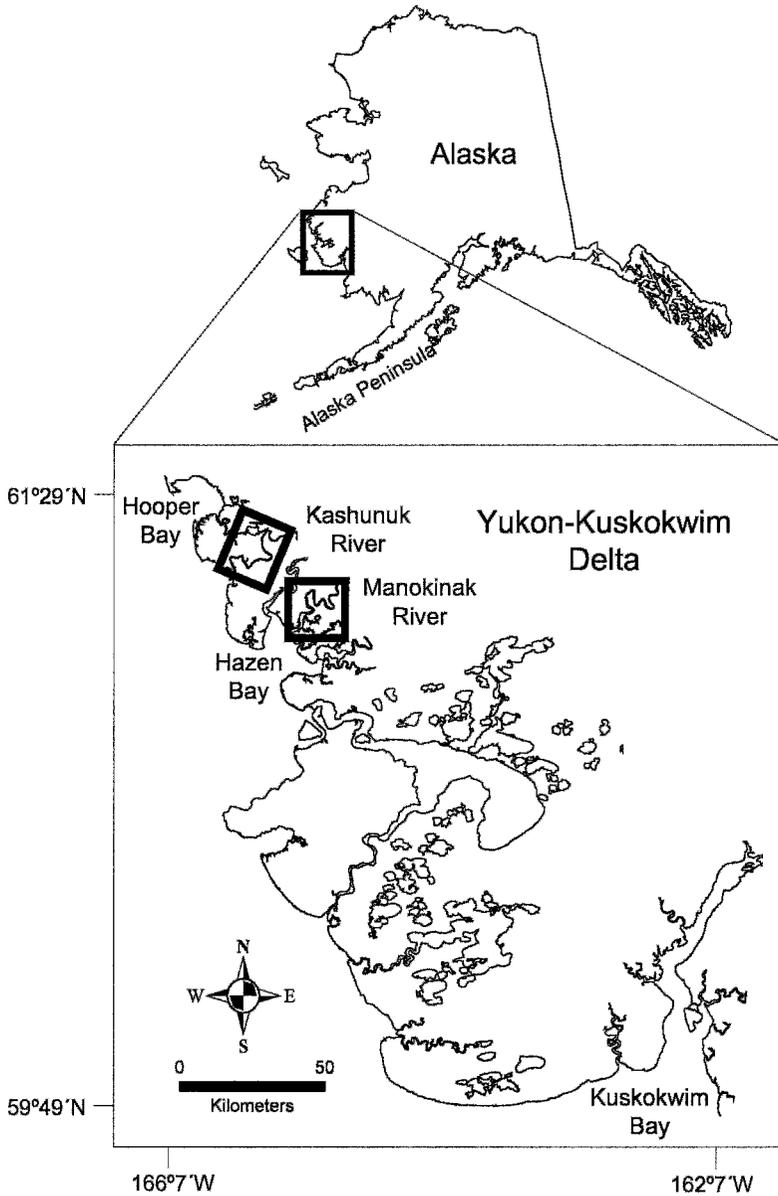


FIGURE 1. Locations of Kashunuk and Manokinak River study areas on the Yukon-Kuskokwim Delta in western Alaska. Adult female Emperor Geese were captured and radio-marked at these areas in 1999, 2002, and 2003, and their prelaying intervals were studied in 2000, 2003, and 2004.

Yukon-Kuskokwim Delta, Alaska (hereafter Yukon Delta; Fig. 1). We selected females that showed evidence of a brood patch and transported them from capture sites to nearby temporary surgical facilities where a veterinarian surgically implanted either a 26 g VHF radio-transmitter, or a 45 g (1999) or 35 g (2002 and 2003) satellite platform transmitting terminal

(PTT) transmitter in the right abdominal air sac (Korschgen et al. 1996). Transmitter antennas exited the body caudally near the base of the tail. We used implanted transmitters because externally attached transmitters can affect reproductive effort of Emperor Geese (Schmutz and Morse 2000), whereas abdominal transmitters with percutaneous antennas have minimal

impacts on behavior and reproduction in Canada Geese (*Branta canadensis*; Hupp et al. 2003, Hupp et al. 2006). We marked 55 (15 PTT, 40 VHF), 40 (20 PTT, 20 VHF), and 41 (18 PTT, 23 VHF) females in 1999, 2002, and 2003, respectively. Geese were held for at least 90 min to allow recovery from surgery before they were released at the capture site.

