

## OPTIMIZING NEST SURVIVAL AND FEMALE SURVIVAL: CONSEQUENCES OF NEST SITE SELECTION FOR CANADA GEESE

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*Abstract.* We examined the relationship between attributes of nest sites used by Canada Geese (*Branta canadensis*) in the Copper River Delta, Alaska, and patterns in nest and female survival. We aimed to determine whether nest site attributes related to nest and female survival differed and whether nest site attributes related to nest survival changed within and among years. Nest site attributes that we examined included vegetation at and surrounding the nest, as well as associations with other nesting birds. Optimal nest site characteristics were different depending on whether nest survival or female survival was examined. Prior to 25 May, the odds of daily survival for nests in tall shrubs and on islands were 2.92 and 2.26 times greater, respectively, than for nests in short shrub sites. Bald Eagles (*Haliaeetus leucocephalus*) are the major predator during the early breeding season and their behavior was likely important in determining this pattern. After 25 May, when eagle predation is limited due to the availability of alternative prey, no differences in nest survival among the nest site types were found. In addition, nest survival was positively related to the density of other Canada Goose nests near the nest site. Although the number of detected mortalities for females was relatively low, a clear pattern was found, with mortality three times more likely at nest sites dominated by high shrub density within 50 m than at open sites dominated by low shrub density. The negative relationship of nest concealment and adult survival is consistent with that found in other studies of ground-nesting birds. Physical barriers that limited access to nest sites by predators and sites that allowed for early detection of predators were important characteristics of nest site quality for Canada Geese and nest site quality shifted within seasons, likely as a result of shifting predator-prey interactions.

*Key words:* daily survival rate, female survival, nest site selection, nest survival, predator-prey relationships, vegetation.

### Optimización de la Supervivencia de Nidos y Hembras: Consecuencias de la Selección de Sitios de Nidificación para *Branta canadensis*

*Resumen.* Examinamos la relación entre los atributos de los sitios de nidificación y los patrones de supervivencia de los nidos y de las hembras de *Branta canadensis* en el Delta del Río Copper, Alaska. Nuestro objetivo fue determinar si los atributos de los sitios de nidificación relacionados a la supervivencia de los nidos y de las hembras eran diferentes, y si los atributos relacionados con la supervivencia de los nidos cambiaban en un mismo año o entre los años. Los atributos de los sitios de nidificación que examinamos incluyeron tanto las características de la vegetación en y alrededor del sitio del nido, como las asociaciones con otras aves nidificantes. Las características óptimas del sitio del nido difirieron, dependiendo de si era examinada la supervivencia de los nidos o de las hembras. Antes del 25 de mayo, la probabilidad de supervivencia diaria de los nidos ubicados en sitios con pastos largos y en islas fue 2.92 veces y 2.26 veces mayor, respectivamente, que la de los nidos en sitios con arbustos bajos. Las águilas *Haliaeetus leucocephalus* son los depredadores más importantes durante la etapa temprana de la época reproductiva y el comportamiento de estas águilas fue probablemente importante en determinar el patrón observado. Después del 25 de mayo, cuando la depredación por parte de las águilas disminuyó debido a la disponibilidad de otras presas, no se encontraron diferencias en la supervivencia de los nidos ubicados en los diferentes tipos de sitios. Además, la

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supervivencia de los nidos se relacionó positivamente con la densidad de otros individuos de *B. canadensis* presentes en las cercanías del nido. A pesar de que el número de mortalidades detectadas para las hembras fue relativamente bajo, se encontró un patrón bastante claro: la mortalidad de las hembras fue tres veces más probable en sitios dominados por una alta densidad de arbustos dentro de un radio de 50 m del nido, que en sitios dominados por una baja densidad de arbustos. La relación negativa entre la cobertura del nido y la supervivencia de los adultos es consistente con aquella encontrada en otros estudios de aves que nidifican en el suelo. Las barreras físicas que limitan el acceso de depredadores a los nidos y los sitios que permiten la rápida detección de depredadores representaron características importantes para la calidad de los sitios de nidificación para *B. canadensis*. Además la calidad de los sitios de nidificación varió dentro de una misma época reproductiva, probablemente como resultado de las interacciones cambiantes entre los depredadores y sus presas.

## INTRODUCTION

Characteristics of nest sites selected by breeding birds have direct impacts on avian fitness (Martin and Roper 1988, Kaminski and Weller 1992, Götmark et al. 1995). As a result, they are likely to be an important target of natural selection (Clark and Shutler 1999) and may help structure variation in life history strategies among species (Martin 1995). These relationships make the consequences of nest site selection an important focus for the study of avian-habitat relationships (Martin 1993, Morrison 2001). Most previous studies of nest site selection have focused on nest survival. However, survival rates of incubating birds also are likely to be affected by the habitat in which a nest is placed (Götmark et al. 1995). Further, measures of relative fitness for many species are sensitive to small changes in female survival during the breeding season (Schmutz et al. 1997, Hoekman, Mills et al. 2002, Hartke et al. 2006).

