

REPRODUCTIVE ECOLOGY OF EMPEROR GEESE: ANNUAL AND INDIVIDUAL VARIATION IN NESTING¹

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Abstract. I studied the nesting ecology of adult female Emperor Geese (*Chen canagicus*) from 1982–1986 on the Yukon-Kuskokwim Delta (YKD), Alaska. I evaluated variation among and within years in date of migration, nest initiation date, clutch size, nesting success, and nesting frequency of 90 individually marked females. Geese arrived on their nesting areas at the same relative date of the season each year and initiated nests five days after their arrival on the study area. Individuals initiated nests at the same relative time of the season each year. There was no significant repeatability for clutch size, nor did mean clutch sizes vary among years. This may be related to geese having ready access to foods during spring migration and a relative short distance (600 km) between migration staging areas and nesting grounds. When data were pooled, clutch sizes declined as the season progressed; however, this decline was not significant within individuals among years. The proportion of adult females that nested annually varied from 38.5–52.0%; the probability of nesting was independent of clutch size or nesting success the previous season. This low nesting frequency may reflect high annual mortality resulting in a high proportion of newly paired birds each year (thus less likely to nest). Emperor Geese remain at food-rich, spring staging areas until nest sites are available, initiate nests early, lay large clutches, and frequently forgo nesting.

Key words: Reproductive ecology; annual variation; individual variation; nesting; *Chen canagicus*; Alaska.

INTRODUCTION

Studies of breeding biology of birds frequently deal with average population statistics such as clutch size or hatching success. Selection, however, acts on individuals. Understanding variation in reproductive success within and among individuals over the lifetime of the individual can lead to a more complete understanding of population demography, adaptation, and selection (e.g., Clutton-Brock 1988, Newton 1989).

Studies of waterfowl suggest that some individuals may consistently produce more offspring than others (e.g., Raveling 1981, Owen and Black 1989, Bacon and Andersen-Harild 1989). Although variation inevitably exists within populations, individual birds are often consistent, migrating to nesting areas about the same time each year (Rees 1989), laying eggs on similar dates, and laying similar clutch sizes each year (Ko-

skimies 1957, MacInnes and Dunn 1988, Gauthier 1989, Lessells et al. 1989). Some of these traits are heritable (Cooke 1987, van Noordwijk and van Balen 1988), although population averages may change with annual variation in weather and other proximate factors.

To better understand how reproductive success may vary among individuals within a population, I studied the nesting ecology of female Emperor Geese (*Chen canagicus*). The Emperor Goose is a maritime species that nests primarily along the coastal fringe of the Yukon-Kuskokwim Delta (YKD), Alaska and winters throughout the Aleutian and Komandorski islands (Gabrielson and Lincoln 1959). Emperor Geese are monogamous and nest either dispersed or semi-colonially, primarily along elevated shorelines of ponds and sloughs (Eisenhauer and Kirkpatrick 1977, Portenko 1981). In this paper I evaluate the variation within and among years in arrival, nest initiation, clutch size, nesting success, and frequency of nest initiation for individual adult female Emperor Geese. I also compare this variation with other goose species nesting on the YKD

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to gain a more complete understanding of how these species may vary in similar environmental conditions.

METHODS

STUDY AREA

I conducted this study on a 760-ha area near Kokechik Bay, YKD, Alaska (63°39'N, 165°51'W) from 1982–1986. This area included the entire study site used by Eisenhauer and Kirkpatrick (1977) in 1971–1973, plus adjacent area (Petersen 1990). The area contains a mixture of lowland, intermediate, and upland tundra similar to that described by Ely and Raveling (1984). Lowland tundra is generally less than 0.5 m elevation above mean high tide and dominated by grasses and sedges. Upland tundra is ≥ 0.5 m of elevation and characterized by prostrate willows (*Salix* spp.), dwarf birch (*Betula nana*) and Labrador tea (*Ledum palustre*), and contains pingos similar to those described by Burns (1964). Intermediate tundra contains plants characteristic of both upland and lowland tundra. The flora, fauna and physical features are described by Holmes and Black (1973), Eisenhauer and Kirkpatrick (1977) and Jackson (1981). Nesting Emperor Geese use similar habitats on the northern Chukotka Poluoostrov, Siberia (Kistchinski 1971, Portenko 1981) and elsewhere on the YKD (Spencer et al. 1951).

NESTS

I determined clutch sizes, nesting success (proportion of nests in which one or more eggs hatched), and hatching success (proportion of eggs that hatched in successful nests) of 746 Emperor Goose nests. Clutch size data were also collected for Greater White-fronted Goose (*Anser albifrons*), Cackling Canada Goose (*Branta canadensis minima*), and Black Brant (*B. bernicla nigricans*) nests found on the study area. Nest searching methods were similar to those used by Raveling (1978) and Ely and Raveling (1984). I determined some nest initiation dates by direct observations of birds building nests and laying eggs. For nests found during egg laying, I determined initiation dates by backdating from the date the nest was found, using an egg-laying rate of 1.2 days/egg (Eisenhauer 1976, Krechmar and Kondratiev 1982). For nests found after incubation began, I assumed the same egg-laying rate and a 24-day incubation period to backdate from

hatch dates (Eisenhauer 1976, Krechmar and Kondratiev 1982). For nests containing eggs laid by more than one female (see below) I excluded obvious parasitic eggs before calculating initiation dates. Parasitic eggs are all eggs added to a nest after incubation begins, extra eggs added during egg laying (i.e., more than one egg laid/day), eggs laid outside a nest and then found in the nest, and eggs with viable embryos that were not completely developed after most eggs hatched and the brood had abandoned the nest. Clutch size includes all but obvious parasitic eggs of Emperor Geese incubated in the nest.

