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REPRODUCTIVE ECOLOGY OF EMPEROR GEESE: SURVIVAL OF ADULT FEMALES[1]

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Abstract. Life history theory predicts a decrease in survival with increased reproductive effort of individuals. This relationship, however, is highly variable among and within species. I studied the nesting success and survival of adult female Emperor Geese during 1982–1986 and found no direct evidence that differential reproductive effort as measured by the number of eggs laid or hatching success had a significant negative effect on survival to the next breeding season. Incubated clutch size, hatched clutch size, number of parasitic eggs, nest initiation date, hatch date, and mass at hatch were not related to subsequent survival. Of the factors I examined, only an attempt to nest the previous season was related to survival of a female. I suggest that the higher probability of survival among non-nesting adult female Emperor Geese was primarily related to hunting pressure on the nesting area between spring and fall migration. The probability of survival was increased for females with larger clutches, suggesting a positive relationship between brood size and survival.

Key words: Reproductive ecology; annual survival; female survival; Chen canagicus; *Alaska*

INTRODUCTION

Current theory predicts that when clutch size increases there is a decrease in survival of adults due to increased parental effort (Williams 1966, Charnov and Krebs 1974). Survival rates of breeding birds have been correlated with age, nesting experience, brood size raised (Nur 1987, Boyce and Perrins 1987), and timing of egg laying (McCleery and Perrins 1988). However, the relationship between reproductive effort, as measured by clutch size or brood size, and subsequent adult survival has been quite variable among species. For example, clutch (brood) size did not correlate with subsequent survival of Great Tits (*Parus major* [McCleery and Perrins 1988]), but correlated positively with survival of Black-legged Kittiwakes (*Rissa tridactyla* [Thomas and Coulson 1988]), and negatively with survival of Pied Flycatchers (*Ficedula hypoleuca* [Askenmo 1979, Harvey et al. 1988]). To date, few studies of waterfowl have examined the relationship between fecundity and mortality. Studies of Barnacle Geese (*Branta leucopsis* [Owen and Black 1989]) revealed that females with young in fall were in better condition than females that nested but had no young; however, condition had no detectable effect on survival through fall migration. Migratory Giant Canada Geese (*B. canadensis maxima*) survived equally well irrespective of reproductive success as measured by presence or absence of a brood in late summer (Raveling 1981). Brood size in introduced, non-migratory Canada Geese had no effect on adult survival, but enlarged broods delayed the timing of nesting the following year (Lessells 1986).

To examine the relationship between reproduction and survival, I studied the nesting ecology of a marked population of migratory adult 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). They exhibit variation in arrival date, nest initiation date and clutch size among years (Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Petersen 1992). My objective was to evaluate the timing of arrival and nest initiation, clutch size, hatching success, and nesting frequency (as defined as

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known nesting attempts) of individual adult female Emperor geese in relation to their subsequent survival.

METHODS

STUDY AREA

I conducted this study on a 760 ha area near Kokechik Bay, YKD, Alaska (63°39′N, 165°51′W). The area contains lowland, intermediate, and upland tundra similar to that described by Ely and Raveling (1984). More complete descriptions of the area are contained in Holmes and Black (1973), Eisenhauer and Kirkpatrick (1977), Jackson (1981), and Petersen (1990). Emperor Geese nest in similar habitats at the northern Chukotsky Peninsula, Siberia, (Kistchinski 1971, Portenko 1981) and elsewhere on the YKD (Spencer et al. 1951).

