

# RELATIVE EFFECTS OF SURVIVAL AND REPRODUCTION ON THE POPULATION DYNAMICS OF EMPEROR GEESE

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**Abstract:** Populations of emperor geese (*Chen canagica*) in Alaska declined sometime between the mid-1960s and the mid-1980s and have increased little since. To promote recovery of this species to former levels, managers need to know how much their perturbations of survival and/or reproduction would affect population growth rate ( $\lambda$ ). We constructed an individual-based population model to evaluate the relative effect of altering mean values of various survival and reproductive parameters on  $\lambda$  and fall age structure (AS, defined as the proportion of juv), assuming additive rather than compensatory relations among parameters. Altering survival of adults had markedly greater relative effects on  $\lambda$  than did equally proportionate changes in either juvenile survival or reproductive parameters. We found the opposite pattern for relative effects on AS. Due to concerns about bias in the initial parameter estimates used in our model, we used 5 additional sets of parameter estimates with this model structure. We found that estimates of survival based on aerial survey data gathered each fall resulted in models that corresponded more closely to independent estimates of  $\lambda$  than did models that used mark-recapture estimates of survival. This disparity suggests that mark-recapture estimates of survival are biased low. To further explore how parameter estimates affected estimates of  $\lambda$ , we used values of survival and reproduction found in other goose species, and we examined the effect of an hypothesized correlation between an individual's clutch size and the subsequent survival of her young. The rank order of parameters in their relative effects on  $\lambda$  was consistent for all 6 parameter sets we examined. The observed variation in relative effects on  $\lambda$  among the 6 parameter sets is indicative of how relative effects on  $\lambda$  may vary among goose populations. With this knowledge of the relative effects of survival and reproductive parameters on  $\lambda$ , managers can make more informed decisions about which parameters to influence through management or to target for future study.

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Populations of emperor geese in Alaska have declined to half the level observed in the mid-1960s (Petersen et al. 1994). These geese nest primarily on the coastal fringe of the Yukon-Kuskokwim Delta (Spencer et al. 1951, Eisenhower and Kirkpatrick 1977). The delta is populated by numerous villages of native Yupik people, who lead a subsistence lifestyle that includes harvest of geese (Klein 1966; C. Wentworth, U. S. Fish and Wild. Serv., Anchorage, Alas., unpubl. data). This harvest occurs throughout the time geese are on the Yukon-Kuskokwim Delta, but is most common during spring when geese first arrive (C. Wentworth, unpubl. data). Some subsistence harvest also occurs while emperor geese are in migratory and winter habitats on the Alaska Peninsula and Aleutian Islands (Fall and Morris 1987). Legal sport harvest was closed in 1986 (U.S. Fish and

Wildl. Serv., unpubl. data). The extent of subsistence harvest and its relative contribution to population declines have been subject to debate (Raveling 1984, King and Derksen 1986). To begin quantifying how harvest (or other sources of variation in demographic parameters) may affect goose populations, wildlife managers need to know how sensitive population growth is to changes in survival and/or reproduction.

The restricted distribution of emperor geese (Eisenhower and Kirkpatrick 1977) and history of data collection by U.S. Fish and Wildlife personnel (Petersen et al. 1994) makes this species particularly amenable to modeling. A series of annual aerial surveys of nesting and staging areas samples nearly the entire population and thus produces measures of annual population change. These data can then be compared to population change projected from reproductive

and survival data gathered from intensive field studies (Petersen 1992a,b; Schmutz et al. 1994). Our objective was to develop a model that projected the population growth rate and age structure reflected in independent aerial surveys and then to use that model to quantify the response of population growth and age structure to changes in either reproductive success or survival.

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## POPULATION STATUS

Virtually all emperor geese stage on the Alaska Peninsula in both spring and fall, using a series of large lagoons on the north coast (Eisenhauer and Kirkpatrick 1977, Petersen and Gill 1982, Schmutz and Kondratyev 1995). Since 1981 FWS personnel have conducted aerial surveys of emperor geese each spring to estimate population size (R. J. King, U.S. Fish and Wildl. Ser., Fairbanks, Alas., unpubl. data) (Fig. 1). We estimated population growth rate,  $\lambda$ , from these data (1985–94) using log-linear regression (Eberhardt 1985) and found that this population may be increasing slightly ( $\lambda = 1.025$ ), although not significantly ( $P = 0.220$ ). Data from aerial surveys on the Yukon-Kuskokwim Delta, with methods detailed by Butler et al. (1995a,b), indicate comparable estimates of  $\lambda$  (W. I. Butler, FWS, Arlington, Va., unpubl. data). Additional aerial surveys during September and October provide annual data on the proportion of juveniles (age-ratio) and the total number of geese in the fall population (Petersen et al. 1994; W. I. Butler and R. J. King, unpubl. data).