Evidence of hatching included pipped and hatched eggs, goslings in the nest, and egg shells with the inner membrane intact but separated from the shell. For eggs that failed to hatch, I determined the type of predator from direct observation of predation events or from physical evidence at the nest. Evidence of arctic fox (*Alopex lagopus*) predation included tooth marks on eggs eaten near the nest, scat in the nest, foot prints to the nest, or remains of an adult killed near the nest. Foxes normally removed and cached the entire clutch (Stickney 1989, pers. observ.). Evidence of avian predation (gulls [*Larus* spp.] and jaegers [*Stercorarius* spp.]) included eggs with holes pecked in them or large fragments with peck marks. Gulls and jaegers ate eggs in the nest or removed a single egg if disturbed by the goose (Strang 1976, pers. observ.).

MARKED GEESE

I marked 90 nesting female geese with individually-coded yellow neck collars and standard USFWS leg bands. Geese were trapped on their nests when hatch began (68 birds) or after 10 days of incubation (22 birds) using modified Weller (Weller 1957) traps (85 birds) or by hand (3, plus 2 with a dip net). Daily observations of geese from blinds allowed me to determine arrival dates of these marked females during subsequent springs. Nesting frequency is defined as the number of known nesting attempts of geese returning to the nesting area as determined by direct observations of marked geese during egg laying or incubation.

WEATHER AND SNOW CONDITIONS

Temperatures on the wintering area and spring staging areas are from National Oceanographic and Atmospheric Administration monthly summary sheets of local climatological data. Consis-

tent yearly winter weather data are available only from Cold Bay, Alaska, a location on the north-easterly portion of the primary winter range of Emperor Geese (Gabrielson and Lincoln 1959, Dement'ev and Gladkov 1952). Data on early spring weather are from Cold Bay, and data on weather during spring migration are from King Salmon and Port Heiden, Alaska. Port Heiden is a major spring staging area (Petersen and Gill 1982) approximately 650 km SE of Kokechik Bay; however, long term weather data for the spring staging area are available only from King Salmon, 250 km NE of Port Heiden.

STATISTICAL ANALYSIS

I expressed annual variation in arrival, clutch initiation, and hatch dates in relation to the first date of the event in a given year. I determined repeatability estimates of arrival date, nest initiation date, clutch size, and hatch date following Lessells and Boag (1987) and standard errors of the repeatability estimates following Becker (1984). Statistical tests were conducted with SPSS* (SPSS* 1986). I used bootstrapping to determine the standard errors of coefficients of variation in clutch sizes among other goose species (50 samples/species). Preliminary assessment of the data suggested that nest mortality rates were constant throughout the nesting period in some years and variable in others, and in some years detectability of destroyed nests was high whereas in others it was low (due to high predation rates during egg laying). Thus, neither the Apparent or the Mayfield procedures were useful for comparing nest success (Johnson and Shaffer 1990). Success of nests were therefore calculated using the Kaplan-Meier procedure (Kaplan and Meier 1958), as modified by Pollock et al. (1989), to permit comparisons of data throughout the nesting period and to include nests found at various stages of the egg-laying and incubation cycle. I used the log-rank test modified for staggered entry design (Pollock et al. 1989) to compare survival rates of nests at five-day intervals among years.

RESULTS

ARRIVAL

The first Emperor Geese arrived at the nesting area in early to mid-May, with large influxes of geese occurring two to 16 days later (Table 1). Marked geese arrived within two to seven days

of the first migrants and continued to appear well into the nesting period (Fig. 1). Marked geese arrived on similar relative days of the migration period in different years (Table 2). Based on the timing of snow melt, I considered 1982, 1985 and 1986 to be late seasons and 1983 and 1984 to be early seasons (Petersen 1990). There was a tendency for marked geese to arrive more synchronously in late seasons than in early seasons (Fig. 1). Conditions on the nesting grounds were not indicative of conditions the preceding winter on the wintering area (Table 3). General conditions on the spring staging areas, however, were similar to conditions in spring on the nesting areas.

NEST INITIATION

Median dates of nest initiation varied from 20 May to 3 June (Table 1), and only in late years (1982, 1985 and 1986) coincided with snow melt and drainage of water from nesting areas (Petersen 1990). Marked geese initiated nests five days after they were first seen on the study area (Table 4). There was no significant difference in the length of time marked geese were present before initiating nests either among years or between early and late seasons. Nest initiation dates of individuals were significantly repeatable (Table 2); the timing of nest initiation for an individual was similar each year.

CLUTCH SIZES

Mean clutch sizes were similar among years (Table 1), and did not vary significantly between early and late seasons (ANOVA $F_{1,470} = 0.71$, $P = 0.41$). Clutch sizes of marked geese were similar to clutch sizes of unmarked geese (ANOVA $F_{1,470} = 0.42$, $P = 0.52$). Clutch sizes of marked geese were also similar in both early and late seasons (ANOVA $F_{1,130} = 1.00$, $P = 0.32$). The most common clutches were 4–6 eggs (Fig. 2) and the median clutch size was five eggs.

Repeatability of clutch size was not significant (Table 2); individual geese did not consistently lay the same number of eggs each year. Differences in clutch size for marked geese averaged less than one egg between years, although several individuals had wide variations in clutch size. No individual consistently laid large (>6) or small (<4) clutches.