NESTS

Between 1982–1986, I determined clutch sizes, nesting success (nests in which one or more eggs hatched), and hatching success (proportion of eggs that hatched) of 93 marked Emperor Geese. Techniques of nest searching were similar to those used by Raveling (1978) and Ely and Raveling (1984). For some nests I determined nest initiation dates by direct observations of birds building nests and laying eggs. For nests found before incubation began, I determined nest initiation dates by backdating from the date the nest was found using an egg-laying rate of 1.2 eggs/day. For nests found after incubation began, I determined nest initiation dates by backdating from hatch dates using the same egg-laying rate and a 24-day incubation period (Eisenhauer 1976, Krechmar and Kondratiev 1982). Conspecific nest parasitism occurs in Emperor Geese (Eisenhauer and Kirkpatrick 1977, Petersen, in press). Clutch size incubated included all eggs incubated in the nest, and clutch size laid included all but obvious parasitic eggs. Parasitic eggs included (1) all eggs added to a nest after incubation began, (2) eggs laid outside a nest and then found in the nest, (3) eggs with viable embryos that were not completely developed after most eggs hatched and the brood had abandoned the nest, and (4) eggs laid by one marked female in a nest that were subsequently incubated by another female (e.g., Yom-Tov 1980, MacWhirter 1989). Evidence of hatching included pipped and hatching eggs, goslings in the nest, and egg shells with an intact inner membrane that was separated from the shell.

MARKED GEESE

I marked nesting female geese on the study area with individually coded yellow neck collars and standard U.S. Fish and Wildlife Service (USFWS) leg bands. Geese were trapped on their nests at hatch (68 birds) or within 14 days of hatch (22 birds) with modified Weller (Weller 1957) traps (85 birds) or by hand (3, plus 2 with a dip net). An additional three adult females that nested on the study area were marked when captured when flightless during banding drives. Captured females were weighed to the nearest 50 gm. Arrival dates of marked females during subsequent springs were determined from daily observations from blinds.

STATISTICAL ANALYSIS

I controlled for annual variation in arrival, clutch initiation, or hatch dates by expressing dates relative to the first day of that event for that year. For females with two or more years of data, clutch sizes and dates for each individual were averaged (Martin and Bateson 1986:30). Data were analyzed following Conover (1980), and statistical tests were executed with SPSS^x (SPSS 1986). Because new geese were marked each year, I calculated survival rates using the Kaplan-Meier procedure (Kaplan and Meier 1958) as modified by Pollock et al. (1989). Resighting probabilities were calculated using Jolly-Seber models and the computer program SURVIV (White 1983). Survival and resighting probabilities are presented as $\bar{x}$ ± SE (95% CL) and include only the 90 adult females trapped on their nests.

ASSUMPTIONS FOR ESTIMATED SURVIVAL

Estimating survival with the Pollock et al. (1989) modification of the Kaplan-Meier procedure requires several assumptions: (1) adult females have been sampled randomly; (2) survival times are independent for each female; (3) capturing and marking has no influence on future survival; (4) the mechanism with which an animal is censored is random (i.e., not related to the animal's fate); (5) emigration or collar loss is zero; (6) survival from the time origin is similar for each individual; (7) newly collared individuals have the same survival function as previously collared animals;

and (8) all collared birds that are alive are seen each year.

The individuals in this study are believed to have been a random sample of successfully nesting females because I attempted to collar every female on the study area that hatched eggs. Females with eggs that hatched during inclement weather were not captured, but I assume hatch date was independent of daily weather conditions. Survival times were assumed to be independent for each female. Geese frequently remain in family groups until the following spring, and survival of each adult female of each family is assumed to be independent of the fate of all other families or pairs. The influence of neck collars on survival of Emperor Geese is unknown but assumed to be minimal. No marked Emperor Geese were seen by other field investigators outside (but within 10 km of) the study area, although emigration could not be ruled out. I assumed collar loss was minimal because no banded females without collars were recaptured at hatch or as flightless adults in brood drives in subsequent years. Factors other than whether the goose nested that influence survival from the time of marking to subsequent nesting seasons were assumed to be similar for birds collared in each year.

