



The Auk 123(1):198–210, 2006
© The American Ornithologists' Union, 2006.
Printed in USA.

NEST SURVIVAL IN DUSKY CANADA GEESE (*BRANTA CANADENSIS OCCIDENTALIS*): USE OF DISCRETE-TIME MODELS

JAMES B. GRAND,^{1,4} THOMAS F. FONDELL,² DAVID A. MILLER,^{3,5} AND
R. MICHAEL ANTHONY²

¹U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, 108 White Smith Hall,
Auburn University, Auburn, Alabama 36849, USA;

²U.S. Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, USA; and

³Alabama Cooperative Fish and Wildlife Research Unit, 108 White Smith Hall, Auburn University, Auburn,
Alabama 36849, USA

ABSTRACT.—The Dusky Canada Goose (*Branta canadensis occidentalis*) population that breeds in the Copper River Delta, Alaska, has declined substantially since the late 1970s. Persistent low numbers have been attributed to low productivity in recent years. We examined patterns in survival rates of 1,852 nests to better understand ecological processes that influenced productivity during 1997–2000. We compared 10 nonparametric models of daily survival rate of nests (DSR) that included variation among years, calendar dates, nest initiation dates, and nest ages with equivalent models based on parametric functions. The unequivocal best model included patterns of DSR that varied among discrete periods of years, calendar dates, and nest ages. Generally, DSR was low early in the nesting season and higher midseason. Across years, patterns in DSR were most variable early and late in the nesting season. Daily survival rates of nests declined between the first and second week after initiation, increased until the fourth week, and then declined during the last week before hatch. Nest survival probability estimates ranged from 0.07 to 0.71 across years and nest initiation dates. Mean rates of nest survival ranged between 0.21 and 0.31 each year. We suggest (1) considering models that do not limit estimates of daily nest survival to parametric forms; (2) placing greater emphasis on sample size when nests are rare, to obtain accurate estimates of nest survival; and (3) developing new techniques to estimate the number of nests initiated. Received 7 July 2004, accepted 2 July 2005.

Key words: Alaska, *Branta canadensis occidentalis*, Copper River Delta, discrete-time models, Dusky Canada Goose, Horvitz-Thompson estimator, nest success, nest survival, nonparametric models.

Supervivencia de los Nidos en *Branta canadensis occidentalis*: Uso de Modelos de Tiempo Discreto

RESUMEN.—Las poblaciones del ganso *Branta canadensis occidentalis* que crían en el delta del Río Copper, Alaska, han declinado substancialmente desde el final de los 70s. Estos números persistentemente bajos han sido atribuidos a una baja productividad en los últimos años. Examinamos los patrones en las tasas de supervivencia de 1,852 nidos para comprender mejor los procesos ecológicos que influenciaron la productividad entre 1997 y 2000. Comparamos 10 modelos no paramétricos de tasas

⁴E-mail: grandjb@auburn.edu

⁵Present address: Department of Natural Resource Ecology and Management, 124 Science II, Iowa State University, Ames, Iowa 50011, USA.

de supervivencia diaria de nidos (TSD) que incluyeron variación entre años, fechas de calendario, fechas de iniciación de los nidos y edad de los nidos con modelos equivalentes basados en funciones paramétricas. El mejor modelo incluyó patrones de la TSD que variaron entre períodos discretos de años, fechas de calendario y edad de los nidos. De modo general, la TSD fue baja al principio de la estación de cría y mayor en el medio de la estación. Entre años, los patrones de la TSD fueron más variables al principio y al final de la estación de cría. Las tasas de supervivencia de los nidos disminuyeron entre la primera y la segunda semana posterior al inicio de los nidos, incrementaron hasta la cuarta semana y luego disminuyeron durante la última semana antes de la eclosión. Las estimaciones de la probabilidad de supervivencia de los nidos variaron entre 0.07 y 0.71 entre los años y las fechas de inicio de los nidos. Las tasas medias de supervivencia de los nidos variaron entre 0.21 y 0.31 cada año. Sugerimos (1) considerar modelos que no limiten las estimaciones de supervivencia diaria de los nidos a formas paramétricas; (2) poner mayor énfasis al tamaño de muestreo cuando los nidos son raros, para obtener estimaciones exactas de la supervivencia de los nidos; y (3) desarrollar nuevas técnicas para estimar el número de nidos iniciados.

THE COPPER RIVER DELTA (CRD) in south-central Alaska contains the largest known concentration of breeding Dusky Canada Geese (*Branta canadensis occidentalis*; hereafter “duskies”). This population has declined steadily since the 1970s as a result of low recruitment, despite successful efforts to improve overwinter survival (Bromley and Rothe 2003). Apparent nest success (the portion of discovered nests that hatch at least one egg) for duskies on the CRD was estimated at 87% in 1959 (Hansen 1961) but had fallen to 43% in the early 1980s (Campbell 1990), and more recent estimates suggest that apparent success was <10% (Campbell and Rothe 1990). Current estimates of the influence of environmental and demographic factors on productivity are critical for determining why the population has not recovered. Thus, unbiased estimates of nest survival (the portion of all nests that hatch at least one egg) and a clear understanding of patterns in daily survival rate (DSR) of nests are of increasing importance in determining management options for reversing this population decline.

Dusky nest survival varies in complex patterns related to date and nest abundance as a result of the predator–prey dynamics in the area (Miller et al. 2006). The CRD was uplifted ~1.9 m during a 1964 earthquake, which resulted in immediate changes in hydrology and long-term changes in vegetative structure (Campbell 1990). Related changes in the predator community are correlated with the decrease in dusky recruitment. Bald Eagles (*Haliaeetus leucocephalus*; hereafter “eagles”) and brown bears (*Ursus arctos*) are the two most frequent predators on

dusky nests (Anthony et al. 2004). Survival of dusky nests appears to vary with abundance of eagles and eulachon (*Thaleichthys pacificus*; Miller et al. 2006), a small anadromous fish that is an important prey species for eagles (Marston et al. 2002). Brown bears frequent nesting areas used by duskies beginning in late May (J. B. Grand et al. unpubl. data). Further complexity results from the variation in abundance of dusky nests from late April through early July (see below).