There was no consistent trend for the 18 marked individuals from which two or more years data are available to lay fewer eggs when nesting later

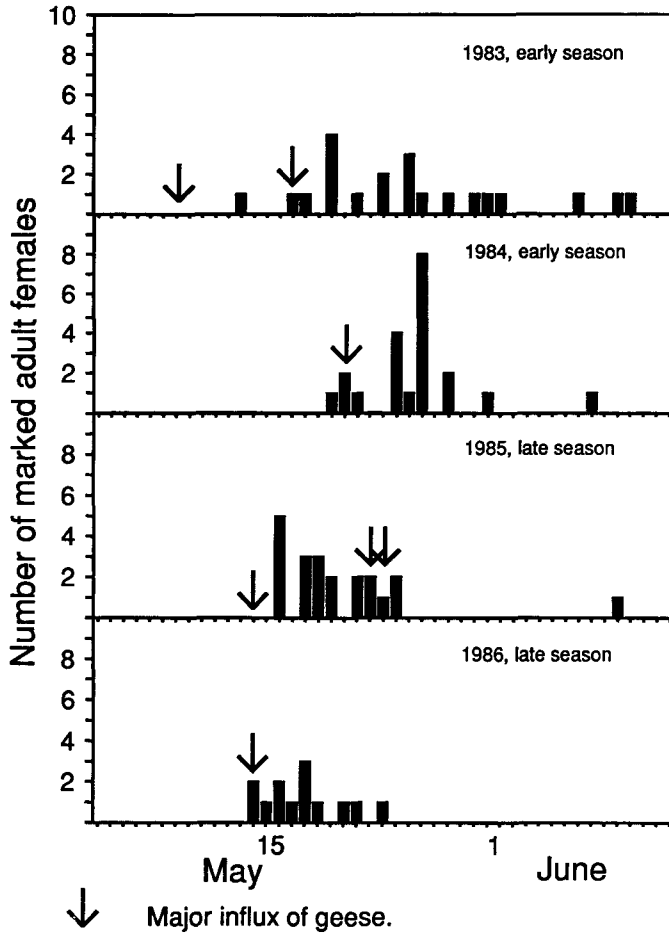


FIGURE 1. First observations of individually marked geese and major influxes of unmarked geese in spring.

in relation to the median nest initiation date than in other years. Only for one individual was this trend significant over four years ($r^2 = 0.9259$, $n = 4$, $P = 0.04$). Six individuals showed no or only a slight change in clutch size with later nesting, one an increase in clutch size, and eight a decrease in clutch size. Two individuals laid the same number of eggs beginning on the same date each year for three years and two years, respectively.

Clutch size of all Emperor Geese declined continuously throughout the nesting season (Fig. 3) at similar (ANCOVA $F_{4,456} = 0.73$, $P = 0.57$) rates each year. Clutch sizes of marked geese exhibited a similar trend at a slightly higher, although not significantly different (ANCOVA $F_{1,458} = 2.43$, $P = 0.12$), rate of daily decline.

NESTING FREQUENCY

When data from all individuals which survived to the next year are combined, 51.5% of 68 females that nested one year nested the next year, while 72.0% of 25 females that failed to initiate a nest one year failed to nest the following year (Table 5). Nesting frequency was independent of clutch size the previous year (Median test $\chi^2 = 0.02$, $df = 1$, $P = 0.90$), although not independent of nesting status the previous year ($\chi^2 = 4.07$, $df = 1$, $P = 0.04$) (Table 5). The frequency with which females nested ranged from five times in five years to once in five years (Table 6). Fifteen of 45 geese (33.3%) nested each year and, on average, a female nested 69.8% of the years she was known to be alive. The overall proportion

TABLE 1. Arrival, nesting chronology, and clutch sizes of Emperor Geese.

Year	First arrival	Major influxes	First nest initiation	Median nest initiation (n)	Clutch size $\bar{x} \pm SE$ (n)	Eggs/clutch hatched $\bar{x} \pm SE$ (n)
1982						
All geese ¹			29 May	3 June (54)	4.9 \pm 0.2 (74)	4.6 \pm 0.2* (65)
Marked geese			29 May	3 June (34)	5.0 \pm 0.3 (36)	4.6 \pm 0.3 (34)
1983						
All geese	7 May	23 May	12 May	20 May (105)	5.1 \pm 0.2 (111)	4.7 \pm 0.2* (102)
Marked geese	13 May	17 May	15 May	21 May (28)	5.0 \pm 0.2 (29)	4.7 \pm 0.2 (29)
1984						
All geese	8 May	13, 22–23 May	17 May	23 May (73)	4.8 \pm 0.2 (88)	3.8 \pm 0.2 (85)
Marked geese	15 May	18 May	19 May	24 May (22)	5.3 \pm 0.3 (21)	4.4 \pm 0.2 (20)
1985						
All geese	17 May	19 May	25 May	1 June (110)	4.8 \pm 0.1 (109)	4.5 \pm 0.2* (109)
Marked geese	19 May	26 May	27 May	31 May (30)	4.9 \pm 0.2 (30)	4.6 \pm 0.2 (30)
1986						
All geese	5 May	7, 16 May	21 May	28 May (55)	5.0 \pm 0.2 (72)	4.3 \pm 0.2* (56)
Marked geese	12 May	23 May	23 May	28 May (16)	4.8 \pm 0.3 (16)	4.4 \pm 0.3 (14)
Total						
All geese					4.9 \pm 0.1 ² (472)	4.4 \pm 0.1 ⁴ (417)
Marked geese					5.0 \pm 0.1 ³ (132)	4.6 \pm 0.1 ⁵ (127)

¹ Includes marked and unmarked geese nesting on the study area.

² $F_{4,467} = 0.941$, $P = 0.44$. Clutch size among years.

³ $F_{4,127} = 0.533$, $P = 0.71$. Clutch size among years.

⁴ $F_{4,127} = 5.016$, $P = 0.0005$. Number of eggs hatched per successful nest among years.

⁵ $F_{4,127} = 0.522$, $P = 0.72$. Number of eggs hatched per successful nest among years.

* Similar clutch sizes; LSD test, $P > 0.05$.

of geese nesting each year was similar ($\chi^2 = 1.87$, $df = 3$, $P = 0.60$), and ranged from 38.5% in 1986 ($n = 26$) to 52.0% in 1984 ($n = 25$) with intermediate values for 1983 (44.4% of 18) and 1985 (50.0% of 24). Marked geese successfully nested at least once (the year they were nest trapped), and geese that did not hatch eggs in at least one year were not sampled. The sample of marked individuals is probably biased toward older, more successful females. Thus the overall nesting frequency of 69.8% based on the average of individual geese that were known to be alive is probably a maximum and 42.6% based on average annual nesting frequency a minimum

proportion for adult females on the Kokechik Bay study area.