I assumed that the probability of a bird returning to the breeding area (given that the bird was alive) and the detection probability did not differ between birds that did and did not nest the previous year. I also assumed that all geese alive were seen. Resighting rates during the study were 100% in two of four seasons (25 of 28 [89%] geese known to be alive in 1983 were seen, 23 of 25 [92%] in 1984, 27 of 27 [100%] in 1985, and 26 of 26 [100%] in 1986 for an annual resighting rate of 95%). One individual was not seen for two years and three individuals were not seen one year before they returned to the study area. Resighting probabilities, as estimated using Jolly-Seber models, were different among years ($\chi^2 = 7.85$, df = 1, $P = 0.01$); however, differences could not be attributed to a single year and probably reflect the few number of birds not seen during years they were known to be alive. The probability of a bird being resighted the first year after banding was not different from subsequent years ($\chi^2 = 0.32$, df = 1, $P = 0.57$). The annual resighting probability during the study was 0.89 ± 0.05 (0.79–0.98).

RESULTS

ANNUAL SURVIVAL

Annual survival of adult female Emperor Geese with nesting experience was low and averaged 58.7% (range 43.9–67.5%) (Table 1). The annual survival estimate derived using Jolly-Seber models was also low (58.6%, range 49.8–67.5%). The two estimates (mean of all years; 58.7 ± 6.3% and Jolly-Seber model; 58.6 ± 4.5%) are similar. The cumulative survival of adult females over the five-year study period was only 11.3 ± 0.03% (Table 1). Differences among years were not evident because similar proportions of marked individuals returned each year ($\chi^2 = 5.34$, df = 3, $P = 0.15$).

COMPARISON OF NESTING AND NON-NESTING FEMALES

The proportion of adult female Emperor Geese that survived to the following summer was significantly higher among geese that did not nest (50.0%, $n = 18$) than among geese that nested (23.0%, $n = 74$) ($\chi^2 = 5.22$, df = 1, $P = 0.02$). However, survival of nesting geese did not differ among females whose eggs did not hatch (14.3%, $n = 7$) and females whose eggs hatched (23.9%, $n = 67$) ($\chi^2 = 0.33$, df = 1, $P = 0.57$) the previous summer.

SURVIVAL AMONG NESTING GEESE

Among nesting females, individuals that survived had laid a significantly larger clutch the previous summer than individuals that did not survive to the following season (Kolmogorov-Smirnov test $Z = 1.28$, $P = 0.04$) (Fig. 1). The two groups did not differ significantly in the clutch size incubated (clutch size plus parasitic eggs, Kolmogorov-Smirnov test $Z = 0.76$, $P = 0.30$), the clutch size hatched (Kolmogorov-Smirnov test $Z = 0.80$, $P = 0.28$), or the number of parasitic eggs incubated (Kolmogorov-Smirnov test $Z = 0.71$, $P = 0.35$) the previous summer (Fig. 1). In addition, surviving females and females that did not survive did not differ significantly in timing of nest initiation (Kolmogorov-Smirnov test $Z = 0.48$, $P = 0.49$) or hatch (Kolmogorov-Smirnov test $Z = 0.84$, $P = 0.24$) the previous summer; arrival dates the previous spring also appeared to be similar for the two groups, although sample sizes were too small for meaningful statistical comparison (Fig. 2).

With clutch size and culmen as covariates, weights of adult females at hatch did not differ significantly between females that survived and females that did not survive to the following summer (ANCOVA $F_{2,49} = 0.02$, $P = 0.90$).

DISCUSSION

ANNUAL SURVIVAL

Annual survival estimates of adult female Emperor Geese (44–69%) were lower than adult survival rates for the similarly sized Snow Goose

TABLE 1. Survival estimates for adult female Emperor Geese.

Year	No. at risk	Annual survival[1]	Cumulative survival[2]	Survival variance	95% CL	
					Upper	Lower
1983	41	0.439	0.439	0.0026	0.540	0.338
1984	40	0.625	0.274	0.0014	0.347	0.202
1985	34	0.675	0.187	0.0008	0.242	0.129
1986	41	0.610	0.113	0.0003	0.146	0.081

[1] Proportion surviving from prior year: 1983 is proportion surviving from summer 1982 to summer 1983, 1984 is proportion from summer 1983 to summer 1984, etc.