In studies in which the consequences of nest site choice have been related to the costs for incubating parents, the focus has usually been on thermal characteristics of the nest (Gloutney and Clark 1997, Shutler et al. 1998, Hoekman et al. 2002, Fast et al. 2007). Few studies have directly examined the relationship between nest site characteristics and predation risk for incubating adults (Wiebe and Martin 1998), despite the potential for nest site characteristics to affect the ability of an incubating adult to escape the nest site when attacked (Götmark et al. 1995). Given that nest site characteristics can have important consequences for the survival of both nests and incubating adults, and that these relationships may differ, there exists a potential for trade-offs to occur (Spencer 2002, Amat and Masero 2004, Forstmeier and Weiss 2004). This

trade-off has been hypothesized as a likely cause for discordance between preferred nest site attributes within populations and the associated fitness value as gauged by individual measures such as nest survival or thermal costs (Götmark et al. 1995, Amat and Masero 2004, Fast et al. 2007). To test this hypothesis there is a need for additional studies that measure the relationship between adult survival and nest site attributes, and to contrast these results with relationships for nest survival.

The relationship between nest site attributes and their fitness consequences may vary within breeding seasons and among years. Predator-prey relationships (Miller et al. 2006) and vegetation relationships (Montgomerie and Weatherhead 1988) can vary within breeding seasons for nesting birds and, as a result, optimizing nest site attributes may depend on the timing of nest initiation within the breeding season. The degree to which this occurs has important implications for understanding habitat relationships in breeding birds. Recent advances in techniques for the estimation of nest survival provide a flexible and robust framework for examining temporal relationships and how these interact with habitat effects (Dinsmore et al. 2002).

We measured attributes of nest sites of Canada Geese (*Branta canadensis*) in the Copper River Delta, Alaska, and examined their relationship to nest survival and to the probability of an incubating female surviving a nesting attempt. Optimal nest sites are those that maximize relative fitness through the combination of the two rates (i.e., lead to the greatest contribution of current and future offspring to subsequent generations; Williams 1966). Predation accounts for the majority of current nest loss and female mortality for Canada Geese in the Copper River Delta

(Bromley and Rothe 2003, Grand et al. 2006). Bald Eagles (*Haliaeetus leucocephalus*) are the primary nest predator, and account for almost three-quarters of annual predation (Anthony et al. 2004). However, predation by Bald Eagles is largely limited to the early part of the breeding season when eulachon (*Thaleichthys pacificus*), a small anadromous fish that is preferred by eagles, are not available (Miller et al. 2006). Thus, predation also has a temporal component, with high predation rates from Bald Eagles early in the nesting season and lower predation rates, attributable to a more diverse set of mammalian predators, during the latter part of the nesting season (Anthony et al. 2006, Grand et al. 2006, Miller et al. 2006). Shifting predator-prey dynamics in concert with vegetation emergence within seasons make it likely that optimal nest site attributes change within a single breeding season.

Vegetation adjacent to a nest site can play an important role in determining predation rates of nesting birds. Vegetation may act as a barrier that can obstruct nests, nesting birds, and predators both visually and physically (Martin 1993). Vegetation at the nest site may also interact with defensive behavior of nesting birds and as a result affect predation rates (Montgomerie and Weatherhead 1988). For waterfowl, high quality nest sites have been hypothesized to be associated with high vegetation density (Baldassarre and Bolen 1994), especially when predation is predominantly from aerial predators that depend on visual cues to detect nests (Clark and Nudds 1991). Alternatively, dense vegetation may reduce the ability of nesting birds to identify an approaching predator and thus lower their ability to avoid detection and capture of the nest or the female (Götmark et al. 1995), or hinder the female's escape from the nest. Further, the role that vegetation plays as a visual or physical barrier will depend on the phenology of leaf-out and on changes in the composition of the predator community, both of which shift within breeding seasons in the Copper River Delta (Grand et al. 2006, Miller et al. 2006).

Other nest site attributes may also be important for this goose population. Bald Eagles spend much of their time perching (Stalmaster and Gessaman 1984) and often detect prey from perch sites (Beuhler 2000). The availability of perch sites may affect habitat use

by eagles and thereby affect encounter rates of eagles with nests. Associations with other nesting birds may also affect predator-prey relationships. Higher densities of Canada Goose nests may result in increased survival rates by enhancing early detection of predators by geese or by diluting predation (Massoni and Reboreda 2001). Alternatively, nest predators may prefer to feed in areas with high nest density, thus increasing the encounter rate of predators with nests in these areas (Niemuth and Boyce 1995). Finally, nesting in association with other species of birds that aggressively defend nest sites from predators may affect predation (Väänänen 2000). Both Mew Gulls (*Larus canus*) and Arctic Terns (*Sterna paradisaea*) actively and aggressively defend their nesting colonies.