Because these patterns result in complex temporal variation in dusky nest survival, it is unlikely that they can be modeled accurately on the basis of relationships with continuous parametric forms (e.g. linear), which require *a priori* decisions regarding the functional form of the variation in DSR. Here, we present a comprehensive analysis of nest survival for duskies using DSR models based on discrete-time covariates, which represent groupings of nests with similar characteristics such as date, age, and nest initiation period. We also compare the efficacy of discrete-time models with that of models based on linear and quadratic functions of time. Further, we use these results to estimate annual (population) nest survival and confidence intervals for the population of duskies nesting on our study area in the western CRD during 1997–2000.

METHODS

FIELD METHODS

We located nests by searching a 13-km² area on the western CRD. The area has been

described previously (Boggs 2000). The study area was searched thoroughly twice each year, 1997–2000, and each search took approximately three weeks to complete. Nests found incidentally during other activities were also included in analyses. We estimated the age of embryos by candling eggs (Weller 1956), and we numbered each egg to determine viability and to detect partial predation. To facilitate relocation, we mapped nests on aerial photographs and recorded Universal Transverse Mercator (UTM) coordinates using global positioning system (GPS) receivers. We revisited nests at 10-day intervals until termination. During each visit, we recorded presence or absence of the female, condition and number of eggs, and stage of incubation. As hatching dates approached, nests were often visited more frequently to mark females and young and to better assess the fate of eggs. Nests were considered to have survived if at least one egg was being incubated or at least one egg hatched by the end of an observation interval.

Nest initiation dates were calculated for nests found during laying by subtracting 1.5 days per egg laid (Bromley and Jarvis 1993) from the date the nest was found. For nests found during incubation, we also subtracted the age of embryos. We assumed an incubation period of 26 days and an average nest age at hatch of 35 days (J. B. Grand et al. unpubl. data). Nests found after abandonment or predation and those with all dead or infertile eggs were not included in any calculations. In estimating nest survival, nests that were abandoned as a result of our activity (i.e. nests abandoned with no sign of disturbance by a predator) were right-censored on the date of the previous visit.

MODELING NEST SURVIVAL

Initially, we cast 10 models (Table 1) that incorporated annual and intra-annual variation in nest survival during discrete periods on the basis of the following criteria. All of our models included differences in DSR among years. Our assumption was that nest survival varied among years and our ability to discriminate among those differences was limited only by sample size. Some models included the effect of nest age to account for hypothesized variation in female behavior across stages of incubation and heterogeneity in female and nest-site quality. However,

TABLE 1. Discrete-time models used to examine the annual and intra-annual sources of variation in daily survival rates (DSR) of Dusky Canada Goose nests, western Copper River Delta, Alaska, 1997–2000. Analogous models using continuous effects of date, age, and initiation dates and quadratic terms were also examined, but are not shown here.

Model	Description
DSR_y	DSR varies among years but is constant within years.
$DSR_{y,d}$	DSR varies among years and calendar dates. Patterns among calendar dates are consistent across years.
$DSR_{y,i}$	DSR varies among years and initiation dates. Patterns among initiation dates are consistent across years.
DSR_{y^*d}	DSR varies among calendar dates. Patterns among calendar dates vary across years.
DSR_{y^*i}	DSR varies among initiation dates. Patterns among initiation dates vary across years.
$DSR_{y,a}$	DSR varies among years and nest ages. Patterns among nest ages are consistent across years.
$DSR_{y,d,a}$	DSR varies among years and calendar dates and nest ages. Patterns are consistent across years.
$DSR_{y,i,a}$	DSR varies among years, initiation dates, and nest ages. Patterns are consistent across years.
$DSR_{y^*d,a}$	DSR varies among calendar dates and nest ages. Patterns among calendar dates vary across years.
$DSR_{y^*i,a}$	DSR varies among initiation dates and nest ages. Patterns among initiation dates vary across years.

Abbreviations: y = year, d = 10-day date periods, i = 10-day nest initiation periods, and a = 7-day age classes. Asterisk (*) indicates effect interactions; otherwise, effects are additive.

we assumed that the effect of nest age would be consistent among years and calendar dates or initiation dates; thus, where age effects were included, they were always additive sources of variation (e.g. $DSR_{y,a}$). The most important comparisons were among models where DSR varied with nest initiation date or calendar date (time). We hypothesized that differences in DSR related

to nest initiation date were related to condition and experience of nesting females. Furthermore, these patterns might be similar among years, as in a model with an additive effect of year and initiation date ($DSR_{y,i}$), or they might vary as in a model containing the interaction between year and initiation date ($DSR_{y,i}$). Similarly, we also included models of DSR that varied by calendar date, with patterns that were similar ($DSR_{y,d}$) or variable ($DSR_{y,d}$) among years, to incorporate hypothesized variation in predator distribution and abundance.

For discrete-time models, we used 10-day intervals for both calendar date and initiation date and 7-day intervals for nest age. We used shorter intervals for age categories because our sample contained a relatively even distribution of nest exposure days across nest ages. We pooled data in the first two and last two calendar-date intervals and the last three initiation date intervals each year, because they included <10 nests. This resulted in six calendar-date intervals, four initiation-date intervals, and five nest-age intervals. Data were standardized across all years by Julian date, and the first interval began with the earliest observed nest exposure date (27 April) and initiation date (24 April). We then cast continuous-time models equivalent to our discrete-time models, replacing the discrete-time covariates of date, initiation date, and nest age with linear and quadratic functions of the three covariates (Table 1). Our global model included the interaction between year and date intervals and an additive effect of nest age. Because of the lack of a widely accepted method (Dinsmore et al. 2002), we were unable to assess the fit of our global model.