[2] Probability of surviving from summer 1982.

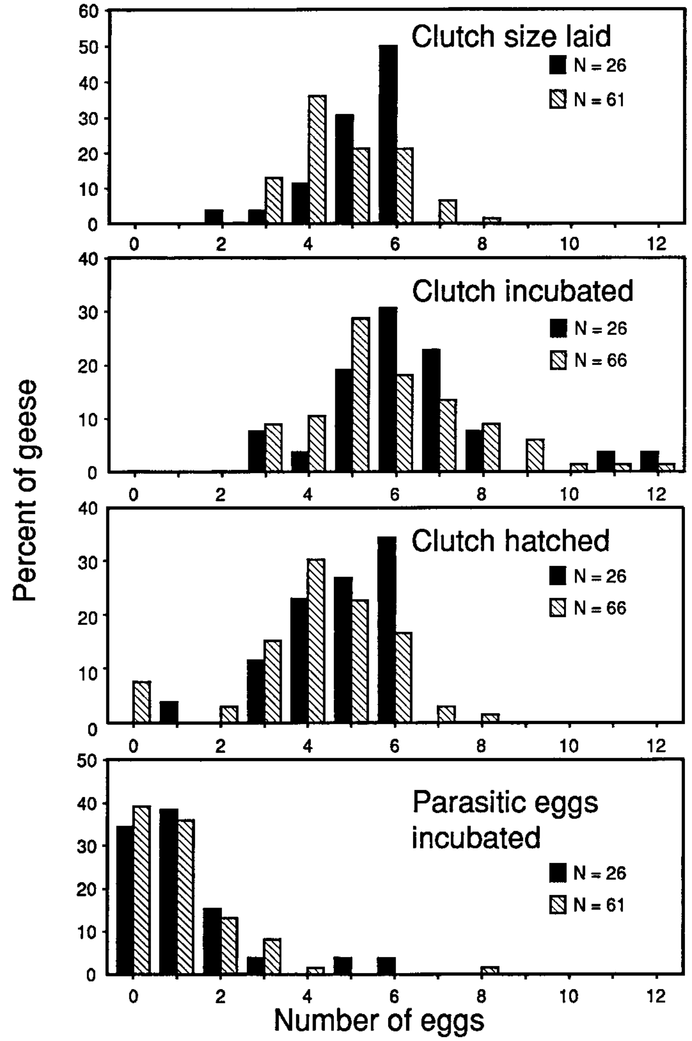

FIGURE 1. Clutch sizes laid, number of eggs incubated, number of eggs hatched, and number of parasitic eggs in nests of adult female Emperor Geese surviving and dead. Data are rounded to the nearest whole number for individuals observed more than one year. Solid bar—percent of birds that survived to the subsequent year. Hatched bar—percent of birds dead by the subsequent year.