## MODEL DEVELOPMENT

### Modeling Approach

We used an individual-based modeling (Huston et al. 1988, DeAngelis and Gross 1992) approach for this study. We expected most of our

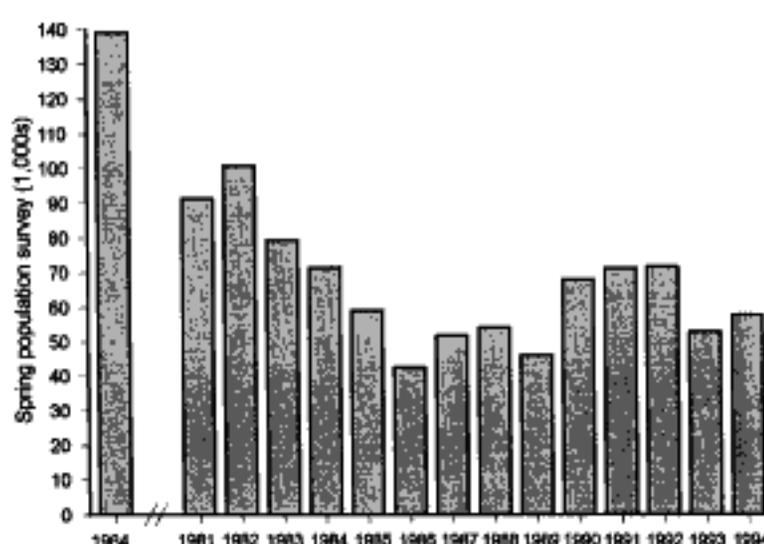


Fig. 1. Population numbers of emperor geese in Alaska as determined from aerial surveys. Surveys are one-time counts during early May of all geese on the Alaska Peninsula (R. J. King, U. S. Fish and Wild. Serv., Fairbanks, Alas., unpubl. data; Petersen et al. 1994). Average annual growth rate ( $\lambda$ ) during 1985–94 was 1.025.

results from individual-based models to be equivalent to those obtainable from the more traditional approach using Leslie (1945) matrices (Caswell 1989; H. Caswell, pers. comm.; DeAngelis et al. 1993). However, we wanted to add the complexity of inducing correlations among subsets of parameters for certain individuals, and the individual-based modeling approach is quite amenable to this objective.

Our model does not contain actual data histories on individual geese studied in the field. Instead, our model uses a simulated population of discrete individuals that each independently survive and reproduce according to rates determined from field studies. We followed these computer-generated individuals through time, subjecting them to various survival and reproductive events, and tallied their numbers to arrive at estimates of both  $\lambda$  and age structure (AS—the proportion of juv during fall migration). We compared these estimates to those independently obtained from spring ( $\lambda$ ) and fall (AS) aerial surveys during a 9-year period. By using 2 population metrics,  $\lambda$  and AS, instead of just one as often done in previous studies, we improved our ability to assess the fit of the model to independent data from surveys. We calculated relative effects, or elasticities (deKroon et al. 1986, Caswell 1989), of parameters to evaluate how changes in each component of reproductive success and survival affected our model projections of  $\lambda$  and AS. Elasticities are metrics from matrix population models that measure the proportional change in  $\lambda$  that results from a proportional change in a given parameter. For

Table 1. Population parameters used to model demographics of emperor geese. Definitions for the various parameter sets are given in the text.

Parameter <sup>a</sup>	Parameter set used in model					
	Resight set	Resight set with correlation structure	Alternate set 1	Alternate set 2	Survey set 1	Survey set 2
Breeding propensity <sup>1,2</sup>						
2 yr olds	0.50	0.50	0.50	0.50	0.50	0.50
3+ yr olds	0.70	0.70	0.70	0.91	0.70	0.70
Clutch size <sup>1</sup>	5.07	5.07	5.07	5.07	5.07	5.07
Nest survival <sup>1</sup>	0.90	0.90	0.90	0.90	0.90	0.90
Total brood survival <sup>3,4</sup>	0.80	0.80	0.88	0.80	0.80	0.80
Gosling survival <sup>3,4,5</sup>	0.70	0.70	0.70	0.63	0.70	0.70
Fall survival						
0 yr olds <sup>6</sup>	0.50	0.50	0.30	0.50	0.50	0.50
1 yr olds <sup>7,8,9</sup>	0.75	0.75	0.90	0.90	0.97	0.99
2+ yr olds <sup>7,8,9</sup>	0.95	0.95	0.99	0.99	0.97	0.99
Winter survival <sup>7,8,9</sup>						
0 yr olds	0.10	0.10	0.20	0.40	0.76	0.46
1+ yr olds	0.70	0.70	0.84	0.84	0.92	0.92
Spring survival <sup>7,8,9</sup>						
0 yr olds	0.95	0.95	0.99	0.99	0.84	0.59
1+ yr olds	0.95	0.95	0.99	0.99	0.98	0.98

<sup>a</sup> Parameter values used in these parameter sets were derived from the following data sources, as indicated by numerical superscript. Where parameter estimates for emperor geese were not available, we used approximations from the goose literature: <sup>1</sup> Petersen (1992a); <sup>2</sup> Cooke and Rockwell (1988); <sup>3</sup> Flint et al. (1995); <sup>4</sup> Williams et al. (1993); <sup>5</sup> Schmutz (unpubl. data); <sup>6</sup> Stehn and Schmutz (unpubl. data); <sup>7</sup> Schmutz et al. (1994) with adjustments for appropriate season lengths; <sup>8</sup> Owen and Black (1989); <sup>9</sup> Butler and Stehn (unpubl. data).

example, estimated elasticities can be used to ascertain whether a 10% reduction in adult harvest would have the same effect on  $\lambda$  as a 10% reduction in egg collection.