We examined variation in DSR and estimated nest survival using the maximum-likelihood (ML) estimators in MARK (White and Burnham 1999). Thus, we were able to construct models with DSR estimates that differed among intervals. We used a logit link to constrain estimates between zero and one, and we used Akaike's Information Criterion (corrected for small sample sizes, AIC_c) to select among our set of candidate models (Burnham and Anderson 1998).

Output in MARK allowed us to examine the effects of each parameter in our best model via the coefficients in the logit equation (β s) and their standard errors. Although this was a useful method for obtaining estimates of parameters of interest, variances were estimable only by

approximation through the delta method or bootstrap simulation. We used bootstrap resampling of the encounter history data (500 samples with replacement up to the original sample size for each of the four years; Efron and Tibshirani 1994). Because MARK does not provide a convenient method for running large numbers of analyses using different data sets, we analyzed bootstrap samples in MATLAB, release 13 (Mathworks, Natick, Massachusetts), and used a quasi-Newton optimization routine to obtain ML estimates based on the same estimator used in MARK (Dinsmore et al. 2002).

We calculated the estimates of DSR for each combination of age, date, and year in the study period. When estimating nest survival during periods prior to the discovery of nests, we used DSR on the first day of monitoring. Thus, nest survival for the period was estimated as

$$\prod_{i=1}^j DSR_i$$

where DSR_i is the DSR of a nest of age i on the first day of nest observation and j is the number of days from nest initiation to discovery of the first nest.

NEST INITIATION AND SURVIVAL

Our observed daily nest initiation frequencies were biased low, because we only used active nests (i.e. nests found during laying or incubation). Nests located that were destroyed or abandoned before we found them were not included in these analyses, because we could not estimate their age or initiation date. Therefore, we estimated the number of nests initiated on each day of the nesting season using DSR estimated by our nest survival model and the Horvitz-Thompson estimator described by Dinsmore et al. (2002). This estimator assumed that if nests were not destroyed they were eventually found prior to hatching. If we also assumed that all surviving nests initiated on the same day had similar probability of discovery, then the inverse of the probability of survival until discovery for a given nest estimated the number of nests in the population represented by that nest. Thus, we summed the inverse of the probability of survival until discovery for all nests initiated on each day to produce an expected nest initiation distribution.

We also calculated nest survival for nests initiated on each day using our estimates of DSR and a 35-day expected nest life from the day the first egg was laid until hatch (1.5 eggs day⁻¹ * 6 eggs + 26 days of incubation). We then used the estimated nest initiation frequencies in a weighted average of nest survival probabilities to calculate mean annual nest survival for the population (Horvitz and Thompson 1952). We produced these estimates for the original data set and each of the 500 bootstrap samples, and used the 0.025 and 0.975 quantiles of the bootstrapped estimates to approximate 95% confidence limits (CL) on the number of nests initiated each day, total nests initiated, and total nest survival each year.

RESULTS

Among all the models we examined, the best model of DSR was unequivocally DSR_{y^{*}d^{*}a ($w_i = 0.98$; Table 2). This discrete-time model included different intra-annual patterns in DSR each year across calendar dates and a consistent pattern of DSR variation with respect to nest ages based on discrete periods. Models that included variation among discrete periods of nest initiation performed poorly ($\sum w_i < 0.01$) in comparison with models based on discrete date periods ($\sum w_i >$}

0.99). Similarly, the model with constant DSR within years (DSR_y) was virtually unsupported by our data. Despite their parsimony, models based on linear functions of date, initiation date, and age also were not supported by our data ($\sum w_i < 0.01$).

DAILY SURVIVAL RATE ESTIMATES

Because it was clearly the best model supported by our data, we examined variability in DSR estimates based only on the model DSR_{y^{*}d^{*}a. We found some similarity in patterns of DSR by calendar date among years. Daily survival rate of nests was low early in the nesting season (before 16 May) and higher midseason (16 May–27 June; Fig. 1). Late-season (after 27 June) patterns were most dissimilar, and DSR declined after 27 June in 1998 and 2000 and increased during the same period in 1997 and 1999. In 1999, DSR started highest of all years and was relatively consistent throughout the nesting season. Overall, variability in DSR was greatest early and late in the nesting season each year.}

Our candidate model set did not include interactions between age and date or age and year; therefore, patterns of DSR across age classes were constrained to be similar among dates and among years. Across nest ages, DSR

TABLE 2. Selection of the best daily survival rate (DSR) model for Dusky Canada Goose nests on the western Copper River Delta, Alaska, 1997–2000, was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c). The top nine models are presented here, along with the model of constant DSR within years. Effective sample size = 1,793.

Model	AIC _c	Δ AIC _c ^a	AIC _c weight ^b	k^c	Model deviance
DSR _{y[*]d[*]a}	1,817.53	0.00	0.98	28	1,760.61
DSR _{y[*]d}	1,825.62	8.10	0.02	24	1,776.95
DSR _{y[*]d[*]a}	1,836.53	19.00	0.00	13	1,810.33
DSR _{y[*]d}	1,857.07	39.54	0.00	9	1,838.97
DSR _{y[*]II²A}	1,910.08	92.55	0.00	7	1,896.02
DSR _{y[*]II²AA²}	1,911.10	93.57	0.00	8	1,895.02
DSR _{y[*]ia}	1,911.12	93.59	0.00	11	1,888.97
DSR _{y[*](I²)A}	1,912.77	95.24	0.00	13	1,886.57
DSR _{y[*](I²)AA²}	1,913.85	96.33	0.00	14	1,885.62
DSR _y	2,088.48	270.95	0.00	4	2,080.46

Abbreviations: y = year, d = 10-day date periods, i = 10-day nest initiation periods, a = 7-day age classes, A = age (continuous), and I = initiation date (continuous). Asterisk (*) indicates effect interactions; otherwise, effects are additive.