NESTING SUCCESS

The proportion of nests having one or more eggs hatch varied markedly among years (90.6% in 1982 to 0.1% in 1986) (Table 7). Nesting success of marked geese was similar to unmarked geese.

In years when few nests were destroyed (1982–1983), nests were lost to avian and mammalian predators in similar proportions ($\chi^2 = 0.15$, $df = 1$, $P = 0.70$). In contrast, during years when predation rates were high (1984–1986), the relative number of nests destroyed by mammals

TABLE 2. Repeatability of arrival date, nest initiation date, clutch size, and hatch date for individual female Emperor Geese.

	F ratio	df	P	Repeatability	SE
Arrival date	2.46	17, 33	0.013	0.341	0.164
Nest initiation date	2.23	18, 34	0.021	0.274	0.144
Clutch size	0.83	19, 34	0.660	-0.179	0.142
Hatch date	1.89	16, 30	0.065	0.240	0.175

TABLE 3. General weather conditions experienced by Emperor Geese during winter, late-winter, spring staging and summer.

	Winter	Late-winter	Spring staging		Summer
	Aleutian Islands ¹ Dec.-Mar. -1.8°C ⁴	Cold Bay Apr. 0.6°C	King Salmon Apr.-May 2.6°C	Port Heiden ² Apr.-May 1.1°C	Kokechik Bay ³ May-Jun 3.1°C
1981-1982 conditions ⁵	Warm	Cold	Very cold	Cold	
1982-1983 conditions	Warm	Very warm	Very warm	Very warm	Very warm
1983-1984 conditions	Warm	Cold	Average	Average	Average
1984-1985 conditions	Very warm	Very cold	Very cold	Cold	Very cold
1985-1986 conditions	Average	Average	Cold	Average	Cold

¹ Aleutian Island weather based on Cold Bay reported monthly summaries.
² Port Heiden weather based on average min.-max. monthly temperatures, no information on deviation of temperature from long term normal available. General weather conditions based on differences in temperatures among years.
³ Kokechik Bay weather based on average min.-max. temperatures from 10 May-10 June taken at the field camp. General weather conditions based on differences in temperatures among years.
⁴ Long term mean.
⁵ General weather condition categories based on deviation from long term mean temperatures: Very cold < -2.0°C, Cold -2.0° to -0.4°C, Average -0.5° to 0.6°C, Warm 0.7° to 2.0°C, Very warm > 2.0°C.

was high while the number destroyed by birds remained low (Table 8). The arctic fox was the primary mammalian predator on the study area and two pairs were present each year.

Predators frequently destroyed nests early in the nesting season before females began incubating (Fig. 4). Only in 1985 were any nests destroyed by predators after the first 10 days of incubation. When few nests were sampled before incubation began (1982 and 1983), the probability of a nest surviving to hatch appeared to be very high. However, too few nests were visited early in those years to accurately determine pre-incubation loss rates. With the exceptions of 1984 and 1986, rates of nest loss were similar between years (log rank tests, $P > 0.05$) (Fig. 4). Predation rates in 1984 were similar only to 1985 (log rank tests, $P > 0.05$). The predation rate in 1986 was different from all other years (log rank tests, $P < 0.005$).

The mean number of eggs in successful ($\bar{x} = 5.0 \pm 0.1$, $n = 398$) and unsuccessful clutches (\bar{x}

$= 4.1 \pm 0.3$, $n = 34$) was similar among years (ANOVA $F_{34,398} = 1.51$, $P = 0.08$). Smaller clutches were less likely to be successful than larger clutches ($\chi^2 = 17.84$, $df = 4$, $P = 0.0013$) when all years were pooled. Small clutches (≤ 3) were combined because of small sample sizes, as

TABLE 4. Length of time between date of first observation and nest initiation for individually marked geese.

Year	Season type	n	Days present	
			Median	Range
1983	Early	4	5	3-6
1984	Early	8	4	0-7
1985	Late	11	6	2-10
1986	Late	4	4	1-8
Total		27	5 ^{1,2}	0-10

¹ Among years, Kruskal-Wallis $\chi^2 = 3.74$, $df = 3$, $P = 0.29$.
² Among seasons, Kruskal-Wallis $\chi^2 = 1.32$, $df = 1$, $P = 0.24$.

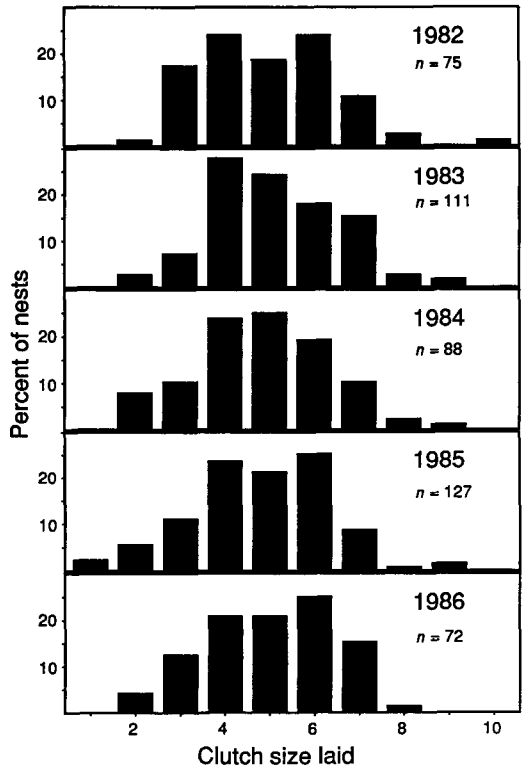


FIGURE 2. Clutch size distribution of Emperor Geese by year.