Because initial estimates of  $\lambda$  and AS from our model did not correspond to estimates from independent survey data (see RESULTS), we examined  $\lambda$ , AS, and parameter elasticities associated with several sets of estimates of reproduction and survival derived either from other studies (Table 1) or from fall aerial surveys. We also explored how correlation between particular parameters could affect estimates of  $\lambda$ , AS, and elasticities of reproductive and survival parameters. Such correlations rarely have been considered in population models (but see Van Tienderen 1995), yet both negative (Nur 1988) and positive (Thomas and Coulson 1988) correlations have been observed in intensive studies of individuals. Therefore, we simulated (for 1 of 6 sets of parameter values, see Parameter Inputs and Parameter Correlation) a positive correlation between a female's clutch size and survival of her progeny. Goslings in large broods of some species of geese grow faster (Cooch et al. 1991) and are dominant over those in small broods (Black and Owen 1989, Gregoire and Ankney 1990), and larger goslings have higher post-fledging survival (Schmutz 1993, Sedinger

et al. 1995), thus suggesting such a relation may exist in emperor geese.

### Model Description

We represented the annual cycle of emperor geese as a series of state variables and transitions (Fig. 2). State variables corresponded to estimates of population size and age structure at particular points within the annual cycle; transitions corresponded to reproductive events, survival, and aging between years. State variables corresponded in time with the series of annual surveys discussed above and thus allowed us to compare  $\lambda$  and AS projected from reproductive and survival rates to those obtained by survey.

Each female of each age class of the pre-breeding age distribution (Fig. 2) passed through 5 reproductive transitions. We assigned an outcome for each transition for each female by comparing random numbers to mean estimates from field studies for each of these reproductive transitions. We drew each random number from a uniform distribution spanning from 0 to 1. For example, if mean total nest success is 0.9 and one drew a random number  $\leq 0.9$ , then that individual was denoted as having successfully nested, whereas if the random number was  $> 0.9$  then she was denoted as having failed in her nesting attempt. We considered all parameters

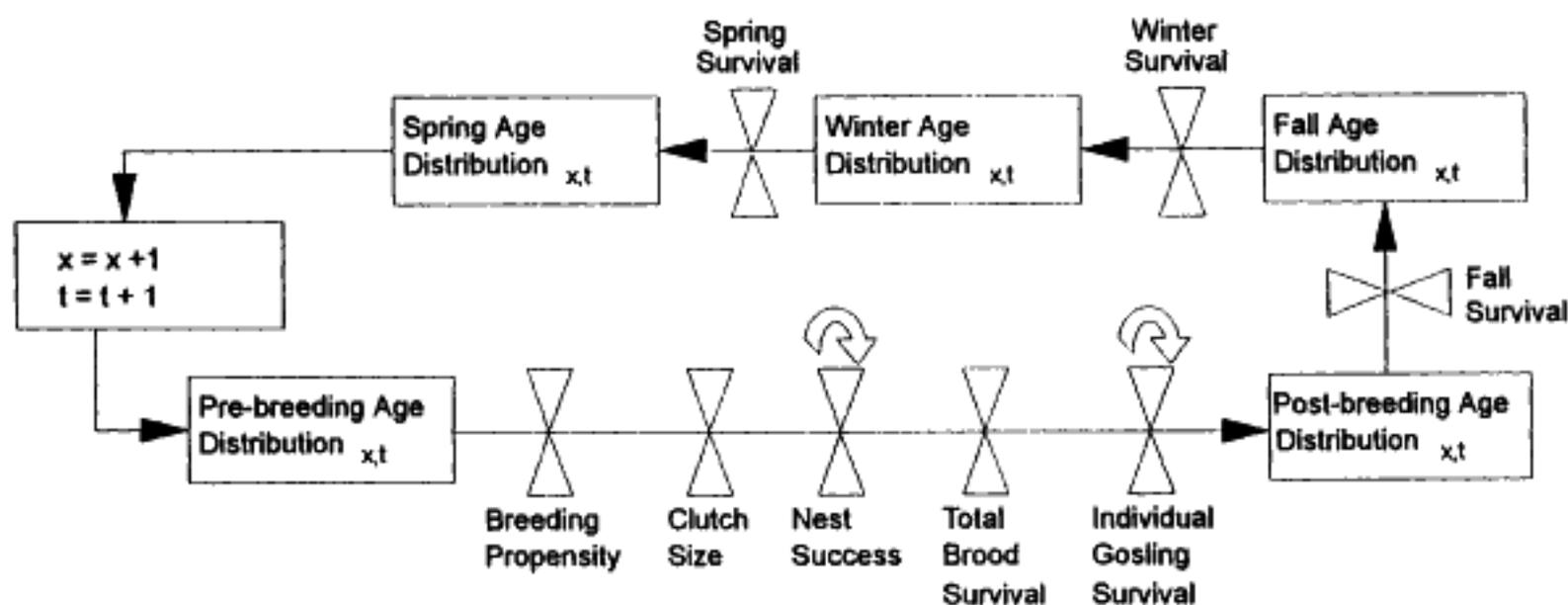


Fig. 2. Emperor goose annual cycle divided into a series of state variables (rectangles) and transitions (bow ties) that correspond to estimates of age-structured population size and life history parameters. We applied transitions to individuals except for nest success and brood survival, which were applied to the entire clutch or brood of a given female.

as binomial except for clutch size. We built an empirical distribution of clutch sizes from 472 nests observed during 1982–85 (Petersen 1992a), and then drew random clutch sizes from this distribution.