^a Δ AIC_c = (AIC_{c*i*} - minimum [AIC_c]).

^b $w_i = \exp(-1/2\Delta$ AIC_{c*i*})/sum (exp [-1/2 Δ AIC_c]).

^c k = Number of estimated parameters.

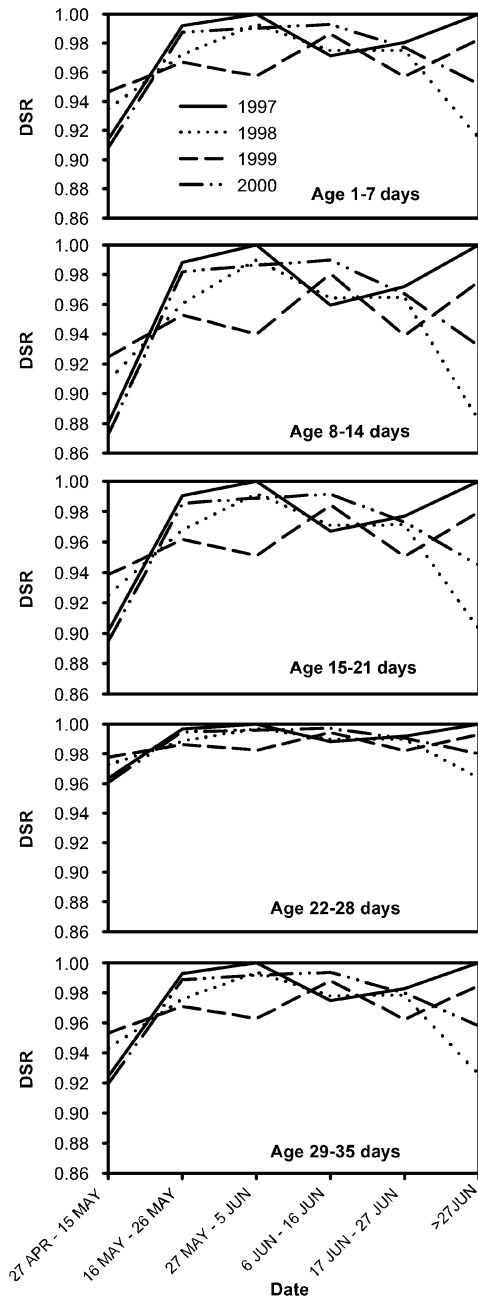


FIG. 1. Patterns in daily survival rates (DSR) for each age group of Dusky Canada Goose nests by date each year, 1997–2000, on the western Copper River Delta, Alaska. Daily survival rates were lowest early and late in the nesting season, and patterns across nest ages were similar.

declined from the first week (laying, ages 1–7 days) to the second (late laying and early incubation, ages 8–14 days), increased until the fourth week (approximately the third week of incubation, ages 15–21 days and 22–28 days), and declined during the last week before hatch (ages 29–35 days; Fig. 2). Daily survival rate of nests was lowest during late laying and early incubation and highest during the third week of incubation, and this pattern was increasingly attenuated as DSR increased.

NEST SURVIVAL

Many (25–45%) of the nests we located each year were inactive (destroyed or abandoned) when found (Table 3). This portion was smallest in 1997 and greatest in 1998, but more inactive nests were found on early dates in 1997, whereas their discovery was more evenly distributed in other years. Although the general shape of the observed nest initiation curves based on nests found active were similar to the initiation curves estimated using the Horvitz-Thompson method, the estimated curves suggested substantially greater numbers of nests initiated on most days (Fig. 3). Additionally, the estimated number of nests initiated each year was similar to the numbers of nests we found in 1998 and 1999, but substantially higher than the numbers found in 1997 and 2000 (Table 3).

We estimated nest survival using only the model $DSR_{y,d,a}$ because we found such strong support for it (i.e. low uncertainty in model selection; Table 2). Nest survival for each initiation date was estimated by the product of DSR from the date of nest initiation until the eggs hatched 35 days later; therefore, patterns of DSR by date were exaggerated (Fig. 4; compare with Figs. 1 and 2). Thus, because DSR was low at early dates, survival was lowest for the first nests initiated in all four years. Additionally, in 1997, 1999, and 2000, nest survival increased through midseason, peaked just after mid-May, and then declined for the remainder of the nesting season. Survival in 1999 was distinct in that it steadily increased throughout the nesting season but never reached the 0.50–0.70 survival of nests initiated midseason in the other three years. Nest survival varied from 0.21 in 1997 (95% CL: 0.13–0.29) to 0.31 in 1998 (95% CL: 0.21–0.42), 0.29 in 1999 (95% CL: 0.15–0.39), and 0.24 in 2000 (95% CL: 0.13–0.38).