In this study, we did not examine the preference of Canada Geese for different attributes when selecting nest sites, but instead addressed the outcome of variation in attributes of nest sites selected by Canada Geese. We examined the relationship of nest and female survival to vegetation at immediate nest sites, vegetation surrounding nest sites, and associations with nests of other geese and aggressive nest-defending birds. In the process we examined two questions of specific interest: Do nest site attributes that are beneficial to nest survival differ from those that benefit female survival? Do optimal nest site attributes differ within and among nesting seasons as they relate to nest survival? We predicted that female survival would be more dependent than nest survival on nest site attributes that promote early detection of predators (i.e., nests associated with high densities of Canada Goose, Mew Gull, and Arctic Tern nests, and low density of vegetation surrounding the nest site) and easy escape from the nest site (i.e., low density of cover at the immediate nest site). In addition, we predicted that nest survival should be higher for nests with dense overhead cover early in the breeding season when Bald Eagles dominate predation, and higher on island sites late in the season when predation by a diverse suite of mammalian predators accounts for the majority of predation.

## METHODS

### STUDY AREA AND DATA COLLECTION

We conducted our study in a 13 km<sup>2</sup> area of the western Copper River Delta, Alaska, from 1997

to 2002. The area was characterized by high densities of small wetlands and tidal sloughs dammed by beavers (*Castor canadensis*) and high Canada Goose nesting densities relative to other parts of the Copper River Delta (Grand et al. 2006). Since an earthquake in 1964 uplifted the Copper River Delta, this portion has been invaded by woody vegetation consisting primarily of shrubs, including alder (*Alnus crispa*), sweetgale (*Myrica gale*), and willow (*Salix* spp.), with scattered trees including Sitka spruce (*Picea sitchensis*) and black cottonwood (*Populus trichocarpa*). A more complete description of the vegetation of the Copper River Delta is provided by Boggs (2000). The occurrence of Canada Goose nests throughout the range of vegetation types and across a broad range of local nest densities allowed for examination of habitat relationships across a wide range of potential nest site attributes.

Nests were located by systematic searches of the study area. We revisited nests once every ten days and considered a nest successful if we found one or more hatched egg membranes in the nest bowl. We considered females to have been depredated while incubating the nest if we found whole carcasses, bones, large numbers of contour feathers, or flight feathers in association with an abandoned or depredated nest. Our method served as an index to female mortality rate because we could not detect females depredated during incubation breaks away from nests and deaths may also have occurred at the nest site without leaving any evidence. We eliminated island nests from the analysis of female survival because most islands were  $\leq 1.5$  m wide; thus, females killed on islands were more likely to go undetected because carcass remains could float away or be carried to onshore sites. In addition, some proportion of carcasses found at nests were males that likely died while helping to defend nest sites. However, based on molecular sex determination of a subset of remains (Griffiths et al. 1998), we believe this proportion was small (eight of nine carcasses for which remains could successfully be identified were identified as females; TFF, unpubl. data). We also found neck collars or leg bands associated with carcasses at three nests, which in all cases came from female birds. Thus, of 12 mortalities of known sex in this study, 11 were females and only one was a male.

We mapped vegetation using a vector-based GIS coverage developed from aerial photography and ground-truthing (Miller 2004). We classified vegetation based on the density (i.e., percent canopy cover) and structure (i.e., height) of shrubs, which in combination described the potential for vegetation to visually and physically obstruct a nest site. Other ground cover was primarily composed of sedges, grasses, and herbaceous species that provided little cover. We classified shrub density into low, medium, and high canopy closure (0%–20%, 21%–60%, and 61%–100%, respectively) and shrub structure by short and tall types (<2 m and  $\geq 2$  m, respectively). The short shrub category was dominated by sweetgale and low willow species, which were characterized by high stem densities and provided relatively dense horizontal cover but little overhead cover. The tall shrub category included alder and tall willow species, which had low stem density and a dense, closed canopy of woody vegetation and thus provided dense vertical overhead cover with little horizontal obstruction. We treated islands as a separate cover type irrespective of shrub density and height due to their small area and insular nature, which made them unique. We determined the vegetation category for each nest site location and calculated the percentage of low-density shrub cover (an index of how open a site was) and length of the perimeter of tall shrub cover (an index to eagle perch site availability) within 50 m, 200 m, and 350 m of nest sites.