All satellite transmitters were programmed to broadcast locations for 8 hr within each 30-hr period beginning in late April of the spring following deployment until batteries failed 1–4 months later, with the exception of three PTTs that transmitted at three-day intervals. We received data through the Argos Data Collection and Location System (Largo, Maryland). Location quality was assigned following Harris et al. (1990). When we received multiple locations for a PTT during an 8-hr transmission, the position that had the highest location quality was selected to represent the animal's location. We did not include questionable locations with errors of >1 km (location quality = 0, A, or B) unless the position was confirmed by similar locations of higher quality on different days. PTTs transmitted data on battery potential and body temperature so we could determine when the battery failed or if the female died. VHF radios increased pulse rate if the female died.

We monitored movements of females with PTTs from their wintering sites to the Yukon Delta in spring 2000, 2003, and 2004. We monitored return dates of females with VHF radios during aerial radio-tracking flights along the coast of the Yukon Delta in each year. We initiated flights from 30 April to 8 May depending on when snow melted, and conducted five radio-tracking flights at 1–5 day intervals in 2000 and 2003. Flights were more frequent (1–3 day intervals) near the peak of arrival. We were able to conduct only three radio-tracking flights at 3–6 day intervals in 2004 due to poor weather. During each flight observers flew north along approximately 350 km of the coast from Kuskokwim Bay to Hooper Bay (Fig. 1) and returned along a route approximately 10 km inland from the coast. On each flight, we visually classified snow cover at the study areas as 0%, 1%–10%, 11%–50%, 51%–90%, or >90%.

When geese were incubating eggs in early June, we noted areas where there were repeated

locations of females with PTTs, and used aerial radio-tracking flights to search for females marked with VHF radios in approximately 200 km<sup>2</sup> regions near the Kashunuk and Manokinak River capture sites. We then conducted ground searches in areas where we suspected nests were located. We used a handheld frequency scanner to facilitate location of females with PTTs and tracked females with VHF radios with a receiver and handheld Yagi antenna. We tried to visually observe each marked female to confirm her reproductive status. We assumed females had not nested or failed in their nesting attempts if they were found in flocks or moved long distances during the nesting period. Upon locating a nest, we recorded clutch size, candled (Weller 1956) or floated (Westerkov 1950) eggs to estimate embryo age, and recorded nest location with a Global Positioning System receiver. We revisited nests near the end of incubation to ascertain hatch date and nest fate. Survival of discovered nests was high (95%), enabling us to estimate initiation dates (date first egg was laid) of most nests based on time required for incubation and egg-laying. We assumed incubation required 24 days starting when the final egg was laid, and the laying interval was 1.2 days between eggs (Eisenhauer and Kirkpatrick 1977, Petersen 1992). Initiation dates of failed nests were based on embryo age at discovery. We obtained data on daily temperatures from a coastal weather station at Hooper Bay, approximately 40–60 km from the study areas.

#### STATISTICAL ANALYSIS

We assessed percent snow cover observed on telemetry flights, dates of ice breakup on the Kashunuk River, and mean temperatures at Hooper Bay from 20 April–20 May to compare when snow melted among years. We considered a marked female's arrival date at the Yukon Delta to be the date she was first detected north of Kuskokwim Bay (Fig. 1). We used that date as the start of the prelaying interval rather than return date to the Kashunuk or Manokinak River study area because uniformity in coastal tundra habitats likely enabled females to acquire forage comparable to that on the nesting areas as soon as they reached the Yukon Delta. Most PTTs transmitted daily, increasing the likelihood that a female was

detected on the day she arrived at the Yukon Delta. For females whose PTTs transmitted at intervals of >1 day, we considered arrival date as the midpoint between the date of first detection on the Yukon Delta and date of the previous location prior to arrival. Likewise, we estimated arrival date of females with VHF radios as the midpoint between date of first detection and the date of the previous radio-tracking flight. In each year, from one to five females with VHF radios were detected on the Yukon Delta during the first radio-tracking flight of the season. In 2000 and 2004 these females were assigned the same arrival date as the earliest-arriving female with a PTT, which was the same date as the telemetry flight, or the day prior. In 2003, no females with PTTs were present prior to our first flight, so we assumed the three females with VHF radios detected on that flight had arrived the previous day. We believe this assumption is justified because a U.S. Fish and Wildlife Service aerial survey of the Yukon Delta two days prior to our first radio-tracking flight did not detect any radios and determined that <0.02% of the Emperor Goose population was present on the Delta at that time (C. Dau, unpubl. data).