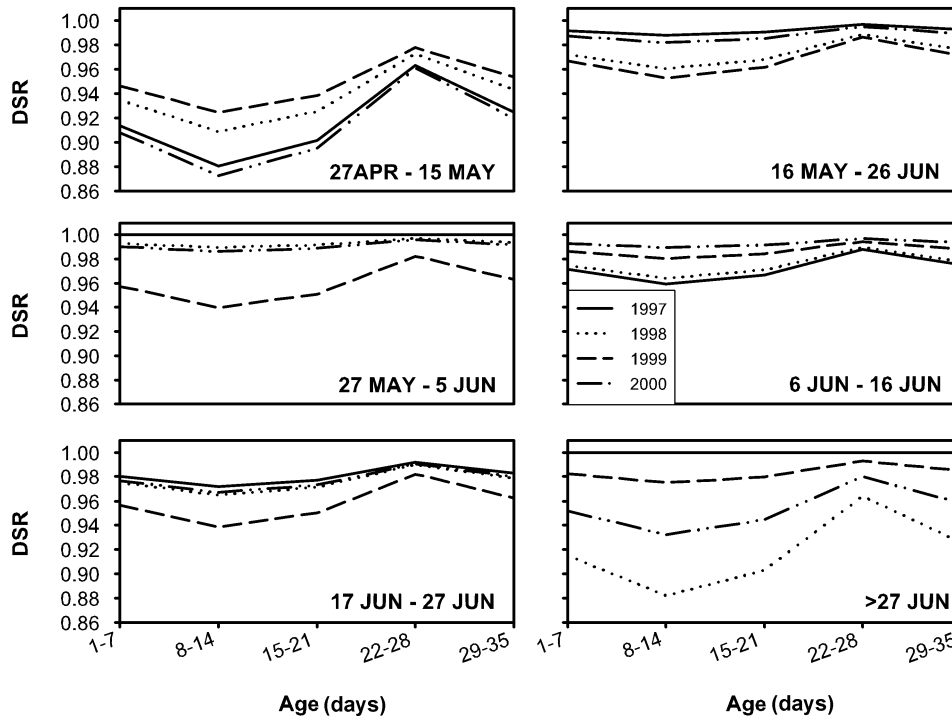


FIG. 2. Daily survival rate (DSR) by nest age for each date period of Dusky Canada Goose nests on the western Copper River Delta, Alaska, 1997–2000. Daily survival rates were lowest during late laying and early incubation, but increased through the second and third weeks of incubation, before decreasing slightly during the final week of incubation. Patterns across dates were similar but increasingly attenuated as DSR increased.

TABLE 3. Numbers of Dusky Canada Goose nests found active and inactive and total nests found on the western Copper River Delta, Alaska, 1997–2000. We also include the expected number of nests, estimated using the Horvitz-Thompson method.

Year	Nests found (<i>n</i>)			Estimated nests initiated (<i>n</i>)	95% confidence limits
	Active	Inactive	Total		
1997	306	104	410	769	578–1,104
1998	280	233	513	510	404–691
1999	295	128	423	490	387–896
2000	304	202	506	782	528–1,382
Total	1,185	667	1,852		

DISCUSSION

MODELING NEST SURVIVAL

We made several assumptions in the *a priori* model-building process that were necessary for casting models that made biological sense

and were parsimonious. We argue that many of these considerations apply widely to studies of avian nest survival. Temporal structure has been incorporated into ML estimators of DSR by assuming that survival is a continuous, logit-linear function of time (Dinsmore et al. 2002) and that these lower-order linear

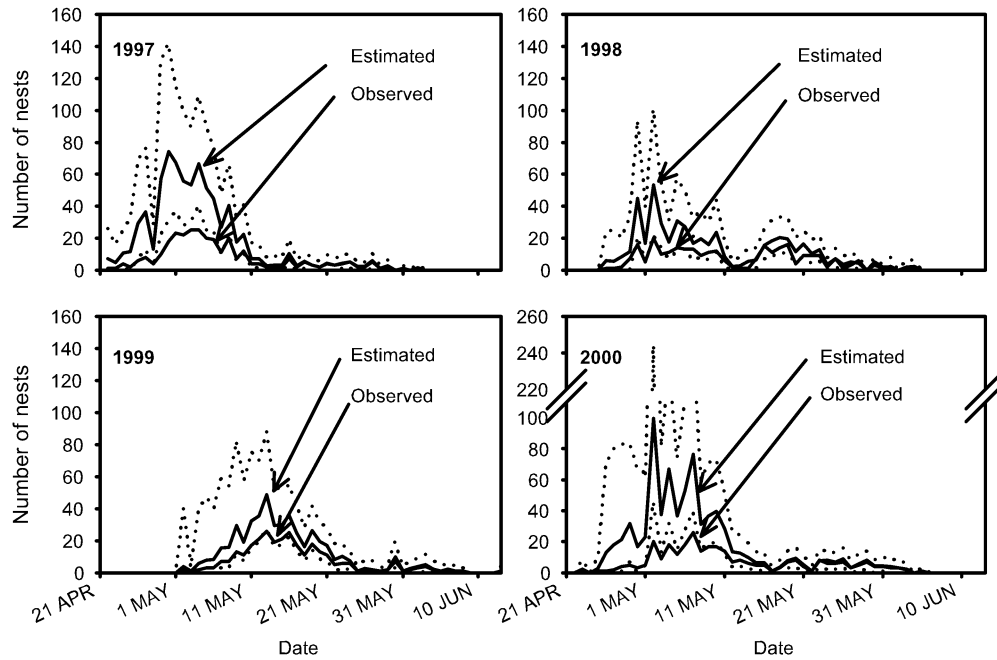


FIG. 3. Number of nest initiations each day from actual nests found and expected number estimated using the Horvitz-Thompson method for Dusky Canada Geese on the western Copper River Delta, Alaska, 1997–2000. Dotted lines indicate 95% bootstrapped confidence limits for the expected number of nests initiated each day. In concordance with Figure 2, the largest discrepancies between the observed and expected nest initiation plots occurred during the early nesting season when DSR was low.

functions offer a parsimonious approach to modeling temporal structure. However, we felt that an *a priori* assumption of a continuous linear pattern in DSR was unjustified because of observed variation in the behavior of females and in the behavior and abundance of predators and alternative prey that were neither linear nor continuous (Miller et al. 2006). Further, the choice of a parametric logit-linear or other type of model requires strong assumptions regarding the factors influencing DSR. Thus, we chose to estimate nest survival for discrete intervals of age and time as Klett and Johnson (1982) did. Although assignment of lengths and placement of intervals for the estimation of DSR were arbitrary, we felt that the relaxation of assumptions about the pattern of variation justified this non-parametric approach.