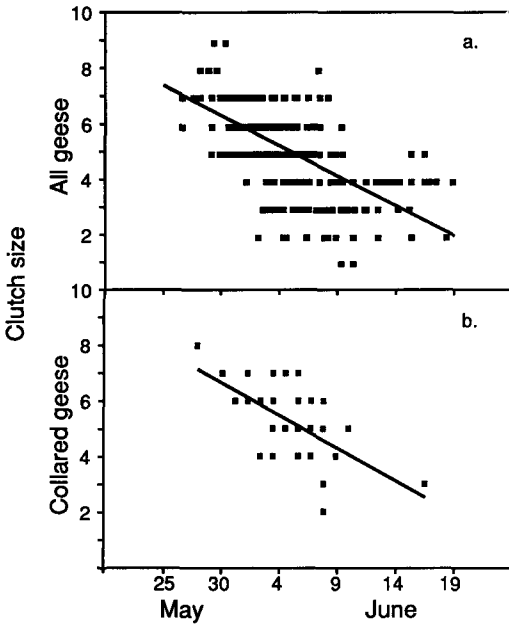


FIGURE 3. Clutch size as related to date of first egg. a. $r^2 = 0.32$, $n = 366$, $y = 37.75 + (-0.21)x$; b. $r^2 = 0.36$, $n = 18$ birds, 49 clutches, $y = 45.44 + (-0.26)x$.

were large clutches (≥ 7). Sample sizes are too small for statistical comparison of nesting success by clutch size by year. However, among completed clutches, small clutches were destroyed in significantly higher proportions than larger clutches in late years when fox predation was severe (1985 and 1986; $\chi^2 = 22.01$, $df = 4$, $P = 0.0002$) (Fig. 5).

HATCHING SUCCESS

The mean number of eggs hatched per nest varied significantly among clutch sizes (ANOVA

TABLE 5. Status of adult female geese in relation to clutch size and reproductive history the previous year.

Status or clutch size in year t	Number (%) of geese returning in year t + 1	
	Nested	Not nested
Not nested	7 (28.0%)	18 (72.0%)
Nested	35 (51.5%)	33 (48.5%)
Clutch size		
≤3	4 (57.1%)	3 (42.9%)
4	7 (58.3%)	5 (41.7%)
5	6 (42.9%)	8 (57.1%)
6	10 (41.7%)	14 (58.3%)
7	4 (66.7%)	2 (33.3%)
≥8	2 (100%)	0 (0%)
Unknown	2 (66.7%)	1 (33.3%)

TABLE 6. Number of nesting attempts of 45 marked geese known alive.

Years observed	Number of years nested				
	5	4	3	2	1
5	1	2	0	1	2
4		3	3	1	2
3			4	3	5
2				7	11

$F_{9,422} = 70.505$, $P < 0.0001$), but not among years (ANOVA $F_{4,422} = 2.288$, $P = 0.06$) (Fig. 5). Among successful nests, the number of eggs hatching per nest increased with increasing clutch size. This pattern was consistent for each clutch size in each year (year \times clutch size interaction, ANOVA $F_{28} = 1.21$, $P = 0.06$). The most common clutches (4–6 eggs/clutch) frequently lost one or more eggs ($\chi^2 = 22.21$, $df = 5$, $P = 0.0005$) (Table 9).

DISCUSSION

NESTING CHRONOLOGY

Weather influences nesting chronology in several species of geese (Cooch 1958, Barry 1962, Hudec and Kux 1971, Ryder 1972, Newton 1977 and citations therein, Raveling and Lumsden 1977), including Emperor Geese. Emperor Geese arrived at later dates and initiated nests at later dates when freezing temperatures and snow and melt-water covered the nesting area (Eisenhauer and Kirkpatrick 1977, Mickelson 1975, Petersen 1990). Delayed nesting seasons, however, did not result in changes of relative arrival patterns of individual Emperor Geese. Individuals that arrived before the median arrival date in mild years arrived early in cold years, and birds that arrived after the median arrival date in mild years arrived late in cold years. This consistency in arrival patterns suggests that birds responded similarly to the same environmental cues for initiation of migration each year. Weather conditions at spring staging areas along the Alaska Peninsula reflected conditions on the nesting grounds on the YKD and may provide a reliable cue regarding the availability of nest sites. In other species of geese, older birds initiated nests earlier in the season than younger, less experienced geese (Brakhage 1965), and adult geese initiated nests about the same time (as modified by weather) each year (Findlay and Cooke 1982, but see MacInnes and Dunn 1988). No trend of earlier nest initiation dates in subsequent seasons was apparent for female Emperor Geese trapped

TABLE 7. Survival of Emperor Goose nests until hatch.

	Pollock et al. (1989) method				Apparent method			
	n	% surv.	Var.	95% c.l.	Uncollared geese		Collared geese ¹	
					n	% surv. ^{3,4}	n	% surv. ³
1982	63	90.6	0.18	82.2–99.0	80	96.3		
1983	118	78.6	0.23	69.2–87.9	102	94.1	7	100
1984	105	37.6	0.15	29.9–45.3	129	67.4	14	78.6
1985	134	48.5	0.22	39.3–57.7	135	71.8	17	88.2
1986	171	0.1	0.00	0.0–0.1	151	33.8	10	40.0

¹ Includes only geese marked in previous years.

² Nests found after egg laying had begun were included in analysis. This is the probability of a nest surviving to hatch.

³ Hatching success calculated using the Apparent method (n hatching/ n found) (Johnson and Shaffer 1990).

⁴ Includes only geese not collared in previous years.

at hatch, suggesting that the females sampled were experienced, older females. No data are available, however, from known-aged individuals.