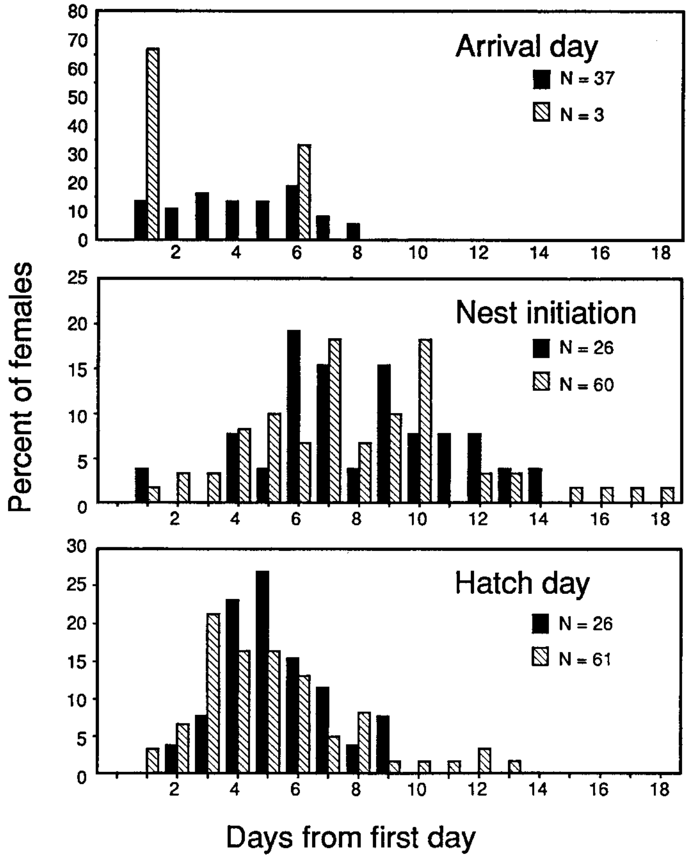

FIGURE 2. Arrival, nest initiation, and hatch dates of adult female Emperor Geese surviving and dead. Data are rounded to the nearest whole number for individuals observed more than one year. Solid bar—percent of birds that survived to the subsequent year. Hatched bar—percent of birds dead by the subsequent year.

(*Chen caerulescens*) (71–85% [Sulzbach and Cooke 1979]), Brant (59–98% [Kirby et al. 1986]), and Barnacle Goose (87–91% [Owen 1982]). I assumed that annual survival was equivalent to annual return rates, thus the lower survival for Emperor Geese could have been an artifact of unrecorded emigration of non-resightings of birds that were still alive and marked. However, analysis of the data using Jolly-Seber models that take into account resighting rates suggests survival rates were low and equivalent to annual survival as estimated from annual return rates. The probability of a goose being alive and being seen in a given summer was high. Marked geese that nested in areas immediately adjacent to the study area were rare, and all marked geese were found within 500 m of the study area. Because adult female geese that have nested in an area have a strong tendency to return to that area in subsequent years (Cooke et al. 1975, Lessells 1985), I believe that most Emperor Geese that were alive were seen.

The lower than anticipated survival rate paralleled a continued population decline of Emperor Geese. The spring population dropped from almost 101,000 geese in 1982 to just over 42,000 geese in 1986 (R. King and C. P. Dau, unpubl. report, USFWS, Fairbanks, Alaska). During this period the population declined at about 20% annually, and the proportion of young in the population averaged 19% (calculated from Petersen and Gill 1982 and W. I. Butler, Jr., unpubl. report, U.S. Fish and Wildlife Service, Anchorage, Alaska). Thus the average annual survival rate of 58.7% by adult females is consistent with the magnitude of the population decline in 1982–1986.

COMPARISON OF SURVIVAL RATES OF NESTING AND NON-NESTING GEESE

Several factors could explain why adult female Emperor Geese that did not nest survived at higher rates than females that did nest. Non-breeding birds may have (1) lower energy costs due to non-breeding (Barry 1962, Hanson 1962, Newton 1977, Raveling and Lumsden 1977, Owen 1982), (2) reduced exposure to predation on the nest (Kruuk 1964) and perhaps during brood rearing, and (3) reduced mortality from hunting during the flightless period (Blurton Jones 1972) and nesting period.

Nesting success was not significantly related to survival of adult female Emperor Geese. This is similar to the results reported for Giant Canada Geese (Raveling 1981) and Barnacle Geese (Black and Owen 1989b), although which Giant Canada and Barnacle geese attempted to nest was not determined. Results of my study did not support the hypothesis of higher survival rates by non-nesting birds than by nesting birds from reduced exposure to predation on the nest. Only five (0.67%) adult female Emperor Geese were killed on their nests while incubating.