We also made several other assertions during model-building that, we suggest, apply to many other species of birds. First, we estimated different DSR each year because it is important to understand how observed patterns of intra-annual variation influence interannual

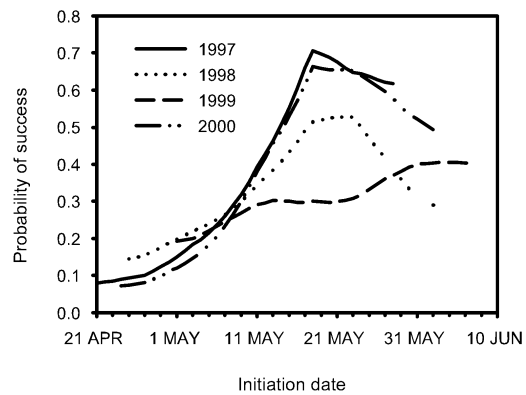


FIG. 4. Estimated survival rate of Dusky Canada Goose nests on the western Copper River Delta, Alaska, increased rapidly through the third week of May in 1997, 1998, and 2000, reaching levels well above 50%. Survival in 1999 increased throughout the nesting period, but never reached 50%. Estimates of survival are based on daily survival rates depicted in Figures 1 and 2, and 35-day nest age at hatch.

variability in nest survival. Nest survival is likely to vary among years, and if models without year effects are selected on the basis of any criteria, it is likely the result of our inability to estimate DSR precisely (Johnson 1999). In addition, estimating annual variation in nest survival is important in understanding population dynamics. Second, we assumed that the influence of nest age would be consistent across years and dates, because it is reflective of risk related to variation in dusky behavior through the nesting period and heterogeneity in female and nest-site quality within the population (Johnson 1979), not variation in extrinsic factors influencing nest survival, such as weather, predator distribution, or predator behavior. Third, we believed that models of DSR that varied among dates, which reflected when nest loss occurred, would fit better than models that estimated variation in DSR among nesting cohorts (i.e. nest initiation dates). We make this assertion because many of the causes of nest failure (e.g. weather, changes in predator distribution) vary independently of the structure of the nesting population. However, in many species of waterfowl, nest initiation date is related to age and experience, and could more directly capture the effects of female age structure and heterogeneity (Finney and Cook 1978).

It should be noted that even though patterns in DSR are best described by calendar date and nest age, nest initiation date and age provide equivalent information about individual nests. Perhaps more significantly, we suggest that DSR frequently varies over the various periods (year, age, calendar date, initiation date) as a result of abrupt or complex patterns in the risk of nest loss, which also may apply to many other bird populations. Thus, it is difficult at best to adequately model the variability observed in large data sets using relatively simple parametric forms. Ideally, these patterns of variation should form the basis for nonparametric models of DSR.

PATTERNS OF VARIATION IN DAILY SURVIVAL RATE ACROSS NEST AGES

The patterns we observed in DSR across nest ages likely result from abrupt changes in dusky behavior, and from heterogeneity as a result of nest-site selection. Although differential nest vulnerability would lead to a steady increase in

DSR across nest ages (Natarajan and McCulloch 1999), we observed a decrease in DSR from the first to the second week of incubation that corresponded to a shift in behavior among nesting females that occurred near the transition between those periods. During late laying (days 6–8, eggs 4–5), female duskies add structure to the nest and begin to line the nest with down (Cooper 1978). In addition, at this time females begin incubation bouts that increase rapidly in duration until laying is completed and nearly constant incubation begins. This abrupt change in behavior and corresponding change in DSR likely applies to many ground-nesting birds with precocial young and is not gradual in nature; thus, a linear model should not fit the pattern well.

As would be expected from individual heterogeneity (Zens and Peart 2003), DSR increased from late laying through mid- and late incubation. This pattern of increasing nest survival with nest age has been observed in several other waterfowl studies (Klett and Johnson 1982, Grand 1995, Garrettson and Rohwer 2001) and may well apply to most species of birds as the result of differential vulnerability to predation. Nests that are located in particularly obvious (vulnerable) sites are quickly eliminated from the population by predators, so that as age increases, only nests that have a high probability of surviving remain. Additionally, risk-taking by females may increase with nest age. Forbes et al. (1994) found that the distance at which females flush from nests when approached by an observer decreased as nest age increased in a number of duck species, which likely reduces detection rates by some terrestrial predators.

However, as our data illustrate (Fig. 2), the increasing DSR expected to result from individual heterogeneity cannot completely explain patterns in DSR across the entire life of the nest. Daily survival rate of dusky nests decreased during the last week of incubation. Bromley (1984) observed an increase in frequency and duration of nest breaks taken by duskies during the final 10 days of incubation, which was related to a loss of lipid and protein (i.e. energy) stores during incubation (Bromley and Jarvis 1993). Bromley (1984) also observed that the rate of weight loss slowed sharply during the final week of incubation; and, in light of observed decreases in nest attentiveness during the same period, he suggested that females had reached a

nutritional threshold (Bromley and Jarvis 1993). Furthermore, increased activity and vocalization by duskies near the nest during the final stages of incubation may provide visual and auditory clues to predators. These types of behavioral changes undoubtedly influence DSR of nests, are common among waterfowl, and likely are common to other birds that rely heavily on endogenous reserves during incubation.

Although higher-order polynomial models could be used to precisely describe complex patterns of DSR as a continuous function of nest age, the estimated coefficients of quadratic and higher-order functions are largely uninterpretable from a biological perspective. We suggest that, if parametric models are used to estimate nest survival, researchers seek models that estimate biologically meaningful parameters. Still, it may not be possible to incorporate the effects of abrupt changes in nest survival, such as the transition from incubation to nestling stages in passerine birds (Mayfield 1961 and many others) without the use of classification into discrete periods or states.