We estimated nest density each year using a two-dimensional kernel density estimator (Silverman 1986). Kernel density estimators are commonly used to generate smoothed probability estimates across two-dimensional surfaces (e.g., home range estimates; Seaman and Powell 1996). Estimates were generated by placing a bivariate normal kernel at each nest location and then combining all kernels to make a single surface that served as an estimate of a nest site occurring at any point within the two-dimensional space of our study area. This method weighted the contribution of other Canada Goose nests as an inverse function of the distance from the nest site of interest and therefore our measure of density was most affected by nearby nest sites. We corrected estimates for edge effects by weighting estimates

by the proportion of total kernel volume that occurred within our study area (Miller 2004). We scaled probability estimates for all years by a factor of 435, the mean number of nests found per year, to convert the measure from the probability of a single nest occurring at a point to the observed density of nests at a location, which we measured as nests  $\text{km}^{-2}$ .

We calculated distance from each nest to the nearest Mew Gull or Arctic Tern nesting colony. We assumed that the influence of these aggressive nest-defending species would decline with distance until the maximum distance at which nests were defended was reached. Based on this assumption and our observations of these species we imposed an a priori threshold on the effect of gulls and terns by assigning a maximum value of 500 m for nests that occurred  $\geq 500$  m from a colony. We used only colonies with  $\geq 10$  pairs because these colonies were readily detectable during nest searches, consistent in location among years, and, due to the large number of birds, were the most likely to have an effect on predators.

#### MODEL DEVELOPMENT AND SELECTION

*Survival estimators.* We estimated daily survival rate (DSR) of nests using the maximum likelihood estimator of nest survival described by Dinsmore et al. (2002) and fit models to our data using MATLAB release 12.1 (Mathworks, Inc., Natick, Massachusetts). Effects of covariates were estimated using a general linear model with a logit-link function. The maximum likelihood estimator allows for the estimation of temporal effects as well as the effect of continuous and discrete covariates.

We estimated the probability of a female surviving a nesting attempt (i.e., the probability of not finding signs of Canada Goose mortality at a nest site) using logistic regression models. This was done using the known fate model in Program MARK (White et al. 2001), with one interval representing a single nesting attempt. Again, covariates were included using general linear models with a logit-link function. We included all nests that we found when estimating female survival. This included active nests found during egg-laying and incubation as well as nests that had already been depredated when found. We assumed that if a female was depredated when incubating the nest, evidence of the predation event would be left at or near

the nest site and the probability of detecting the mortality would be unbiased among nest site types used in analyses. Thus, the estimate of survival likely reflects a minimum mortality rate of incubating females. In addition, the method excludes mortality away from nest sites, for example during incubation breaks. However, because mortality during breaks was not associated with the nest site it was not relevant to determining the relationship between nest site attributes and female survival.

*Temporal effects.* Patterns in temporal variation may be important for determining the relationship of nest site attributes to survival rates. We addressed temporal variation in both survival rates and in the relationship of nest site attributes to survival. The degree to which we were able to address temporal components differed when estimating nest survival versus female survival due to differences in the way data was collected and in the frequency of predation events.

Temporal patterns in nest survival for this population were previously examined by Grand et al. (2006) and the strength of evidence for different models of temporal variation was not examined again here. However, temporal variation in nest survival could potentially confound the estimation of nest site effects if the proportion of geese using nests with certain attributes varies across time. To avoid a potentially spurious correlation with seasonal changes in nest site preference we included temporal variation in models of DSR based on the best model of temporal variation from Grand et al. (2006). The model included categorical effects of nest age (differences among five seven-day intervals within the nesting period), year, and calendar date (differences among six 10-day intervals within each year). Because of the inclusion of temporal variation, all estimated effects are relative to the average DSR for nests in the same year, on similar dates, and at similar ages.

In cases in which we examined whether habitat effects differed within seasons, we divided the nesting season into an early and late period corresponding to the period prior to 25 May and after 25 May, respectively. This date generally corresponds with a shift from intense predation primarily by Bald Eagles to predation by a diverse suite of mammalian predators (Anthony et al. 2004, Miller et al.

2006). This date also generally corresponds to the timing of vegetation leafing out and therefore to a greater contribution of vegetation to visual obstruction (Miller 2004). Finally, we examined whether the effect of nest site attributes differed among years.

*Nest site attributes.* We selected a similar set of candidate models for analysis of nest and female survival because they could be affected by similar mechanisms and this allowed us to contrast the results for the two vital rates. We ranked candidate models for both nest survival and female survival using Akaike's information criterion (AIC; Anderson et al. 2000). We made inferences regarding the strength of evidence for individual parameters based on whether model-averaged 95% confidence intervals included the value for no effect. We calculated parameter estimates and unconditional standard errors from model averaging based on the subset of models including that parameter.