We similarly evaluated fates of individuals at survival transitions, which were also derived from field studies (Table 1). Survivors from the fall entered their respective age classes, providing the basis for the state variable termed the fall age distribution. We repeated this process for winter and spring survival transitions. Year changed instantaneously after we calculated spring survival, and members of all age classes were then incremented by one. We then repeated this process for the next year.

We calculated  $\lambda$  by dividing the total number of geese for a given state variable by its value for the previous year. We calculated  $\lambda$  and AS at 7 years into each model projection because preliminary analyses beginning with 35,000 females, uniformly distributed among age classes, indicated that both  $\lambda$  and AS stabilized after 7 years. We estimated variances and confidence limits for  $\lambda$  and AS by repeating the simulation as a set of 500 Monte Carlo trials. These variances reflect demographic stochasticity (Gotelli 1995); however, at such large population sizes, demographic stochasticity is relatively unimportant, and thus, our model is essentially deterministic.

### Parameter Inputs

We first used data from Petersen (1992a) and Schmutz et al. (1994) for values for most parameters (Table 1). Petersen (1992a) gathered

reproductive data in 1982–86 whereas Schmutz et al. (1994) obtained survival data in 1988–92. We refer to this initial set of parameter values as the resight set since survival estimates were obtained by mark-resight methods. Because estimates of  $\lambda$  with the resight set were so divergent from  $\lambda$  estimated from independent data from aerial surveys (see RESULTS), we also estimated  $\lambda$ , AS, and elasticities of parameters using 4 additional sets of parameter values. We chose 2 of these data sets in the following manner. We increased or decreased parameter values from the resight set (usually in 10% increments) to arrive at a range of parameter values determined from references cited in Table 1. We then examined all possible combinations ( $3^{10}$  or 59,049) of these parameter values from this range. We did not then iterate this process for each of these combinations; rather, based on the results of the 59,049 evaluations of our model, we selected 2 sets of parameter values for further iterations and calculations of confidence limits. These 2 parameter sets were: alternate set 1—the parameter values that yielded the highest estimate of  $\lambda$  while matching (within 1%) the average AS from the age-ratio survey conducted in fall; and alternate set 2—the values that yielded the highest estimate of  $\lambda$  (Table 1).

For the other 2 additional parameter sets, we used the same reproductive values as in the resight set but used survival values that we derived from analyses of data from aerial surveys conducted in fall (Butler and Stehn, unpubl. data). By applying the tabular methods of Lynch and Singleton (1964) to the fall survey data of pop-

ulation number and age-ratio, Butler and Stehn (unpubl. data) calculated annual survival rates for juveniles and adults combined. The geometric mean of their estimates for 1985–93 was about 0.80. Using a fall proportion of juveniles of 0.22 (approx 1985–94 mean), we calculated all possible values for adult and juvenile survival considered separately that together resulted in the composite survival rate of 0.80. From this set of possible values, we chose 2 sets of adult and juvenile survival rates for further consideration—one where adult and juvenile survival equaled 0.85 and 0.62 (annual survival from fall to fall; survey set 1), and one where adult and juvenile survival equaled 0.95 and 0.27 (survey set 2). To use these annual survival estimates with our model structure, we assumed constancy of survival among seasons and allocated survival proportionately (Table 1).

### Parameter Correlation

We generated a sixth set of predictions of  $\lambda$  and AS from our model, this one using the resight set of parameter values but with a positive correlation between clutch size and subsequent within-year reproductive success (nest success, total brood survival, gosling survival, and fall survival of juv). To induce this correlation, we first randomly selected a clutch size for an individual and compared it to the population mean. The deviation in clutch size from the population mean determined how much better (or worse) this individual performed in subsequent life-history aspects. If, for example, an individual's clutch size was 25% greater than the population mean, then probabilities for all subsequent parameters for reproduction and progeny survival within that year for that female's young were raised by 25%, except for the limitations imposed by bounding all parameters to be  $\geq 0$  and  $\leq 1$ . This procedure induced a correlation of nearly 1.0 within this subset of reproductive parameters.

### Elasticity Analysis

We calculated a statistic, here termed relative effect, that measured the proportional change in mean population growth rate or age structure given a proportional change in the parameter of interest when all other parameters were held constant. We define relative effect as:

$$\begin{aligned} \text{Relative Effect} \\ &= [(R_{\text{changed}} - R_{\text{unchanged}})/R_{\text{unchanged}}] \\ &\div [(PV_{\text{changed}} - PV_{\text{unchanged}})/PV_{\text{unchanged}}] \end{aligned}$$

where  $PV_{\text{changed}}$  and  $PV_{\text{unchanged}}$  are the new and original input values for a given parameter and  $R_{\text{changed}}$  and  $R_{\text{unchanged}}$  are the population growth rates calculated with these respective parameter values. We similarly calculated relative effects of parameters on AS. We calculated relative effects for all 6 sets of parameter values. Relative effects in our individual-based model are homologous and equivalent to lower level elasticity measures calculated from matrix population models (deKroon et al. 1986, Caswell 1989:135, Caswell et al., unpubl. data).