Among females that nested, we estimated the prelaying interval as the number of days between estimated arrival on the Yukon Delta and nest initiation. We computed generalized linear models in PROC GLM (SAS Institute 1989) to examine the effects of when snow melted (years when snow melted earlier compared to years in which snow melted later; we called this variable "snow-melt") and individual arrival date on the Yukon Delta on length of a female's prelaying interval. Because of annual differences in timing of migration, arrival date was scaled to the earliest observed arrival of a marked bird in each year. We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for candidate models that included combinations of the main effects and their interactions. We also evaluated support for a null model in which prelaying interval was invariant. We used the residual sum of squares from each model to compute Akaike's information criterion adjusted for small sample size ( $AIC_c$ ) and Akaike weights ( $w_i$ ) to gauge relative support for models. We added an effect of radio type

(VHF versus PTT) to the most parsimonious models (those with a difference in  $AIC_c$  score from the top model of  $\leq 2.0$ ) to determine if inclusion of that effect improved the models. We did this because we were less likely to detect females with VHF radios immediately upon their arrival, thus there was potential for estimates of the prelaying interval to be shorter for females marked with VHF radios than for those with PTTs. We used model averaging (Burnham and Anderson 2002) to compute weighted parameter estimates of predictor variables.

We examined the effects of arrival date on nest initiation date to determine if females that arrived earlier also nested earlier (Bêty et al. 2003). Due to annual differences in timing, arrival date was scaled to the earliest observed arrival in each year, and nest initiation was scaled to the first observed nest initiation date. We also considered models that included effects of snow-melt, an interaction between arrival date and snow-melt, and a null model in which nest initiation date was invariant. In addition, we examined how clutch size was affected by scaled arrival and nest initiation dates. We again used an information-theoretic approach to gauge relative support for candidate models of nest initiation date or clutch size, and used model averaging to derive parameter estimates when there was uncertainty in model selection (Burnham and Anderson 2002).

We plotted winter locations of females with PTTs in ArcView (ESRI, Inc., Redlands, California) and measured the distance that each female migrated from her wintering site (primary location of a female from 1 Jan to 15 Mar) to the Yukon Delta via spring staging areas. We then examined the correlation between migration distance and annually adjusted arrival date for all females that had active PTTs upon their arrival, and the correlation between migration distance and clutch size as well as annually adjusted nest initiation date for females with PTTs that nested.

We assessed the distribution of all females with PTTs upon their arrival on the Yukon Delta, and measured distance between prelaying locations and nest sites for females with PTTs that nested. We used one location received during each 30–72 hr cycle for each PTT,

TABLE 1. Mean temperature and snow and ice conditions affecting the prelaying intervals of Emperor Geese on the coastal Yukon Delta, Alaska in 2000, 2003, and 2004. Snow cover was estimated at the Kashunuk and Manokinak Rivers during aerial radio-tracking flights. Temperature was measured by a weather station at Hooper Bay, Alaska.

Indicator of spring conditions	2000	2003	2004
20 April–20 May mean temperature (°C)	−0.8	2.1	4.8
Snow cover 1 May (%)	50–90	1–10	1–10
Snow cover 20 May (%)	10–50	0	0
Kashunuk River ice breakup	4 June	13 May	10 May

and only included locations in which location uncertainty was  $\leq 1$  km (location quality = 1, 2, or 3; Harris et al. 1990). We computed distances within which 50%, 75%, and 90% of locations were from nest sites.

## RESULTS

Of the 136 female Emperor Geese marked during the study, 92 (56 VHF, 36 PTT) returned to the Yukon Delta with functional transmitters in the spring after capture. Median dates of arrival for all marked females were 11 May, 7 May, and 6 May in 2000, 2003, and 2004, respectively. The distance females migrated from wintering areas (670–2600 km) had little influence on their arrival dates ( $r^2 = -0.004$ ). Although median arrival date varied by only five days among years, the conditions birds encountered upon returning to the Yukon Delta varied substantially. There was more snow cover and snow melted later in the colder spring of 2000 than the warmer springs of 2003 and 2004 (Table 1).