We included six covariates that fell within three broader categories in our analysis. For vegetation at the immediate nest site, we included shrub height and density. For vegetation surrounding the nest site, we included the percentage of low-density shrub and length of tall shrub perimeter within fixed radii (50 m, 200 m, or 350 m). Finally, for associations with other nesting birds we included the density of Canada Goose nests and the proximity to colonies of aggressive species (Mew Gulls and Arctic Terns).

We conducted model selection for nest survival models using a hierarchical process. First, a set of models was developed for each individual category of nest site attributes. In addition to constant effects across time, we explored models in which vegetation effects differed between the early and late portions of the nesting season. Covariates in best models for each individual category were then combined to create a global model for nest survival and this model was compared to simpler models in which covariates from different categories were systematically left out. Finally, for parameters remaining in the best global model we examined whether there was support for annual variation in the effect size by comparing a model in which the effect was held constant across years to one in which the effect differed among years. This hierarchical approach allowed us to compare the importance of different categories of nest site attributes by examining the fit of

models from individual categories while also examining parameter estimates for effects when all levels were accounted for.

A simpler set of candidate models was examined for the analysis of female survival because we were unable to examine temporal effects for nest site attributes and we restricted models to no more than two covariates to prevent overfitting. This constraint was based on the relatively small number of mortalities and guidelines given by Hosmer and Lemeshow (2000). We compared models with all one and two covariate combinations of the six potential covariates in a single step.

Inference from the logit-link function for the covariates of female and nest survival is estimated by the change in odds of survival per unit change in the covariate (odds ratio; Hosmer and Lemeshow 2000), therefore we present estimates as odds ratios. To place continuous covariates on a similar and comparable scale we present odds ratios relative to a one standard deviation change in the covariate. Effect sizes for categorical variables are presented as the odds ratio between categories. We calculated standard errors and confidence intervals from variance-covariance matrices estimated using Program MARK (White et al. 2001). Nest success (i.e., the probability a nest survives the whole period from initiation to hatching) was calculated as the product of daily survival rates for a 35-day nesting period. For reference, nest success rates were calculated for nests initiated on 26 April and 12 May. For years with average phenology, these dates represent the first week of nest initiation and the completion of initial nest initiation (i.e., before the start of renesting), respectively (Fondell et al. 2006).

## RESULTS

### NEST SURVIVAL

We analyzed the survival of 1599 nests that were active when found. The best model included the effect of shrub structure early in the season, Canada Goose nest density, distance to a Mew Gull or Arctic Tern colony, and the proportion of low-density shrub habitat within 50 m of the nest site (Table 1).

There was strong evidence for higher nest survival at tall-shrub and island nest sites compared to short-shrub sites early in the

TABLE 1. Comparison of top-ranked models examining the relationship of habitat variation to daily survival rate of Canada Goose nests ( $n = 1599$ ) found on the Copper River Delta, Alaska, 1997–2002. All models in analysis include effects for nest age, year, and calendar date based on the analysis of Grand et al. (2006;  $K = 40$  for temporal effects alone). Covariates for vegetation at nest sites, vegetation surrounding nest sites, nest density of geese, and distance to colonies of nest-defending species were examined separately. Best models for each subcategory were then used to build a global model for nest survival. Models were ranked by the difference in second-order Akaike’s information criterion ( $\Delta AIC_c$ ). Models with  $\Delta AIC_c < 5$  are shown.

Model <sup>a</sup>	Deviance	$K^b$	$\Delta AIC_c^c$	Akaike weight
Nest site vegetation				
H <sub>early</sub>	2359.2	42	0.0	0.66
H <sub>early</sub> + D <sub>early</sub>	2357.4	44	2.2	0.20
H <sub>early</sub> + H <sub>late</sub>	2358.7	44	3.5	0.10
Vegetation surrounding nest site				
PLD_50	2365.1	41	0.0	0.49
T_350 <sub>early</sub>	2366.4	41	1.3	0.25
PLD_50 + T_350 <sub>early</sub>	2364.6	42	1.5	0.22
Nesting density				
ND + COL <sub>DIST</sub>	2345.3	42	0.0	0.71
ND	2349.2	41	1.1	0.29
Global				
ND + COL <sub>DIST</sub> + H <sub>early</sub> + PLD_50	2322.7	45	0.0	0.62
ND + COL <sub>DIST</sub> + H <sub>early</sub>	2325.8	44	1.1	0.38