The factor most strongly influencing differential survival of nesting and non-nesting female Emperor Geese remains undocumented in a direct manner. Based on indirect evidence it is likely that hunting pressure during the breeding season on the YKD may have been responsible for lower survival of nesting females. Spring hunting of waterfowl is a traditional activity by residents of the YKD. Estimates of the number of Emperor Geese shot each spring range from 6,500 in the mid-1960s (Klein 1966) to 8,300 in 1980 (Copp and Smith 1981 *in* Pamplin 1986). This continued harvest of geese has been implicated as a factor responsible for the decline of Emperor Goose populations (Raveling 1984, King and Derksen 1986, Pamplin 1986).

Early spring migrants are primarily paired adults, whereas sub-adults and non-breeding adults migrate to the breeding grounds later in spring (Blurton Jones 1972, Petersen and Gill 1982) when travel conditions for humans are more difficult due to ice break-up and fewer birds are available to local hunters. Thus, most birds that are shot in early spring are potential breeding birds. The effects of losing a mate during this time period (pre-nesting nest site establishment, early egg laying) are unknown, but may result in non-nesting (e.g., Raveling 1989).

Non-nesting and failed nesting Emperor Geese migrate from nesting areas during late May through July (Kistchinski 1971, Blurton Jones 1972, Krechmar and Kondratiev 1982) to molting areas on Saint Lawrence Island (Fay and Cade 1959) and elsewhere (Portenko 1981). Individuals in these non-breeding flocks may be less vulnerable to harvest than brood flocks on the nesting areas. Adults and young in brood flocks have been harvested by driving birds into nets (Klein 1966, Jenness 1970) and are shot when encountered along river systems. Spring and summer take of geese on the YKD has been increasing primarily as a result of increases in human populations and efficiency in transportation (Timm and Dau 1979, Raveling 1984, King and Derksen 1986). For Emperor Geese the decreased survival of nesting geese may in part be a result of increased hunting pressure in the spring and summer.

SURVIVAL OF NESTING FEMALES

None of the results of this study supported the idea that the energy costs associated with reproductive effort adversely affected the probability of survival of adult female Emperor Geese. In contrast, nesting geese that survived laid larger clutches than geese that did not survive, and the probability of survival was independent of arrival date, nest initiation date, hatching date, and weight of the female at hatch.

Females that laid more eggs may have been in significantly better physical condition, of generally higher quality, or with better mates and thus more likely to survive than females that laid smaller clutches (i.e., quality of the female; Coulson 1966, Smith 1981, Loman 1982). However, weights of female Emperor Geese at hatch did not differ between geese that survived and geese that did not survive and thus appears to contradict this explanation. Increased clutch size among geese has also been associated with greater experience (Cooke et al. 1981, Aldrich and Raveling 1983) and increasing age (Brakhage 1965, Cooper 1978, Finney and Cooke 1978, Cooke et al. 1981, Rockwell et al. 1983). Because exact age and experience was unknown, I could not assess how they may have influenced survival among female Emperor Geese. Increased overwinter survival could be a result of larger families being dominant and having greater control of access to food and other resources (Boyd 1952, Hanson 1953, Raveling 1970, Lamprecht 1986, Black and Owen 1989a). Family dynamics after fledging, foraging ecology in winter, and behavioral dynamics of Emperor Geese in winter are unknown. Thus the effect of family size and dynamics on over-winter survival is as yet undetermined.

In some species of birds, individuals that initiate nests early in the season have a higher probability of survival than birds that lay eggs later (McCleery and Perrins 1988, Harvey et al. 1988, Gauthier 1989). Emperor Goose survival, however, was independent of nest initiation date and arrival date.

Nesting and raising broods can be stressful, as geese have starved to death on their nests (Harvey 1971, Ankney and MacInnes 1978), and geese that attend young through the winter initiate nests later the following season (Lessells 1986). However, increased reproductive effort had no apparent negative effect on survival of adult female Emperor Geese. Emperor Geese that survived had laid larger clutches than geese that did not survive, and survival was independent of arrival date, nest initiation date, hatching date, or weight of the female at hatch. This is consistent with a study on Barnacle Geese which suggested that pairs that raised families through the following winter did not decrease their survival to the next fall (Black and Owen 1989b).

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