CLUTCH SIZE

Reduced clutch sizes in some years for arctic and sub-arctic nesting geese have been attributed to insufficient food (or insufficient quality) available at spring staging areas and resultant poorer condition of females on their arrival to nesting areas (Newton 1977, Ebbsing et al. 1982, Davies and Cooke 1983, Cooch et al. 1989). In years with delayed snow melt on the nesting areas, reduced clutch sizes were attributed to use of energy reserves by females for maintenance during a prolonged pre-nesting period and subsequent reduction in reserves available for egg laying (Ankney and MacInnes 1978, Raveling 1979a). Seasons severely delayed because of prolonged snow and ice melt can result in non-breeding by significant proportions of arctic goose populations (Barry 1962, Raveling 1978, Cooke et al. 1981, Prop et al. 1984).

Spring weather currently influences Emperor Goose clutch size less than for other geese. Black Brant, Cackling Canada Geese, and White-fronted Geese nesting on the YKD laid fewer eggs in

late years than in early years (Mickelson 1975, Raveling 1978, Dau and Mickelson 1979, Ely and Raveling 1984, pers. observ.). Unlike the other species nesting in the area, Emperor Geese exhibited no significant variation in clutch size between early and late seasons from 1982–1986. The variation in clutch size among these years in the same area for the other goose species was significantly greater than for Emperor Geese ($Z = -2.30$, $P = 0.01$). This suggests that for Emperor Geese the nutrient reserve levels needed for egg production remained high in late seasons during this period. This may be because Emperor Geese have ready access to foods during spring migration, or because they have a shorter migration between staging areas and nesting grounds than do other species of geese.

Similar weather conditions at staging and nesting areas could clue Emperor Geese to remain on staging areas where abundant food is available until nesting areas are accessible. Emperor Geese feed extensively on blue mussels (*Mytilus edulis*) and the bivalve *Macoma balthica* in intertidal regions of lagoons along the north side of the Alaska Peninsula during spring migration (Petersen 1983). The delay in migration in late years would result in geese remaining in these food rich

TABLE 8. Proportion of nests destroyed by mammalian and avian predators. Other losses include nests flooded due to storm tides, deserted nests, and unknown losses.

	Total nests	Total destroyed	Type of loss		
			Mammalian predation % (n)	Avian predation % (n)	Other % (n)
1982	102	8	37.5% (3)	62.5% (5)	
1983	168	13	46.2% (6)	53.8% (7)	
1984	141	53	79.2% (42)	15.1% (8)	5.7% (3)
1985	159	43	81.4% (35)	11.6% (5)	7.0% (3)
1986	176	114	89.5% (102)	8.8% (10)	1.8% (2)

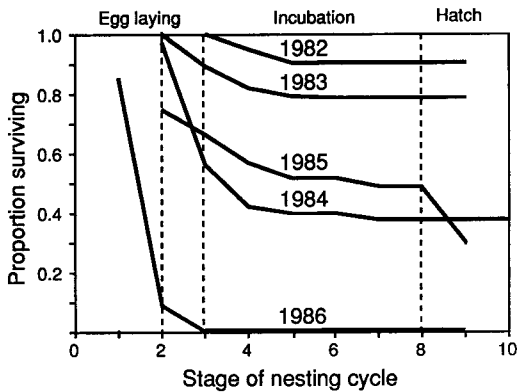


FIGURE 4. Survival probabilities of Emperor Goose nests at stages of the nesting cycle. Distance between each stage is five days. Stages: 1—first nest initiated, 2—median nest initiation, 3—median initiation of incubation, 4 to 7—incubation at 5 day intervals, 8—median hatch, 9 to 10—hatch at 5 day intervals.

areas until nesting areas became available. This would result in reduced clutch size variability between early and late years because geese would not spend prolonged periods on the nesting area and use energy reserves needed for egg formation and incubation.

Reduction of clutch sizes in late seasons could occur because of local depletion of mussel and clam beds by foraging Emperor Geese. Mickelson (1975) and Eisenhauer and Kirkpatrick (1977) reported lower clutch sizes in Emperor Geese in late seasons when populations were much larger (140,000–160,000; Eisenhauer and Kirkpatrick 1977). During the years of this study the spring Emperor Goose population declined from 101,000 in 1982 to 42,000 in 1986 (R. King, U.S. Fish and Wildlife Service, pers. comm.). A density dependent effect on clutch size may have occurred during previous studies, but could have been absent from 1982–1986. Emperor Geese arrive at their nesting area with heavy accumulations of body fat (Portenko 1981). Geese could accumulate additional energy stores after arrival on the nesting grounds, thus reduce the density dependent effect on clutch size. Some forage plants are available during the pre-laying period (Raveling 1979b, pers. observ.) and Emperor Geese feed at this time; however adult female fat and protein levels did not increase significantly after arrival to the nesting area (K. Laing and D. G. Raveling, pers. comm.).

Clutch sizes of Emperor Geese declined within each season from 1982–1986 at a rate similar to

TABLE 9. Clutch sizes in relation to total and partial failure, and number of eggs hatched by Emperor Geese in 1982–1986.

Clutch size	<i>n</i>	% total nests	% total nest failure	% partial nest failure	$\bar{x} \pm SE$ at hatch ¹
1	3	0.6	33.3	0.0	1.0 \pm 0.0*
2	21	4.5	28.6	20.0	1.8 \pm 0.1*
3	52	11.2	19.2	19.0	2.8 \pm 0.1*
4	113	24.3	15.9	30.5	3.6 \pm 0.1
5	104	22.4	8.6	34.4	4.5 \pm 0.1
6	102	22.0	9.8	44.4	5.2 \pm 0.1
7	55	11.8	12.7	52.1	6.0 \pm 0.2**
8	9	1.9	11.1	25.0	7.4 \pm 0.5**
9	5	1.0	40.0	33.3	7.7 \pm 1.3**
10	1	0.2	0.0	0.0	10.00**

* ** Denotes pairs of groups that are similar. Scheffe procedure $P < 0.05$.
¹ ANOVA $F_{9,455} = 65.79, P = 0.0000$.