<sup>a</sup> Model structure given is in addition to parameters related to age, calendar date, and year in which the nest was exposed. H = structure of shrub vegetation at nest site (tall shrub, short shrub, or island), D = density of shrub vegetation at nest site (low-density, medium-density, high-density, or island), PLD\_50 = percentage of low-density shrub vegetation within 50 m of the nest, T\_350 = length of tall shrub perimeter within 350 m of nest, ND = Canada Goose nest density, COL<sub>DIST</sub> = distance to nearest Mew Gull or Arctic Tern colony, early = prior to 25 May, late = after 25 May.  
<sup>b</sup>  $K$  = number of estimated parameters.  
<sup>c</sup>  $AIC_c$  values for best models were as follows: H<sub>early</sub> = 2443.2, PLD\_50 = 2447.1, ND + COL<sub>DIST</sub> = 2429.3, global model 2412.7.  $AIC_c$  value for null model with only temporal effects was 2457.8.

nesting season, with an odds ratio for DSR of 2.92 (95% CI: 1.46–5.83) for tall-shrub to short-shrub and 2.26 (1.37–3.72) for island to short-shrub sites. The odds ratio was 1.29 for tall-shrub to island sites during this period, but the 95% CI included one (0.56–2.98). Nest survival increased with nest density with an odds ratio of 1.23 (1.10–1.38) for each one standard deviation increase in nest density ( $\bar{x} = 46.0$  nests km<sup>-2</sup>, SD = 15.9, range = 6.2–87.4). The strength of evidence for other covariates included in the best model was weaker based on the inclusion of an odds ratio of one within the 95% CI (0.93 [0.83–1.05] and 1.09 [0.99–1.21] for distance to a Mew Gull or Arctic Tern colony and the proportion of low-density shrub habitat within 50 m, respectively). Effects remained consistent among years when annual variation was included in models. Nest density was positively related to nest survival in all years. In five of six years, nests in short-shrub sites had the lowest nest survival among structure types and the percentage of low-

density shrubs within 50 m of the nest site was positively related to nest survival. The effect of distance to a Mew Gull or Arctic Tern colony was the least consistent, with a negative relationship in three out of six years. For all covariates, however, the models including differences in main effects of nest site attributes among years had a  $\Delta AIC_c > 5$ , lending little support for annual variation in habitat effects.

We estimated nest success rates for nests initiated early and in the middle of the nesting season in different nest sites and at varying nesting densities (Fig. 1). Nests in tall-shrub sites and on islands had nest success rates 1.5–2.0 times higher than nests in short-shrub sites when initiated early in the season. Across nest site types, nest success averaged about 20% higher in areas with a nest density of 65 nests km<sup>-2</sup> than in areas with 25 nests km<sup>-2</sup>.

FEMALE SURVIVAL

We used nests that were active and depredated when found in our analyses of female survival

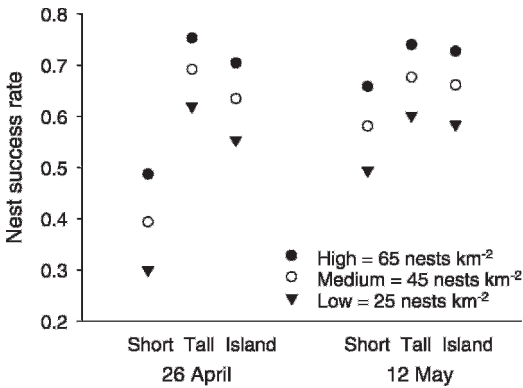


FIGURE 1. Predicted nest success rates for Canada Geese in the Copper River Delta, Alaska, in 1997–2002, increased with increasing nest density. Across nest sites, nest success was higher for nests in tall shrubs and on islands than for nests in short shrubs early in the nesting season, while success rates were similar across sites later in the season. Nest success rates were calculated based on average daily survival rates for all years for nests initiated on 26 April and 12 May for sites in tall shrubs, short shrubs, and on islands at three nest densities. These dates were chosen to demonstrate predicted patterns for early and intermediate nest initiation dates within a nesting season.

( $n = 2414$ ); Canada Goose carcasses were associated with 41 of those that failed. The top model included only the percentage of low-density shrub within 50 m of the nest site (Table 2). However, there was considerable model selection uncertainty and three other models had  $\Delta AIC_c$  values  $< 2$ , so we examined the strength of evidence for each of the parameters further. Parameter weights (sum of the Akaike weights for models including a parameter) were 0.62, 0.30, and 0.17 for the percentage of low-density shrub, nest density, and distance to a colony of Mew Gulls or Arctic Terns, respectively. After model averaging, the percentage of low-density shrub within a 50 m radius ( $\bar{x} = 42\%$ ,  $SD = 31\%$ ) was the only parameter with a 95% confidence interval for the odds ratio that did not include one (1.46 [1.05–2.07]). Therefore, we limited further inference to the effect of low-density shrub within 50 m of the nest site for female survival. The apparent probability that a female survived a nesting attempt in a year with median annual survival decreased from 0.992 to 0.975 as the percentage of low-density shrub decreased from 100% to 0%. This is equivalent to a greater than

three-fold increase in mortality during a nesting attempt in an area with continuous high-density shrub cover within 50 m of the nest site compared to an area with no high-density shrub cover.