We located the nests of 37 Emperor Geese that had active transmitters. However, we suspected that the nests of two females were parasitized by conspecifics based on asynchronous egg development in both nests, and large clutch size (seven eggs) of one of the nests. We eliminated these nests from further analysis, leaving us with a sample of 35 females (14 PTT, 21 VHF) with known arrival and nest initiation dates. We found most of the nests used in our analysis of prelaying intervals in 2000 ( $n = 20$ ) or 2004 ( $n = 13$ ). Only two nests were found in 2003, probably because of high arctic fox (*Alopex lagopus*) predation that year (Fischer et al. 2003). Of 55 females not found on nests, eight died or experienced PTT failure before the onset of nesting, and 34 either did not nest or failed in their nesting attempt based on their occurrence in flocks (18 females), or because

PTT locations indicated they departed the Yukon Delta to molt remiges in Russia or on St. Lawrence Island (Hupp et al., in press). The reproductive status of 13 females was uncertain, either because their VHF radios were not detected after the onset of nesting (indicating radio failure or departure from the study areas), or because they could not be located during ground searches even though their radios were operational and they remained on the Yukon Delta (five females).

Because of similarities in spring weather in 2003 and 2004, and the small sample of nests in the former, we pooled nest data for these years and compared the prelaying interval in two years when snow melted early with 2000, when snow melted late (effect of “snow-melt”). The 35 Emperor Geese that nested spent 4–19 days on the Yukon Delta before they initiated egg-laying. Median dates of nest initiation were 27 May, 21 May, and 15 May in 2000, 2003, and 2004, respectively. The most parsimonious model for variation in length of the prelaying interval included the parameters snow-melt, scaled arrival date of a female on the Yukon Delta, and an interaction between snow-melt and arrival date (Table 2). This model accounted for 71% of the variation in the data (Fig. 2). There was also support for a model that included the main effects of snow-melt and arrival date, but that lacked the interaction term (Table 2, Fig. 2). Inclusion of an effect of radio type did not improve the two models (Table 2), and model-averaged parameter estimates for an effect of radio type suggested little difference in estimates of prelaying interval based on PTTs versus VHF radios ( $\hat{\beta}_{\text{radio type}} = 0.2$ , 95% CI =  $-0.6, 1.0$ ). Based on model-averaged parameter estimates, the prelaying interval of females in 2000 when snow melted late (median = 15 days, range = 12–19 days) was 3.9 days longer (95% CI =

TABLE 2. Candidate set of linear models used to examine the effects of when snow melted ("snow-melt"), individual arrival date, and type of transmitter (VHF versus PTT) on the prelaying interval of 35 radio-marked female Emperor Geese on the Yukon Delta, Alaska, 2000–2004. Estimates of prelaying intervals in 2003 and 2004, when snow melted early, were pooled and compared to a year in which snow melted late (2000). Arrival date was scaled to the earliest observed arrival of a marked goose in each year. Models are ranked according to the increase in Akaike's information criterion adjusted for small sample size relative to the lowest observed value of  $AIC_c$  ( $\Delta AIC_c$ ).  $\text{Log}(\mathcal{L})$  is the maximized log-likelihood value,  $K$  is the number of parameters in the model, and Akaike weights ( $w_i$ ) are the likelihood a given model is the best among the candidate set.

Model	$\text{Log}(\mathcal{L})$	$K$	$\Delta AIC_c^a$	$w_i$
Snow-melt + arrival date + snow-melt*arrival date	-25.4	5	0.0	0.50
Snow-melt + arrival date	-27.5	4	1.4	0.25
Snow-melt + arrival date + snow-melt*arrival date + radio	-25.2	6	2.6	0.14
Snow-melt + arrival date + radio	-26.8	5	2.9	0.12
Snow-melt	-36.2	3	16.2	0.01
Arrival date	-44.2	3	32.3	0.01
Intercept	-47.3	2	36.1	0.01

<sup>a</sup> The lowest  $AIC_c$  value was 62.9.

-7.9, 0.1 days) than during the years of 2003 and 2004 when snow melted early (median = 11 days, range = 4–16 days). The model-averaged estimate for effect of arrival date indicated that the prelaying interval diminished 0.4 days (95% CI = -0.9, 0.0 days) for each day of delay in a bird's arrival. Thus, prelaying intervals for birds that arrived first on the Yukon Delta were about four days longer than for birds that arrived last. In the years when snow melted early, the prelaying interval diminished an additional 0.3 days for each day of delayed arrival (95% CI = 1.0, 0.3 days).