that reported by Rohwer and Eisenhauer (1989) for Emperor Geese on the same study site in 1973. This seasonal decline is found in many species of birds that exhibit variation in clutch size (e.g., Klomp 1970, von Haartman 1971, Perrins and McCleery 1989, but see Eldridge and Krapu 1988). Toft et al. (1984) and Murphy (1986) summarized explanations of reduced clutches within a season. Smaller average clutch sizes later in the season have been attributed to renesting individuals laying smaller clutches later in the season, young or less-experienced individuals laying smaller clutches later in the season, and depletion of nutrient reserves while waiting to nest. Toft et al. (1984) suggested that different optimum clutch sizes may exist for individuals that nest at different times during the season. This is supported by studies confirming the repeatability of clutch size and laying date found in some species (Batt and Prince 1979; van Noordwijk et al. 1980, 1981a, 1981b; Findlay and Cooke 1982, 1983; van Noordwijk 1987; Gauthier 1989).

Although Emperor Geese arrived and initiated nests at the same time each year, they did not always lay the same size clutch. This low repeatability of clutch size is consistent with other species of geese (Canada Geese [MacInnes and Dunn 1988] Lesser Snow Geese [Lessells and Boag 1987]) and does not support Toft et al. (1984) in relation to clutch size in geese. This lack of strong repeatability may reflect variation in physical ability (i.e., energy reserves on arrival) of females to lay their maximum clutch each year (Ankney and MacInnes 1978, Raveling

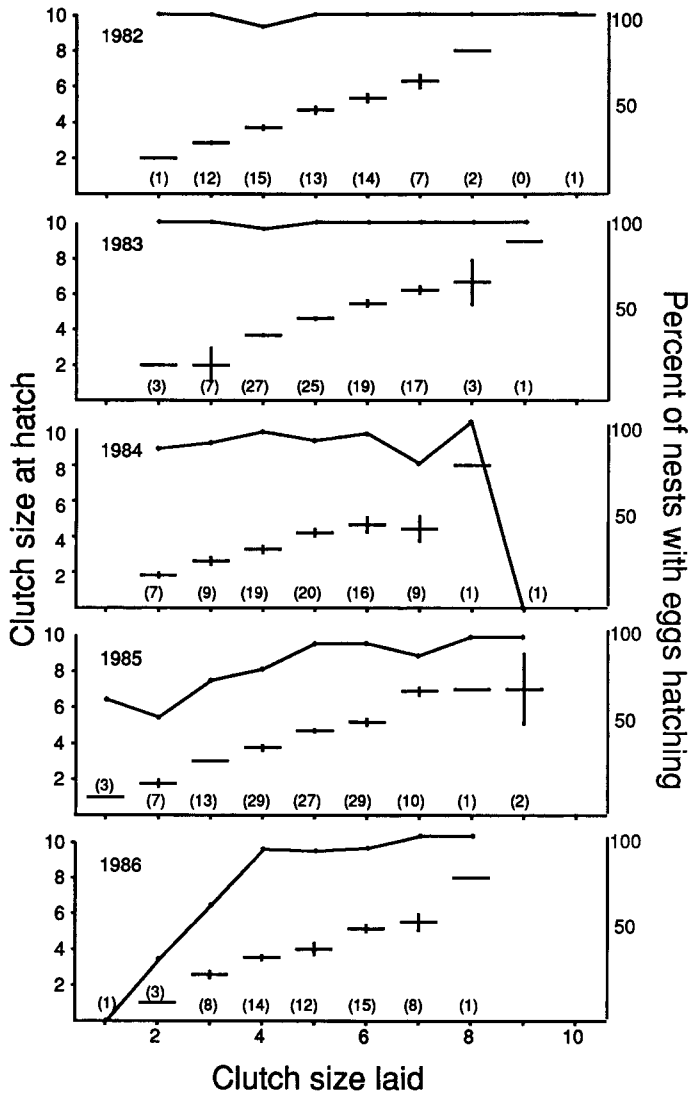


FIGURE 5. Clutch size ($\bar{x} \pm SE$) at hatch and percent of nests having one or more eggs hatch by clutch size laid and year. Sample size (n) included all nests with known fate and clutch size laid.

1979a, Findlay and Cooke 1983, Hamann et al. 1986, Eldridge and Krupu 1988).

NESTING FREQUENCY

In normal conditions most adult geese attempt to nest each season (Craighead and Stockstad 1964, Brakhage 1965, MacInnes et al. 1974, Prop et al. 1984), although non-nesting occurs in some individuals (MacInnes et al. 1974, Cooper 1978). In some years a large segment of the population may not nest because of weather conditions influencing habitat availability (Barry 1962, Prop et al. 1984) or food shortages (Davies and Cooke

1983). It is commonly assumed that after her first nesting season a female goose nests each successive year (Cooper 1978, Cooke and Rockwell 1988). This was not the case for Emperor Geese. Only 42.6–69.8% of adult females nested each year. Nesting frequency was independent of the previous year's nest fate, clutch size, nest initiation date, and arrival date and the current year's arrival date or timing of habitat availability. An estimated 21% of females nest parasitically (Petersen 1991). Although laying eggs, most parasitically laying females were not recorded as nesting birds since few could be pos-

itively identified with nests. Because parasitic females were recorded as non-nesting individuals, their nesting frequency may be higher than indicated.