## DISCUSSION

Understanding how nest site selection affects the fitness of breeding birds depends on knowledge of the relationship between nest site characteristics and both reproduction and adult survival (Götmark et al. 1995). Given the important role of predation in nesting systems (Martin 1993), it is important to understand how predation rates of both nests and adults relate to nest site attributes. Mortality during breeding is often a significant proportion of overall mortality for birds (Schmutz et al. 1997, Hoekman, Mills et al. 2002, Hartke et al. 2006) and mortality can be related to nest site characteristics (Wiebe and Martin 1998, Amat and Masero 2004). Surprisingly, few studies have attempted to measure these relationships for incubating adults (Wiebe and Martin 1998, Amat and Masero 2004). This stands in direct contrast to the many studies that have hypothesized the importance of adult survival in explaining patterns of nest site selection (Montgomerie and Weatherhead 1988, Götmark et al. 1995, Amat and Masero 2004, Fast et al. 2007).

We suspect that the scarcity of attention that has been given to measuring patterns in adult survival has been driven largely by the difficulties in measuring this parameter. Two major limitations that are likely to be encountered in many studies including our own are the relative infrequency of adult mortality in comparison to nest mortality and the difficulty of tracking mobile adults versus immobile nests. Although measures of individual fitness for most avian species are much more sensitive to small changes in adult survival than in nest survival, the relative rarity of adult mortality makes it difficult to detect relationships to nest site characteristics. Even with large sample sizes our power to detect patterns was likely limited. This was illustrated by the much greater standardized effect size and much lower precision of the estimated effect of the percentage of low-density shrub on adult survival than the effect of nest density on nest survival. Likewise, because we were unable to determine the rate at which we detected mortality events, our mea-



TABLE 2. Comparison of top-ranked models examining the relationship of habitat variation to survival rate of incubating Canada Goose females ( $n = 2414$ ) associated with nests found on the Copper River Delta, Alaska, 1997–2002. Year is incorporated into all models as a random effect. Models were ranked by the difference in second-order Akaike's information criterion ( $\Delta AIC_c$ ). Models with  $\Delta AIC_c < 5$  are shown.

Model <sup>a</sup>	Deviance	$K^b$	$\Delta AIC_c^c$	Akaike weight
PLD_50	393.3	2	0.0	0.26
PLD_50 + ND	394.1	3	0.8	0.17
PLD_50 + H	395.1	3	1.8	0.10
PLD_50 + COL <sub>DIST</sub>	395.1	3	1.9	0.10
ND	395.4	2	2.1	0.09
Constant	396.5	1	3.2	0.05

<sup>a</sup> PLD\_50 = percentage of low-density shrub vegetation within 50 m of nest site, ND = Canada Goose nest density, H = height of shrub vegetation at nest site, COL<sub>DIST</sub> = distance to nearest Mew Gull or Arctic Tern colony, Constant = intercept only.

<sup>b</sup>  $K$  = number of estimated parameters.

<sup>c</sup>  $AIC_c$  value for best model was 393.27.

sure of adult survival is an index to true survival. Despite the limitations in our measure of female survival, we believe our results are an important contribution toward understanding the processes affecting nest site selection.

#### EFFECTS OF VEGETATION

Our results did not support any direct trade-offs between nest survival and female survival. This stands in contrast to the results of Wiebe and Martin (1998), who found that nest concealment as measured by the proportion of lateral cover was positively associated with nest survival but negatively associated with the survival of incubating females for White-tailed Ptarmigan (*Lagopus leucurus*). However, our results did indicate that vegetation characteristics related to predation of nests and adults differed and that different mechanisms in the predation process affected the two rates. Nest survival was highest at sites where vegetation created physical barriers to predation, whereas female survival was highest in sites with vegetation that allowed early detection of and easy escape from predators.

Nests in tall shrub habitats are protected by a dense overhead canopy of woody vegetation that is most likely to affect large avian predators that must detect and capture prey from above. Unlike most other populations of Canada Geese, closely related Vancouver Canada Geese (*B. c. fulva*), which breed along the coast of southern Alaska in the presence of dense Bald Eagle populations, place their nests almost exclusively in forested habitat (Lebeda and Ratti 1983). Escape from predation by Bald

Eagles may have had an important role in shaping this nest site preference. The nesting strategy of using tall shrub types may become increasingly important for the Copper River Delta Canada Goose population now that tall shrubs occur in significant numbers across their entire nesting area and the eagle population continues to increase (Bowman et al. 1997).