## RESULTS

### Predictions of $\lambda$ and AS

With the resight set of parameter values (Table 1), our model estimated  $\lambda = 0.665$  (95% CI = 0.659–0.670) and AS = 0.307 (95% CI = 0.302–0.311). These results are markedly different than those predicted from independent surveys ( $\lambda = 1.025$ , AS = 0.221). By inducing a positive correlation between clutch size and juvenile survival parameters, we increased the estimates of  $\lambda$  from 0.665 to 0.696, while AS changed from 0.307 to 0.394.

Using alternate set 1, we estimated  $\lambda = 0.873$  and AS = 0.216; whereas with alternate set 2, we estimated  $\lambda = 0.973$  and AS = 0.295. Survey set 1 and survey set 2 produced estimates of  $\lambda$  of 1.062 and 1.059, respectively. Estimates of AS from these parameter sets were 0.257 and 0.283.

### Relative Effects

Relative effects of adult survival parameters on  $\lambda$  ( $\geq 0.68$ ) were much greater than relative effects of reproductive parameters ( $\leq 0.17$ ) for all 6 sets of simulations (Fig. 3). The inverse was generally true for relative effects on AS (Fig. 4). When moving from 1 parameter set to another, juvenile survival, particularly winter survival of juveniles, was increased proportionally more than adult survival. As juvenile survival was increased across parameter sets, the relative effects of adult survival parameters on  $\lambda$  decreased while relative effects of reproductive parameters on  $\lambda$  increased (Fig. 3).

## DISCUSSION

The population growth rate for emperor geese during 1985–94 was near 1.0, based on 2 independent surveys (Alaska Peninsula in spring and Yukon-Kuskokwim Delta in summer). Assuming these survey-based estimates of  $\lambda$  are

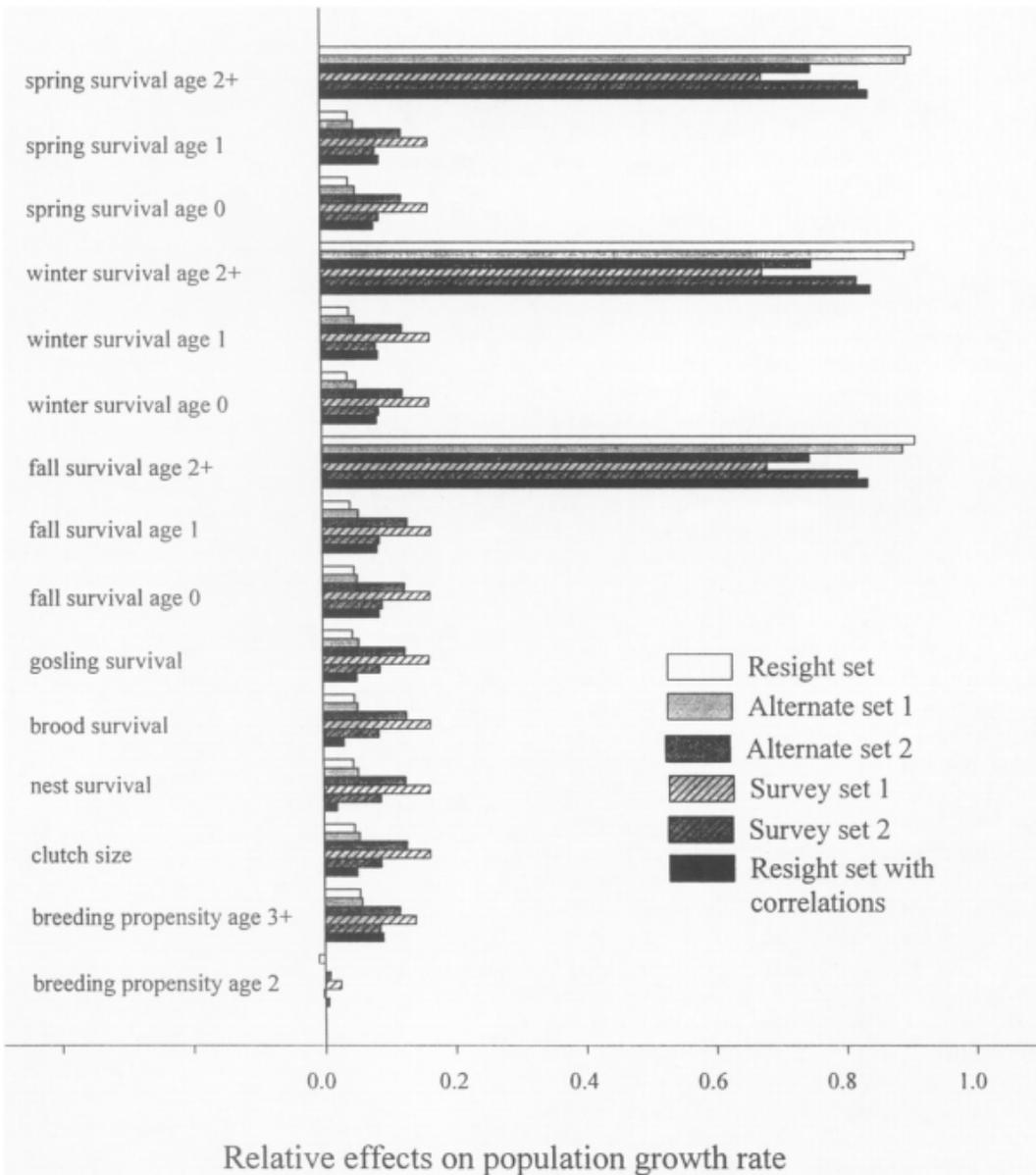


Fig. 3. Relative effects on population growth rate ( $\lambda$ ) of sequentially altering mean values of parameters used to model the dynamics of emperor geese. We derived each estimate of  $\lambda$  as the mean from 500 iterations of a demographically stochastic model. A relative effect of 0.9 means that a 10% change in that parameter will result in a 9% change in  $\lambda$ .