Two almost equally supported models of nest initiation date (adjusted for annual variation) included terms for adjusted arrival date, snow-melt, and, for one model, the interaction between the two terms (Table 3). Each model accounted for 35%–40% of the variation in the data (Fig. 3). The model-averaged parameter estimate for adjusted arrival date suggested that nest initiation date increased approximately 0.5 days (95% CI = 0.1, 1.0 days) for each day a female's arrival was delayed relative to that of the first observed migrant, indicating that females that arrived earliest also nested earliest. Scaled nest initiation dates were slightly earlier in years when snow melted early ( $\hat{\beta}_{\text{snow-melt}} = 0.8$  days), however the 95% confidence limit surrounding the averaged parameter estimate was large (-4.1, 2.5) suggesting the difference was equivocal. However, in years when snow melted early, arrival date had less

of an effect on nest initiation date (Fig. 3) because nest initiation was more compressed ( $\hat{\beta}_{\text{snow-melt*arrival date}} = -0.2$ , 95% CI = -0.8, 0.3). In 2000, 50% of nests were initiated within six days of the first observed nest, whereas in 2003 and 2004, 50% of nests were initiated within three days of the first nest. Migration distance had very little effect on adjusted nest initiation date ( $r^2 = -0.08$ ) among 16 females with PTTs that nested.

Median clutch size (four eggs) was similar between years of early versus late snow-melt. Clutch size was affected more by nest initiation date than by arrival date (Table 4). However, clutch size diminished by only 0.2 eggs for each day of delayed initiation, and nest initiation date explained only 16% of the variation in clutch size (Fig. 4). There was weak support for a null model in which clutch size was invariant (Table 4). Migration distance had minimal effect on clutch size ( $r^2 = -0.02$ ) among the 16 females with PTTs.

Upon arrival at the Yukon Delta, many (57%) females with PTTs initially settled in areas south of Hazen Bay, whereas the remainder (43%) were first detected in the vicinity of Hazen and Hooper bays,  $\leq 20$  km from their original capture sites. Females that initially settled in other regions quickly returned to areas near the Manokinak and Kashunuk Rivers, and by the fifth day after their arrival, 90% were within 20 km of their site of capture. Within 15 days after arrival, all females with

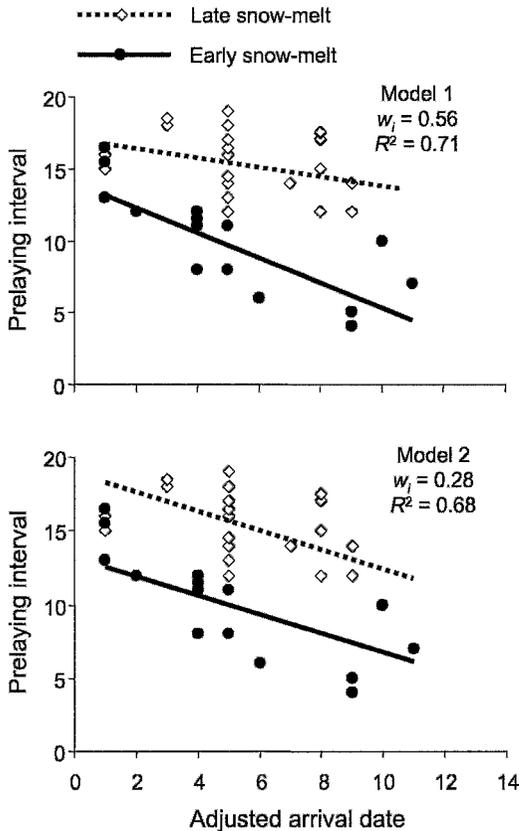


FIGURE 2. Prelaying intervals (days between arrival at the nesting area and nest initiation) of 35 radio-marked female Emperor Geese diminished with their arrival date at the Yukon-Kuskokwim Delta, Alaska and were shorter in years when snow melted earlier (2003 and 2004) compared to a year in which snow melted later (2000). Arrival date was scaled to the first observed arrival of a radio-marked bird in each year. Akaike weights ( $w_i$ ) are provided to show relative support for each model as indicated in Table 2. Model 1 included parameters for when snow melted ("snow-melt"), arrival date, and the interaction between snow-melt and arrival date, whereas Model 2 included parameters for snow-melt and arrival date without the interaction. Overlapping data points are offset so that all points are visible.