Our finding that open habitat beyond the nest site was positively associated with female survival was consistent with our hypothesis that female survival would be more dependent than nest survival on early detection of predators. Open habitat beyond the immediate nest site likely reduces barriers that conceal predators, increasing early predator detection by nesting females and paired males located near the nest site. An association of greater nest concealment with higher adult mortality was also found for White-tailed Ptarmigan (Wiebe and Martin 1998) and Kentish Plovers (*Charadrius alexandrinus*; Amat and Masero 2004), both of which are also ground-nesting birds.

#### EFFECTS OF OTHER NEST SITE ATTRIBUTES

Nest survival was higher for nests on islands and in areas with high densities of other nesting Canada Geese, both site types that may increase the ability of geese to detect predators early and better defend the nest site. Islands occur in open areas by virtue of being surrounded by water, while high nest densities lead to a greater number of male geese in the area that actively warn of the approach of predators by vocalizing and displaying. However, other mechanisms may also explain these patterns, such as water

acting as a barrier to predation (Albrecht et al. 2006) and high nest densities diluting the effect of predators (Massoni and Reboresda 2001).

#### TEMPORAL VARIATION IN EFFECTS

While the relationship between nest site attributes and nest survival remained consistent among years, we found that relationships changed within seasons in response to predictable patterns of within-season phenology. Our results are more consistent with changes in the predator community leading to within-season changes in habitat relationships than changes in vegetation structure, due to the timing of these changes. This is consistent with other studies that have shown differences in optimal nest site attributes that depend on the predator responsible for taking nests (Clark and Nudds 1991, Liebezeit and George 2002, Albrecht et al. 2006). Higher nest survival early in the year in tall shrubs likely resulted from the physical barrier to Bald Eagle predation caused by the dense overhead canopy of branches. Island sites are relatively small and have sparse vegetation, therefore changes in vegetation were minimal within seasons and do not explain why island sites did better than short shrub sites early but not late in the nesting season. Higher nest survival at island sites compared to short shrub nest sites during the early part of the season may have resulted from avoidance of islands by eagles or a better ability of geese to defend nests on islands because of their open nature. Higher nest survival on islands early in the season is less easily attributable to predator changes than higher survival in tall shrub sites, however, given that island sites are generally thought to be a deterrent to mammalian predation (Albrecht et al. 2006).

#### RELATIVE IMPORTANCE OF NEST AND FEMALE SURVIVAL

Measurements of the sensitivity of a measure of individual fitness such as  $\lambda$  to changes in each vital rate would be necessary to definitively determine the actual effect of the observed habitat relationships for both nest and female survival on individual fitness (Caswell 2001). However, based on demographic information from the population we can make some inference as to the magnitude of the effects of each. Although the proportion of nests at which a dead adult was detected was relatively small,

this source of mortality is still likely to be an important selective force on the population. Canada Geese in the Copper River Delta average 1.5 nest attempts annually (Fondell et al. 2006), and, even if we detected all mortality associated with nests, this would mean at least 10% of all annual mortality occurs through predation at the nest site. Because Canada Geese are long-lived, generally delay breeding until 2–4 years of age, and annual reproductive output is relatively low (Mowbray et al. 2002, Bromley and Rothe 2003, Fondell et al. 2006, Grand et al. 2006), relative changes in adult survival are likely to have a much greater impact on fitness than similar relative changes in nest survival. This was demonstrated by Schmutz et al. (1997) for Emperor Geese (*Chen canagica*), which have similar vital rates to Canada Geese. They found that a 1% relative increase in adult survival would lead to a 0.9% increase in  $\lambda$  while a 1% relative increase in nest success would lead to only a 0.1% increase in  $\lambda$  (i.e., a nine-fold difference).

The high degree of correlation between the proportion of low-density shrub habitat and the probability of a mortality event demonstrates that strong relationships can emerge between nest site characteristics and survival of incubating adults, which in turn can help shape patterns in nest site selection. Our results support the hypothesis of Götmark et al. (1995) that adult survival is more likely than nest survival to be negatively affected by concealment and parallels patterns found when the relationship of nest site attributes to adult survival has been examined in other species (Wiebe and Martin 1998, Amat and Masero 2004).

There is a need for more studies to examine the role of adult survival in shaping nest site preferences in birds. Relationships are likely to vary among taxa and to be influenced by a number of factors including body size and cryptic plumage of the incubating adults, behavior of adults in defending nests (Montgomerie and Weatherhead 1988, Albrecht and Klvaňa 2004, Remeš 2005), and life history characteristics of the birds, which may shape trade-offs between current and future reproduction as affected by adult survival (Partridge and Harvey 1988, Ghalambor and Martin 2001). Understanding these relationships will help to shed light on the causes of discordance

between nest site preferences and patterns in nest survival observed in many bird populations (Götmark et al. 1995)

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