PATTERNS OF DAILY SURVIVAL RATE ACROSS DATES

The pattern of variation in DSR across dates likely was related to changes in predator behavior and abundance. Eagles were the primary predator on dusky nests (Anthony et al. 2004, Miller et al. 2006), and we observed marked changes in eagle abundance on the study area through the nesting season. In most years, eagles were abundant early in the nesting season, when we observed them hunting over suitable nesting areas. This behavior continued, and eagle abundance increased until late May, when we observed them feeding in high densities along sandbars on spawning eulachon. These phenomena likely explained not only low DSR during the early nesting season in most years, but also the abrupt increase and relative stability of DSR during midseason, when prey-switching by eagles apparently occurred.

Declines in DSR late in the nesting season in two of four years were probably the result of decreasing availability of spawning eulachon for eagles, and increases in brown bear predation on dusky nests. This pattern was different in 1999; DSR was initially high but failed to increase until June and then declined again sharply. In that year, nesting chronology

was delayed by ~10 days because of late snowmelt. Additionally, when eagles arrived on the study area, alternative prey was not readily available (Miller et al. 2006). Nonetheless, our data support abrupt changes in DSR as a result of changes in predator behavior. Similar relationships may also occur in systems where prey availability fluctuates either rapidly or in discontinuous patterns that result from prey or predator movements or prey-switching by predators.

PATTERNS IN NEST SURVIVAL

Our estimates of nest survival are intermediate in relation to historical estimates of apparent success for duskies. Apparent success typically overestimates the proportion of all nests that hatch, and as nest survival decreases, that bias typically increases (Mayfield 1961). Thus, the 1959 estimate of 87% (Hansen 1961) was likely relatively unbiased, whereas the estimate of 10% success in the late 1980s (Campbell and Rothe 1990) was likely a large overestimate. Nest survival during the early 1980s, when apparent success was 43%, likely was similar to the 21–31% nest survival we observed in 1997–2000. These results suggest that gosling production may have increased since the late 1980s but remains at less than half of that observed before the 1964 earthquake.

Despite the evidence that DSR models based on calendar date fit much better than models based on nest initiation date (Table 2), it is important to understand the variation in nest survival as it relates to the timing of nest initiation, because of the implications for dusky population biology. The low survival rate of nests initiated before mid-May each year represents a departure from the findings of others who have investigated the advantages of early nesting in waterfowl (Flint and Grand 1996, Grand and Flint 1997; but see Grand 1995, Garrettson and Rohwer 2001). This pattern is likely the result of the complex interaction of dusky (prey) and eagle (predator) behavior. Eagle populations in the region have increased substantially in recent decades (Bowman et al. 1997, Jacobson and Hodges 1999). Further, early in the nesting season, the onset of incubation, which makes nests more detectable by predators, coincides with increases in the number of eagles present on the CRD. The result is that nest survival for

females initiating nests in late April and early May was less than half that for females initiating in mid-May in three of four years. This differential in nest survival would appear to be strong selective pressure for females that nest later. However, duskies experience a relatively long nest initiation period (53 days) compared with most geese nesting at similar latitude (Mickelson 1975, Bruggink et al. 1994, Lindberg et al. 1997), and duskies are known to renest (Fondell et al. 2006). Furthermore, in most years, nests initiated late in the season have a high probability of survival. Thus, in terms of female success, the combination of a long nesting period, ability to renest, and high survival rates for late nests likely offsets the low survival rates of nests initiated early in the year.

Although estimates of annual nest survival varied from 21% to 31% during the years of our study, there was considerable overlap in confidence limits each year. Furthermore, estimates of nest survival in 1997 and 2000 were likely biased low, and thus very similar to nest survival rates in 1998 and 1999. This assertion is further supported by large discrepancies among estimates of the number of nests initiated and the number of nests found in 1997 and 2000. These large discrepancies were likely due to inaccurate estimates of DSR in the early portion of the nesting season, which were amplified by the Horvitz-Thompson estimator.

The Horvitz-Thompson approach to estimating the number of nests initiated each day is inversely related to the respective DSR estimates. Thus, underestimation of DSR results in overestimation of nest numbers, and vice versa. When the number of nests under observation is small, as occurred each year early in the nesting season, DSR is very sensitive to the number of nest mortalities. Thus, underestimates are likely because of random events. In comparison with overestimates of DSR of similar magnitude, an underestimate of DSR has a much greater effect on the estimated number of nests. The result is that nest numbers are overestimated during periods when DSR is underestimated, which in turn has a large negative effect on estimated nest survival for the population because periods of low DSR are disproportionately weighted in those estimates. We also point out that the Horvitz-Thompson method estimates the population of nests that would have been discovered had they survived. Thus, the assumption is

that all surviving nests are discovered eventually, and the method should not be applied to studies where search effort is insufficient to do so. Therefore, we suggest caution in the use of the Horvitz-Thompson method, and suggest that further research should be directed toward methods that are less sensitive to underestimation of DSR, and study designs that directly estimate nest detection rates.

ACKNOWLEDGMENTS

This project was funded through a partnership among U.S. Geological Survey, Biological Resources Division, Alaska Science Center; U.S. Fish and Wildlife Service, Region 7, Migratory Bird Management; U.S. Forest Service, Chugach National Forest, Cordova Ranger District; and Alaska Department of Fish and Game. We thank D. V. Derksen, R. L. Leedy, R. M. Oates, D. W. Logan, and T. C. Rothe for their support in this project, and C. R. Rakos for assistance with logistics. We thank the following U.S. Forest Service biologists and technicians for their assistance: E. C. Cooper, E. H. Gray, and especially D. E. Youkey. This project would not have been possible without the exceptional effort made by the following field biologists: M. G. and J. P. Stattleman, J. G. Fode, S. A. Fisher, P. A. Fitzmorris, N. D. Chelgren, B. C. Lake, R. J. Gazda, P. J. Wolf, S. A. Pavey, and S. T. Meade. We also thank P. L. Flint, M. J. Conroy, J. D. Nichols, and T. L. Shaffer for comments on earlier versions of this manuscript.