PTTs were <20 km from their capture sites. Therefore, there was no indication that marked birds nested in areas of the Yukon Delta other than the Manokinak and Kashunuk River study areas. We recorded 120 locations at 1–3 day intervals for 14 females that nested and had functional PTTs during their entire prelaying period. Fifty percent of locations were within 3 km of nest sites, 75% were within 8 km, and 90% were within 75 km.

## DISCUSSION

At the population level, we observed shorter prelaying intervals in warmer years when snow melted earlier. At the individual level, the prelaying interval diminished with later arrival dates and females that arrived later also nested later. Our estimates of prelaying intervals assume the number of eggs laid by a marked female was accurately measured, and that there was no nest parasitism by conspecifics or partial nest predation. We tried to reduce bias due to nest parasitism by removing from analysis two nests that we suspected were parasitized. However, nest parasitism is common among Emperor Geese (Petersen 1992) and we may not have detected it in all nests. Petersen (1991) observed that, on average, nest parasites laid two eggs in host nests. Therefore, any error induced by undetected nest parasitism would have been small relative to the 15-day range in prelaying interval. We cannot account for partial nest predation prior to nest discovery, but believe the effect was minimal. Arctic foxes are the main nest predators of Emperor Geese (Petersen 1992) and their numbers were low in 2000 and 2004 when we found most nests (U.S. Fish and Wildlife Service, unpubl. data).

Spring temperatures, melting of snow cover, and timing of river ice breakup in 2000 were comparable to long-term averages on the Yukon Delta, whereas 2003 and 2004 were years of unusually early breakup (CRE, unpubl. data). If rapid follicle growth for Emperor Geese requires 12 days (Alisauskas and Ankney 1992), all females in 2000 delayed follicle development until after their arrival on the Yukon Delta. Conversely, in the warmer springs of 2003 and 2004, >50% of females likely initiated rapid follicle growth prior to migrating to the Yukon Delta, resulting in prelaying intervals of <12 days. Some females apparently initiated rapid follicle growth as much as one week before they arrived on the Yukon Delta in the warmer springs, resulting in a prelaying interval of only four days. Prior to migrating to the Yukon Delta, Emperor Geese use spring staging areas in coastal lagoons on the Alaska Peninsula, where they feed on intertidal invertebrates (Petersen and Gill 1982, Petersen 1983). Staging areas are 600–700 km from the nesting areas. Females with PTTs spent 30–40 days on spring staging areas,

TABLE 3. Candidate set of linear models used to examine the effects of when snow melted ("snow-melt"; years in which snow melted early versus a year in which snow melted late) and individual arrival date on date of nest initiation by 35 radio-marked female Emperor Geese on the Yukon Delta, Alaska, 2000–2004. Arrival and nest initiation dates were scaled to the earliest observed occurrences of those events each year. Models are ranked according to the increase in Akaike's information criterion adjusted for small sample size relative to the lowest observed value of  $AIC_c$  ( $\Delta AIC_c$ ).  $\text{Log}(\mathcal{L})$  is the maximized log-likelihood value,  $K$  is the number of parameters in the model, and Akaike weights ( $w_i$ ) are the likelihood a given model is the best among the candidate set.

Model	$\text{Log}(\mathcal{L})$	$K$	$\Delta AIC_c^a$	$w_i$
Snow-melt + arrival date + snow-melt*arrival date	–25.3	5	0.0	0.47
Snow-melt + arrival date	–26.7	4	0.1	0.45
Arrival date	–30.0	3	4.3	0.06
Snow-melt	–31.0	3	6.2	0.02
Intercept	–34.2	2	10.1	0.01

<sup>a</sup> Lowest observed  $AIC_c$  value was 62.6.

usually did not use intermediate stopovers between the Alaska Peninsula and Yukon Delta, and most migrated between the two areas in a single day (JWH, unpubl. data). Emperor Geese that initiated rapid follicle development before they arrived on the Yukon Delta must have done so while at spring staging areas. Because the Alaska Peninsula staging areas are on the coast of the Bering Sea, they are often affected by the same weather patterns that influence the Yukon Delta. Indeed, mean daily temperatures between 20 April and 20 May in 2000, 2003, and 2004 at Hooper Bay on the Yukon Delta and Port Heiden, near one of the main staging areas on the Alaska Peninsula, were strongly correlated ( $r^2 = 0.56$ ). Petersen (1992) suggested that similarities in spring weather between the Yukon Delta and Alaska Peninsula serve as a cue for Emperor Geese to time their departure to nesting areas. Our results suggest that conditions on the Alaska Peninsula could also affect timing of follicle development and enable Emperor Geese to initiate nesting more quickly in years in which snow melts early. Spring weather can be an important proximate control of reproductive cycles in waterfowl (Bluhm 1992). Plasticity in timing of follicle development would be advantageous in a variable environment as it would enable females to initiate nests when conditions allowed, without a reduction in clutch size (Raveling 1978). Clutch sizes of Emperor Geese were similar among years when snow melted on different dates, indicating that variable timing in follicle development across years did not negatively affect egg production.