unbiased, then annual survival rates estimated from fall surveys of population numbers and age-ratios provided more accurate predictions of  $\lambda$  than did mark-resight estimates of survival. We therefore believe that our earlier mark-resight estimates of survival (Schmutz *et al.* 1994) are biased low. In that study, we controlled for initial handling and neck collar effects, collar loss, and birds that never visited our sampling

sites in spring and fall migratory staging areas. This adjustment was done by including only those birds seen on staging areas in survival analyses and by beginning the analysis at the time of first observation, not at the time of banding on the Yukon-Kuskokwim Delta. Although birds did not enter in the analysis until they had worn a neck collar for at least 2 months, neck collars potentially have a chronic negative effect (Zicus

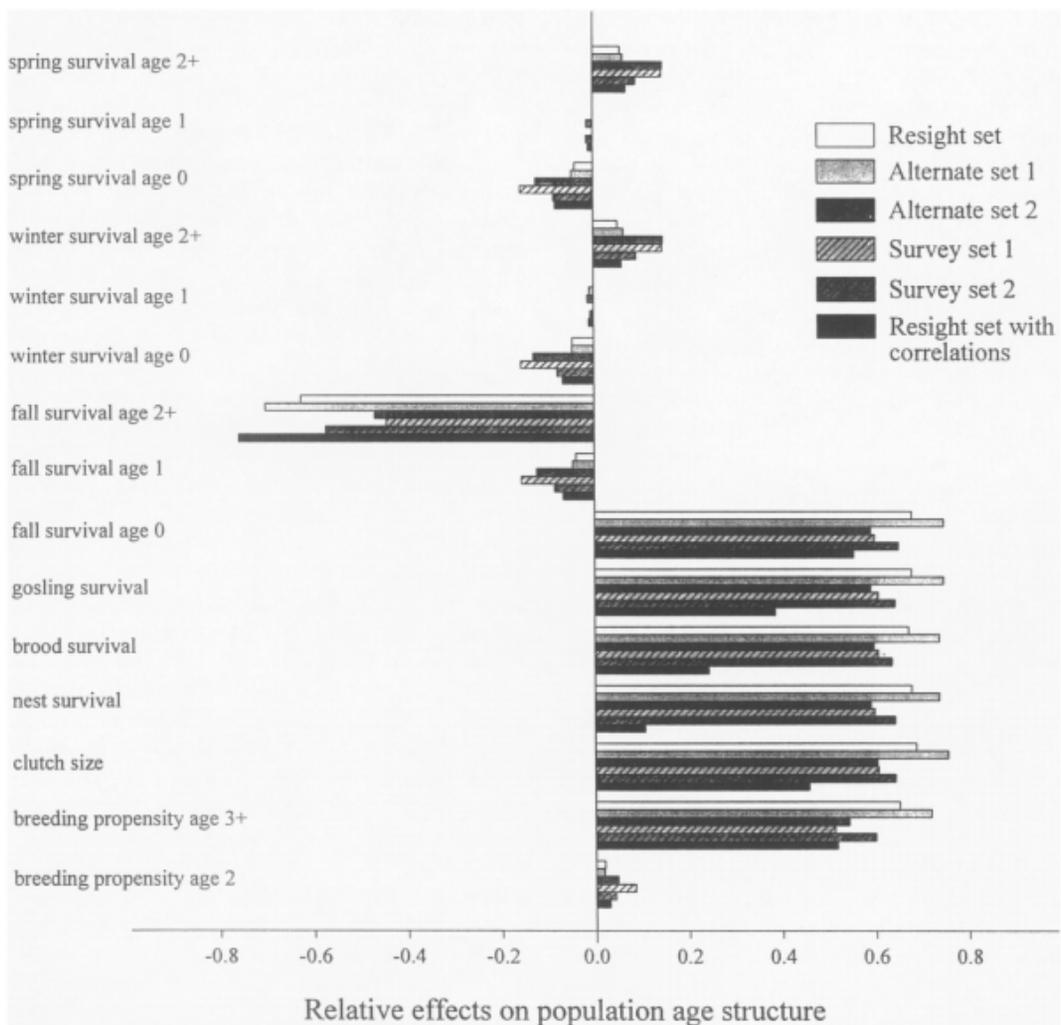


Fig. 4. Relative effects on fall age structure (AS) of sequentially altering mean values of parameters used to model the dynamics of emperor geese. We derived each estimate of AS as the mean from 500 iterations of a demographically stochastic model. A relative effect of 0.9 means that a 10% change in that parameter will result in a 9% change in AS.

et al. 1983). Observed increases in feather wear beneath collars (Schmutz, pers. obs.) may result in increased thermoregulatory costs for this most northerly wintering goose. Alternatively, or in addition, neck collars may exact a biologically significant increase in the energetic cost of flight (Gessaman and Nagy 1988). Testing for negative effects of neck collars, however, has been hampered by our and others' inability to follow a sample of alternatively marked birds to serve as an appropriate control group (but see Samuel et al. 1990).