LITERATURE CITED

- ANTHONY, R. M., J. B. GRAND, T. F. FONDELL, AND B. F. J. MANLY. 2004. A quantitative approach to identifying predators from nest remains. *Journal of Field Ornithology* 75:40–48.
- BOGGS, K. 2000. Classification of community types, successional sequences, and landscapes of the Copper River Delta, Alaska. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-469.
- BOWMAN, T. D., P. F. SCHEMPF, AND J. I. HODGES. 1997. Bald Eagle population in Prince William Sound after the Exxon Valdez oil spill. *Journal of Wildlife Management* 61: 962–967.
- BROMLEY, R. G. H. 1984. The energetics of migration and reproduction of Dusky

- Canada Geese (*Branta canadensis occidentalis*). Ph.D. dissertation, Oregon State University, Corvallis.
- BROMLEY, R. G., AND R. L. JARVIS. 1993. The energetics of migration and reproduction of Dusky Canada Geese. *Condor* 95: 193–210.
- BROMLEY, R. G., AND T. C. ROTHE. 2003. Conservation assessment for the Dusky Canada Goose (*Branta canadensis occidentalis* Baird). U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-591.
- BRUGGINK, J. G., T. C. TACHA, J. C. DAVIES, AND K. F. ABRAHAM. 1994. Nesting and Brood-rearing Ecology of Mississippi Valley Population Canada Geese. *Wildlife Monographs*, no. 126.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model Selection and Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.
- CAMPBELL, B. H. 1990. Factors affecting the nesting success of Dusky Canada Geese, *Branta canadensis occidentalis*, on the Copper River Delta, Alaska. *Canadian Field-Naturalist* 104:567–574.
- CAMPBELL, B. H., AND T. C. ROTHE. 1990. Annual Report of Survey-inventory Activities. Part XIII. Waterfowl. Alaska Department of Fish and Game, Juneau.
- COOPER, J. A. 1978. The History and Breeding Biology of the Canada Geese of Marshy Point, Manitoba. *Wildlife Monographs*, no. 61.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- EFRON, B., AND R. J. TIBSHIRANI. 1994. An Introduction to the Bootstrap. Chapman and Hall, New York.
- FINNEY, G. H., AND F. COOKE. 1978. Reproductive habits in the Snow Goose: The influence of female age. *Condor* 80:147–158.
- FLINT, P. L., AND J. B. GRAND. 1996. Nesting success of Northern Pintails on the coastal Yukon-Kuskokwim Delta, Alaska. *Condor* 98:54–60.
- FONDELL, T. F., J. B. GRAND, D. A. MILLER, AND R. M. ANTHONY. 2006. Renesting by Dusky Canada Geese on the Copper River Delta, Alaska. *Journal of Wildlife Management* 70: in press.
- FORBES, M. R. L., R. G. CLARK, P. J. WEATHERHEAD, AND T. ARMSTRONG. 1994. Risk-taking by female ducks: Intra- and interspecific tests of nest defense theory. *Behavioral Ecology and Sociobiology* 34:79–85.
- GARRETTSON, P. R., AND F. C. ROHWER. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. *Journal of Wildlife Management* 65:398–405.
- GRAND, J. B. 1995. Nesting success of ducks on the central Yukon Flats, Alaska. *Canadian Journal of Zoology* 73:260–265.
- GRAND, J. B., AND P. L. FLINT. 1997. Productivity of nesting Spectacled Eiders on the lower Kashunuk River, Alaska. *Condor* 99: 926–932.
- HANSEN, H. A. 1961. Loss of waterfowl production to tide floods. *Journal of Wildlife Management* 25:242–248.
- HORVITZ, D. G., AND D. J. THOMPSON. 1952. A generalization of sampling without replacement from a finite universe. *Journal of the American Statistical Association* 47: 663–685.
- JACOBSON, M. J., AND J. I. HODGES. 1999. Population trend of adult Bald Eagles in southeast Alaska, 1967–97. *Journal of Raptor Research* 33:295–298.
- JOHNSON, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. *Auk* 96:651–661.
- JOHNSON, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63:763–772.
- KLETT, A. T., AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* 99:77–87.
- LINDBERG, M. S., J. S. SEDINGER, AND P. L. FLINT. 1997. Effects of spring environment on nesting phenology and clutch size of Black Brant. *Condor* 99:381–388.
- MARSTON, B. H., M. F. WILLSON, AND S. M. GENDE. 2002. Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs. *Marine Ecology Progress Series* 231: 229–236.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MICKELSON, P. G. 1975. Breeding Biology of Cackling Geese and Associated Species on the Y-K Delta, Alaska. *Wildlife Monographs*, no. 45.

- MILLER, D. A., J. B. GRAND, T. F. FONDELL, AND R. M. ANTHONY. 2006. Predator functional response and prey survival: Direct and indirect interactions affecting a marked prey population. *Journal of Animal Ecology* 75: in press.
- NATARAJAN, R., AND C. E. MCCULLOCH. 1999. Modeling heterogeneity in nest survival data. *Biometrics* 55:553–559.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111–113.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–138.
- ZENS, M. S., AND D. R. PEART. 2003. Dealing with death data: Individual hazards, mortality, and bias. *Trends in Ecology and Evolution* 18:366–373.

Associate Editor: A. E. Burger