The length of the prelaying interval provides insights into where Emperor Geese likely acquired nutrients for follicle development. Based on isotopic analysis of eggs and forage, Schmutz et al. (2006) found that Emperor Goose eggs collected from nests near the Manokinak River in 1994 contained both a terrestrial signature comparable to forage on the Yukon Delta and a marine signature. Marine nutrients comprised approximately half of the protein in egg yolks, with a higher percentage in eggs that were laid first in a clutch, although there was considerable variation among individuals. We saw little evidence that Emperor Geese used marine habitats after their arrival at the Yukon Delta, so the marine signature was likely derived from invertebrate foods consumed at staging areas. Relative investment of local compared to marine nutrients in eggs may vary among years, with greater investment of marine nutrients in warmer years when rapid follicle development is initiated while geese are still at staging areas. Sources of nutrients for egg-laying may also vary among individuals, with earlier migrants investing more nutrients from the Yukon Delta due to their longer prelaying intervals and later migrants investing relatively more marine nutrients because they are more likely to initiate follicle development on staging areas. Differences among individuals in timing of migration and length of prelaying interval on the Yukon Delta could account for the high individual variation that Schmutz et al. (2006) observed in isotopic signatures of Emperor Goose eggs, although nest parasitism

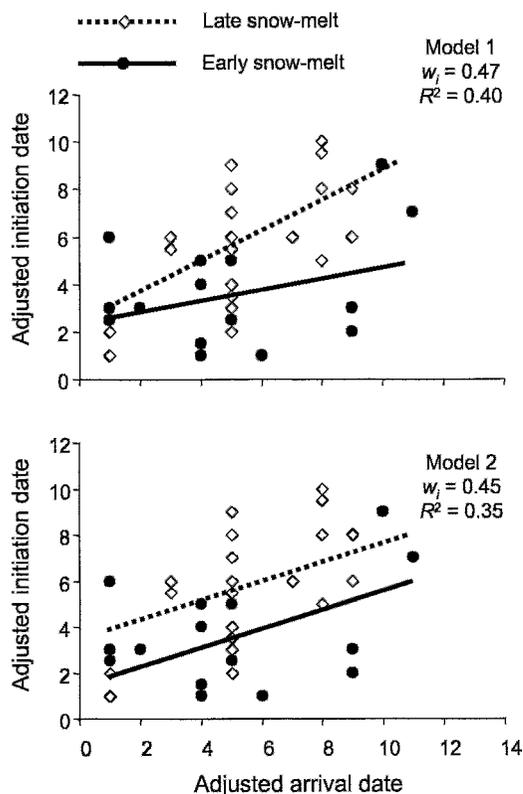


FIGURE 3. Nest initiation date of 35 radio-marked female Emperor Geese increased with individual arrival dates at the Yukon-Kuskokwim Delta, Alaska. Initiation date was scaled to the first observed nest in each year. Arrival date was scaled to the first observed arrival of a radio-marked bird in each year. Nesting tended to occur sooner after arrival in years in which snow melted earlier (2003 and 2004) than in a year when snow melted later (2000). Akaike weights ( $w_i$ ) are provided to show relative support for each model as indicated in Table 3. Model 1 included parameters for arrival date, when snow melted ("snow-melt"), and the interaction between arrival date and snow-melt, whereas Model 2 included parameters for arrival date and snow-melt without an interaction. Overlapping data points are offset so that all points are visible.

by conspecifics could also be a contributing factor.