An additional or alternate source of bias in mark-resight estimates of survival may be a con-

sequence of philopatric behavior of migrating geese. If geese exhibited absolute fidelity to particular staging areas on the Alaska Peninsula, then the adjustment procedure mentioned above and described by Schmutz et al. (1994) would have appropriately accounted for the fact that geese occurred at all staging areas, but only a subset of staging areas was sampled. However, preliminary analyses with newly developed movement models (Nichols et al. 1993, Spindelov et al. 1995) indicate that surviving emperor geese exhibited a 55–80% chance of returning to their previous staging area (Schmutz, unpubl. data). Thus, this partial (<100%) phil-

opatry may have resulted in birds moving away from sampled areas. Although such movement might be biologically termed temporary emigration in that geese were likely to return to their former staging area, it may have functioned statistically as permanent emigration, as birds may have died or the study may have ended before they returned to their previous staging area. Bias would then result, as mark-resight models confound permanent emigration with death (Pollock et al. 1990).

The range of values for survival rates we simulated spans from near the minimum (Timm and Dau 1979, Rexstad 1992) to the maximum (Owen and Black 1989) of the distribution of survival rates estimated from other goose populations (see also Kirby et al. 1986, Francis et al. 1992). We expect that the true survival rates for emperor geese were within the range of values spanned by the various parameter sets used in our model. Clearly, relative effects (elasticities) were fairly insensitive to what parameter set we used; varying adult survival rates consistently had the highest relative effects on  $\lambda$  whereas varying reproductive parameters had the lowest. These results are in general agreement with other recent studies on comparatively long-lived waterfowl species (e.g., harlequin ducks [*Histrionicus histrionicus*; Goudie et al. 1994], and snow geese [*Chen caerulescens*; Brault et al. 1994]). Further, life history theory predicts that elasticities of adult survival will be high in birds with long generation times, whereas they will be comparatively low (relative to those for reproduction) in birds with short generation times (Eberhardt 1985, Lebreton and Clobert 1991).

Despite consistently greater relative effects of survival than reproduction on  $\lambda$ , we did observe that relative effects on  $\lambda$  and AS varied depending upon what set of parameter values was used (Figs. 3, 4). This variation exemplifies how goose populations characterized by differing demographics may differ quantitatively, but not qualitatively, in how much various reproductive and survival parameters affect population change. As survival estimates included in the model were raised, relative effects of survival on  $\lambda$  decreased (from 0.91 to 0.68) and relative effects of reproductive parameters on  $\lambda$  increased (from 0.05 to 0.17). The directional pattern of this variation in relative effects among parameter sets was opposite of what one might initially have predicted from life-history theory,

which predicts that increases in adult survival rate would result in increasing relative effects of this parameter on  $\lambda$  (Lebreton and Clobert 1991, Stearns 1992); but this unexpected pattern occurred because we varied survival of juveniles disproportionately more among parameter sets than survival of adults. Juvenile survival in geese (Francis et al. 1992, Flint et al. 1995) and most organisms (Stearns 1992) is inherently more variable than adult survival. The relation between such parameter variation and elasticities (relative effects) is important to interpretation of long-term demographic studies, such as that for snow geese at La Perouse Bay (Cooke et al. 1995) where systematic changes have been documented in both adult and juvenile survival, but in opposite directions and at differing absolute rates of change (Francis et al. 1992, Cooke et al. 1995).

The management utility of elasticities, or relative effects, can be demonstrated by example. Surveys of subsistence harvest indicate an average annual harvest during 1985–93 of 1,420 ( $n = 8$  yr) emperor geese during the spring period (8 Apr–20 May), typically the time of greatest take (C. Wentworth, unpubl. data). Based on timing of spring migration, geese arriving on the Yukon-Kuskokwim Delta at this time are mostly breeding adults (Schmutz, unpubl. data). Therefore, if we assume that spring subsistence harvest is composed of only adults and that 70% of the 70,000 geese present during the spring population survey are adults (based on the modeled age structure), then harvest accounts for nearly 3% of the adult population  $\{[1,420/(70,000 \times 0.7)] \times 100 = 2.9\%$  and 58% (2.9% harvest mortality / 5% total spring mortality) of mortality during spring (assuming 95% spring survival rate, Table 1). Under this scenario and assuming harvest mortality is additive, reducing spring harvest by 50% (from 1,420 to 710 geese) would result in changing adult survival rates by 1.5% (710 fewer birds harvested / 49,000 total birds available), and thus, with an estimated relative effect of 0.90 for adult survival (approx average for parameter sets shown in Fig. 3), would increase population growth rate by 1.35% ( $1.5\% \times 0.9$ ).

Another example of the management utility of relative effects on  $\lambda$  can be seen in the difference between the elasticities associated with adult survival and those for reproductive parameters such as clutch size and nest success. In the preceding example, reducing harvest of

adults by 710 birds increased their survival rate by 1.5% and resulted in a 1.35% increase in  $\lambda$ . To achieve this same increase in  $\lambda$  by enhancing nest success, overall nest success in the population would need to increase by 13.5% ( $1.35\% / 0.10$  relative effect = 13.5%; again, relative effect of 0.10 is an approx average for parameter sets shown in Fig. 3).