In monogamous birds the death of a mate and subsequent re-pairing may result in non-nesting or failed nesting in the following breeding season. Re-pairing in Snow Geese (*Chen caerulescens*) resulted in no significant reduction of reproductive potential (Cooke et al. 1981). However, in Owen et al. (1988), reproductive potential of Barnacle Geese (*Branta leucopsis*) fell following re-pairing, and it is suggested that re-pairing soon after the previous breeding season reduces the negative reproductive effects of re-pairing. Thus, the reproductive potential of geese re-pairing in early fall should be similar to geese who remain paired into the next breeding season. For Emperor Geese, hunting mortality occurs predominantly in spring during native subsistence harvest activities (Klein 1966, Pamplin 1986). This spring kill coupled with a high annual adult mortality rate from all causes (Petersen 1992) would result in a large proportion of adult geese that are newly paired in spring and less likely to nest. Geese that pair in spring may be physiologically unprepared to nest (Akeson and Raveling 1984). Females who have lost their mates may have insufficient energy reserves for successful nesting, since one role of the male is to allow the female sufficient uninterrupted time to feed (McLandsress and Raveling 1981, Raveling 1988).

Delayed maturity is believed to be an adaptation, exhibited by many species, that results in more viable offspring produced over the lifetime of the individual (Bell 1980). A similar argument could be made for frequent non-nesting. Non-nesting is the apparent strategy used by Emperor Geese when the costs of nesting (higher adult mortality) are high and survival of non-nesting individuals is high (Petersen 1992). An individual should nest only when it is likely to produce its maximum potential number of surviving offspring. Older geese have larger clutches (Brakhage 1965, Cooper 1978, Finney and Cooke 1978), higher hatch rates (Brakhage 1965, Aldrich and Raveling 1983), and higher fledging rates (Raveling 1981).

NESTING SUCCESS

Many species of birds suffer high rates of nest predation. Poor reproduction of several species of arctic waterfowl with wide geographic distributions is correlated with lows in cycles of or-

dens, which are often alternate prey of primary nest predators (Pehrsson 1986, Summers 1986, Summers and Underhill 1987, Mason 1988, but see Owen 1987). At Kokechik Bay in spring 1986, when predation rates were high on Emperor Goose nests, alternative prey (*Microtus* spp.) were as abundant as in 1985 (R. M. Anthony, pers. comm.). High predation apparently occurred in 1986 because foxes did not den successfully that spring and had more time available to search for and cache goose eggs (Stickney 1989).

Most destruction of Emperor Goose nests occurred during laying when geese were seldom at their nests. As with other larger arctic and subarctic nesting geese (e.g., Snow Geese, Harvey 1970; Pink-footed Geese [*Anser brachyrhynchus*], Inglis 1977; Canada Geese, Raveling and Lumsden 1977), incubating Emperor Geese vigorously defended their nests from foxes and reduced losses to avian predators by almost continuous incubation (Thompson and Raveling 1987). Nests are susceptible to egg losses during laying (Harvey 1971, Inglis 1977). During this period arctic foxes were most successful in taking eggs from Emperor Goose nests.

There was no single "best" clutch size for Emperor Geese. Most clutches contained 4–6 eggs, with a few ≤ 3 and ≥ 7 egg clutches each year. Clutches of five and six eggs experienced the least total failure, and clutches of two and three eggs the least partial failure. Clutches of seven, eight, and nine eggs produced the most hatched eggs per successful clutch, and also had the highest variance. Females laying six or more eggs, however, survived at higher rates than birds laying five or fewer eggs (Petersen 1992). Females that laid smaller clutches (3–4 eggs) lost more entire clutches, hatched fewer eggs, and survived at lower rates (Petersen 1992) than geese that laid larger clutches (5–7 eggs). Over half of the geese that nested in any one year, however, laid five or fewer eggs. One explanation for this preponderance of small clutches would be that the smallest clutches are laid by younger, inexperienced geese not yet laying to their full potential (Kossack 1950, Finney and Cooke 1978, Rockwell et al. 1983, Aldrich and Raveling 1983). More young female Emperor Geese may have nested in the two early seasons (1983 and 1984) when a shift toward four and five egg clutches was apparent. This disparity between the mean and optimum clutch size could also reflect differences in female condition due to environmental variability (Rockwell et al. 1987, Ankney

and Afton 1988) and be reflected in among year differences of individual Emperor Geese.

The largest number of eggs laid, eggs hatched, or young fledged is not necessarily the most productive clutch based on return rates and subsequent nesting of offspring (van Noordwijk et al. 1980). Similarly, the most productive clutch one year may not be the most productive clutch the next year (Lack 1966, van Noordwijk et al. 1980). The increased survival of adults laying six or more eggs coupled with clutch sizes of six or more eggs producing the most young suggests that, on average, females laying six or more eggs will produce more offspring than other females. However, the proportion of those offspring surviving to nesting age is unknown.

INDIVIDUAL VARIATION

Emperor Geese exhibited both intra- and inter-individual variation in clutch size. Although the population as a whole exhibited a seasonal decline in clutch size (a trait common to other arctic and temperature waterfowl), individual birds did not exhibit that pattern. Emperor Geese that arrived and initiated nests early in one year tended to do so in other years, despite wide variation of weather conditions and timing of the season. Clutch sizes of individuals, however, were not correlated with nest initiation date. The intra-individual variation in clutch size suggests that individuals are not consistently in peak physiological condition each year.

Individuals that lay eggs late have smaller clutch sizes, on average, than those that lay eggs early. Perhaps individuals nesting early in the season have a larger potential clutch size than individuals that normally nest later. Inter-individual variability in maximum potential clutch, however, is unknown. Small clutch sizes in later initiated nests result in a shorter pre-incubation period such that smaller clutches hatch earlier within a season than would large clutches laid by the same individuals. Early goslings can take advantage of the early availability of high quality foods (Sedinger and Raveling 1986). These goslings should experience increased survival through fall migration since larger goslings survive at higher rates than smaller goslings (Owen and Black 1989). By hatching early, geese also avoid being unable to leave before freeze-up (Cooch 1958).

Emperor Geese remain at food-rich, spring staging areas until nest sites are available thereby

reducing their preincubation maintenance costs; they initiate nests early which subsequently results in increased gosling size and survival to fledging; they lay a large clutch which results in more eggs hatching per female; and adult females frequently forgo nesting thereby increasing their survival.

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