We observed that length of prelaying intervals diminished while nest initiation dates increased with arrival date. Ely et al. (2007) observed similar relationships among Tule Greater White-fronted Geese (*Anser albifrons elgasi*) that nested in Alaska. Bête et al. (2003) also observed similar patterns for Greater Snow

Geese (*Chen caerulescens atlantica*), and found that females that had low indices of abdominal fat (Owen 1981) prior to migration delayed nest initiation after their arrival at the nesting area. Although we could not measure the physiological condition of Emperor Geese before nesting, differences in endogenous reserves could account for some of the individual variation we observed in arrival and nest initiation dates. Female Emperor Geese have high incubation constancy, likely as a predator defense mechanism (Thompson and Raveling 1987). Schmutz et al. (2006) found incubation constancy of Emperor Geese to be positively related to female body mass, and that endogenous reserves available to females during incubation had been derived in marine environments, likely intertidal habitats on the Alaska Peninsula. Emperor Geese may delay their migration to the Yukon Delta, or initiation of nests after their arrival, until they are in adequate condition to enter incubation. However, females that arrive at the nesting area later may have shorter prelaying intervals relative to early migrants due to the diminishing returns associated with delayed nest initiation (Rowe et al. 1994, Bête et al. 2003). Although we observed individual differences in arrival and nest initiation dates, they were not influenced by the distance geese had migrated. Females from different wintering areas may reach similar levels of condition while at spring staging areas.

Even in years of shortened prelaying intervals or among Emperor Geese that arrived at the Yukon Delta relatively late, local forage was likely important during the latter period of follicle development. Our data suggest that birds primarily exploited forage in the vicinity of where they nested. Upon arrival at the Yukon Delta, Emperor Geese quickly returned to the areas where they had been captured the previous year, and among females that nested, 75% of prelaying locations were within 8 km of the nest site. Likewise, Gauthier and Tardif (1991), Ganter and Cooke (1996), and Carrière et al. (1999) observed that prelaying geese fed near nesting areas. Local forage is an important source of nutrients during follicle growth for White-fronted Geese that nest on the Yukon Delta (Budeau et al. 1991) and for some species of geese elsewhere (Bromley and Jarvis 1993, Ganter and Cooke 1996, Gauthier et al. 2003).

TABLE 4. Candidate set of linear models used to examine the effects of spring arrival date and nest initiation date on clutch size of 35 radio-marked female Emperor Geese on the Yukon Delta, Alaska, 2000–2004. Arrival and nest initiation dates were scaled to the earliest observed occurrences of those events each year. Models are ranked according to the increase in Akaike’s information criterion adjusted for small sample size relative to the lowest observed value of  $AIC_c$  ( $\Delta AIC_c$ ).  $\text{Log}(\mathcal{L})$  is the maximized log-likelihood value,  $K$  is the number of parameters in the model, and Akaike weights ( $w_i$ ) are the likelihood a given model is the best among the candidate set.

Model	$\text{Log}(\mathcal{L})$	$K$	$\Delta AIC_c^a$	$w_i$
Nest initiation date	0.7	3	0.0	0.80
Intercept	-2.3	2	3.5	0.14
Arrival date	-1.9	3	5.1	0.06

<sup>a</sup> Lowest observed  $AIC_c$  value was 5.42.

Emperor Geese cannot be strictly classified either as a species that initiates rapid follicle development during migration or that delays follicle growth until arrival at the nesting area. Instead, they exhibited individual and annual variability in timing of nest initiation relative to their arrival at the Yukon Delta nesting area. The proximity of marine staging habitats to their nesting area may provide them with the flexibility to alter timing of follicle development depending on annual conditions, and to vary sources of nutrients invested into eggs. Plasticity in timing of reproduction and sources of

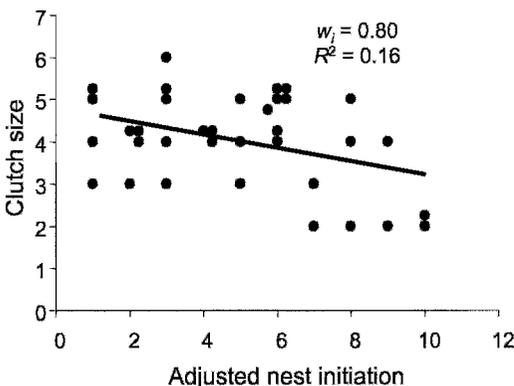


FIGURE 4. Clutch size for 35 radio-marked female Emperor Geese diminished slightly with nest initiation date at the Yukon-Kuskokwim Delta, Alaska in 2000, 2003, and 2004. Nest initiation date was scaled to the earliest observed nest in each year. Overlapping data points are offset so that all points are visible.

nutrients invested in eggs likely has adaptive benefits in a variable environment. Measurement of individual prelaying intervals in other goose species would improve understanding of the timing of follicle development relative to arrival after migration.

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