Changing adult survival by the same proportion during the fall or winter would have the same relative effect on  $\lambda$  as changing it during the subsequent spring (Fig. 3). This equivalence of elasticities is consistent with well-established theory and relates to the fact that an equilibrium  $\lambda$  depends on annual adult survival (the product of seasonal components) rather than the timing of survival relative to reproduction (Caswell 1989). As demonstrated below, this result must be interpreted carefully when applying it to management decisions regarding, for example, fall versus spring harvest.

If we consider only adult harvest, it must be recalled that the equivalent elasticities for these periods are based on changing spring and fall survival by a constant proportion. Thus, increasing spring or fall harvest by 10% (and thus, changing survival from, e.g., 0.90 to 0.81, would reduce  $\lambda$  by approx 9% [ $10\% \times$  the elasticity of 0.9]). Often, however, management plans are focused on absolute numbers of harvested birds, not constant proportions. For example, an increased harvest of 500 adults in fall would have less effect on  $\lambda$  than an increase of 500 adults the following spring simply because the population of available adults that spring would be lower. As such, fall and spring survival would have been changed by different proportions and this would necessarily result in differential changes in  $\lambda$ . In this scenario we are assuming that changes in harvest affect adult survival rates only, and that no changes occur in other parameters, e.g., juvenile survival.

Relative effects quantify population response to a change in a given parameter value. They do not, however, address how frequently such parameter change may occur. If reproductive parameters are more variable than survival parameters, reproduction may contribute more to the dynamics of population change than predicted by just the magnitudes of relative effects. For example, killer whales (*Orcinus orca*) are a long-lived species and adult survival was found to have a much greater elasticity (relative effect) than any other life history parameter; yet, vari-

ation in fecundity was correlated more to annual variations in population size than any other parameter (Brault and Caswell 1993). Greater annual variation in reproduction than in survival commonly has been documented in geese (Owen and Black 1989, Cooke et al. 1995). Further, Petersen et al. (1994) reported that the amount of annual change in spring population size of emperor geese was significantly related to the proportion of juveniles in the fall population, a metric used to index annual reproduction. Our metric for age structure differs from another commonly used metric (no. of juv divided by no. of ad [no juv in the denominator]). Although our metric is the one used by managers of goose populations (e.g., U.S. Fish and Wildl. Serv., unpubl. data), it will produce somewhat larger estimates of relative effects of parameters on AS than if one used the other metric.

Because we used several different parameter sets, our model mimics environmental stochasticity in survival. However, across the 6 simulated parameter sets, we did not vary reproductive rates as much as survival rates, and therefore, we may have underrepresented the potential effects of environmental stochasticity on reproduction, and in turn, the range of effects on  $\lambda$ . Reproduction in arctic breeding geese can be reduced in years with late springs (Barry 1962, Cooke et al. 1995). For emperor geese, late springs in 1985 and 1992 corresponded to the 2 years (since 1985) with exceptionally low fall age-ratios (W. I. Butler, unpubl. data).

Environmental stochasticity probably affects parameters in a correlated fashion. For example, a late spring may depress multiple stages of reproduction. Average clutch size declines with later initiation dates (Petersen 1992a). Also, less absolute time available for gosling growth and declining plant qualities (Sedinger and Raveling 1986) make it likely that goslings are smaller in late years, and thus would have poorer juvenile survival rates (Schmutz 1993) and possibly smaller adult body size, survival, and fecundity (Sedinger et al. 1995). This scenario is more complex than our simple model of a correlation between reproductive parameters. Since we demonstrated that even such simple correlations can influence  $\lambda$ , future studies should consider the correlational structure among parameters.

## MANAGEMENT IMPLICATIONS

Uncertainty about accuracy of parameter estimates led us to examine a range of parameter

values, particularly for survival, that encompasses much of that found in the literature on arctic geese. Across this range, adult survival consistently had much higher relative effects on  $\lambda$  than did reproductive parameters. Thus, life-history patterns of geese are such that a manager's perturbation of survival would be predicted to have qualitatively larger population effects than a similar level of perturbation to reproduction. Further, the variation of relative effects on  $\lambda$  within a parameter (created by using different parameter sets) suggests that quantified predictions of population effects in response to perturbation require accurate estimates of reproduction and survival.

Our measures of relative effects provide estimates of how much change in growth rate or age structure can be expected if a given survival or reproductive parameter is altered through management action. However, the realization of this predicted effect on  $\lambda$  will then be modulated by the frequency and magnitude of variation in unperturbed parameters (e.g., late springs and disproportionately poor reproduction).

A final caveat is that we have assumed no compensatory relations among parameters. Emperor geese are still well below historical numbers, thus partly justifying our additive model, but as densities of geese increase on the Yukon-Kuskokwim Delta the potential increases for density-dependent effects (Cooch et al. 1989, Sedinger et al. 1995) on the modeled parameters. In such a system, relative effects and correlations among parameters probably would change, but the relations are complex and understanding this complexity will require intensive, long-term data on the relation between density and the various life-history parameters.

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