NEST SURVIVAL PATTERNS IN WILLOW PTARMIGAN: INFLUENCE OF TIME, NESTING STAGE, AND FEMALE CHARACTERISTICS

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Abstract. Nest predation is the most important factor limiting reproductive success of Willow Ptarmigan (*Lagopus lagopus*), as it is for many bird species. Using program MARK, we examined patterns of daily nest survival in two widely separated populations of Willow Ptarmigan in Manitoba and British Columbia, Canada, by examining variation among years, over the course of the breeding season or in relation to the age of the nest, or age and condition of the female. At La Pérouse Bay, Manitoba, daily nest survival increased linearly throughout the season, with moderate annual variation. Nests also had higher daily survival during laying and late in incubation, and lower survival early in incubation. At Chilkat Pass, British Columbia, daily nest survival varied strongly by year and nests had higher survival early and late in the season, but survival was not affected by the age of the nest. At both sites, but especially at Chilkat Pass, periods of lower nest survival tended to coincide with peak breeding periods, suggesting predators may adjust their search effort based on the likelihood of locating nests. Neither female age nor condition were included in the best models. Thus, in both ptarmigan populations, nest survival patterns appeared to be influenced more by ecological factors than by individual characteristics of breeding females. The extent of annual variation and seasonal patterns may have differed between sites due to the different predator and alternative prey communities.

Key words: alternative prey, information-theoretic approach, Lagopus lagopus*, nest survival, predator activity, program MARK, Willow Ptarmigan.*

Patrones de Supervivencia de los Nidos de *Lagopus lagopus*: Influencia del Tiempo, de la Etapa en el Ciclo de Nidificación y de las Características de las Hembras

Resumen. Como en muchas especies de aves, la depredación de los nidos es el factor más importante que limita el éxito reproductivo de *Lagopus lagopus*. Utilizando el programa MARK, examinamos los patrones diarios de supervivencia de los nidos en dos poblaciones distantes de esta especie ubicadas en Manitoba y British Columbia, Canadá. Examinamos la variación en la supervivencia entre años, durante el transcurso de la época reproductiva y en relación con la edad del nido y con la edad y la condición de la hembra. En La Pérouse Bay, Manitoba, la supervivencia diaria de los nidos incrementó linealmente a lo largo de la estación, con pequeñas variaciones anuales. Los nidos presentaron una mayor supervivencia diaria durante la postura y a fines de la incubación, y menor supervivencia al inicio de la incubación. En Chilkat Pass, British Columbia, la supervivencia diaria de los nidos varió entre años y los nidos presentaron una mayor supervivencia en la parte inicial y final del período de incubación, pero la supervivencia no fue afectada por la edad del nido. En ambos sitios, especialmente en Chilkat Pass, los períodos de menor supervivencia tendieron a coincidir con el pico de la época reproductiva, lo que sugiere que los depredadores podrían ajustar su esfuerzo de búsqueda con base en la probabilidad de encontrar nidos. Los mejores modelos no incluyeron la edad de las hembras ni su condición. Por lo tanto, en ambas poblaciones, los patrones de supervivencia de los nidos parecieron estar más influenciados por factores ecológicos que por características particulares de las hembras reproductivas. El grado de variación anual y los patrones estacionales podrían haber diferido entre sitios como resultado de las diferencias en las comunidades de depredadores y presas alternativas.

INTRODUCTION

Nest predation is the most influential factor affecting reproductive success of many birds (Martin 1993), but the factors driving patterns of nest predation are not well known. Within species, nest survival varies annually and geographically in relation to the abundance and richness of predator communities (Kurki et al. 1997, Wilson and Arcese 2006), variation in weather (Morrison and Bolger 2002), and habitat structure at local, patch, and landscape scales (Stephens et al. 2005, Tewksbury et al. 2006). Nest survival often varies over the breeding season within a particular site. For example, nest survival might increase in a linear fashion over the season coincident with increases in vegetation cover for nest concealment (Sullivan and Dinsmore 1990, Wiebe and Martin 1998a). Nest survival might also increase linearly if there is a greater abundance of alternative prey late in the season (Bêty et al. 2002). Alternatively, nest survival rates may be high early in the season but decrease over time if predators develop a search image for nests (Nams 1997) or increase their hunting efforts due to elevated nutritional demands for reproduction. Nonlinear patterns might also occur. If predator saturation occurs when nests are most numerous midseason (Niemuth and Boyce 1995), nest survival might be highest in the middle of the breeding period. In contrast, nest survival might be lowest midseason if predators focus their hunting efforts during periods of peak breeding density.

Risk of nest detection by predators may be reduced by selecting sites with high concealment (Schieck and Hannon 1993) or by reducing movement to and from the nest during incubation (Martin et al. 2000). Females may vary in their ability to adopt these behaviors. Older or more experienced females may select more concealed nest sites or exhibit less conspicuous incubation behavior (Sæther 1990). Alternatively, older females may select nest sites with reduced cover to increase their ability to detect approaching predators (Wiebe and Martin 1998a). Females in better condition might have higher nest survival rates if they have greater incubation constancy (Erikstad 1986, Wiebe and Martin 2000). Nest survival may also vary with nest age if changes in female behavior influence nest detection by predators

(Martin et al. 2000). Many species spend less time at the nest during laying than incubation, which could lead to higher survival during the laying period if predators use female activity as a cue to locate nests.

Most earlier studies of nest survival used the Mayfield (1961) or similar methods (Klett and Johnson 1982). While these techniques have been very useful, testing how nest survival varies over time or as a function of covariates requires breaking the data into discrete groups; thus, large sample sizes are required to consider the influence of several factors simultaneously. Recently developed analytical techniques allow for the construction of models that incorporate continuous temporal variation within a season or nesting period, and allow inclusion of covariates such as age, size, body condition, or weather (Aebischer 1999, Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004). In this study, we used the nest survival model in program MARK (White and Burnham 1999, Dinsmore et al. 2002) to investigate patterns of nest survival in two populations of Willow Ptarmigan (*Lagopus lagopus*) in northern Canada.

The Willow Ptarmigan is a monogamous, precocial, ground-nesting grouse that inhabits arctic, subarctic, and subalpine tundra. Ptarmigan produce a single brood per season, but if the initial nest fails, females may make one to three renesting attempts, depending on the age of the female and the date and stage of loss of the first nest (Martin et al. 1989, Hannon et al. 1998). Nest predation is the greatest single factor influencing Willow Ptarmigan fecundity (Martin et al. 1989, Sandercock et al. 2005). Willow Ptarmigan populations across North America are experiencing dramatic habitat change and environmental variation driven by global climate change and other processes (Hassol 2004). An understanding of patterns of nest survival will allow us to evaluate the ability of this species to adjust to changes in nest survival that may result from ecological or environmental variation. Thus, using data from our long-term observational studies, we investigated: 1) temporal patterns in nest survival among years and over the breeding season; 2) temporal variation in nest survival related to nest age; and 3) whether nest survival was related to age or condition of females. We did not explicitly test hypotheses about the mechan-

isms driving the patterns we observed, since our long-term studies were not developed with that in mind. Rather, using newly developed analytical techniques, we hoped to address the above questions about patterns of nest survival and discuss possible ecological and behavioral correlates with the view of developing testable hypotheses for future studies.

METHODS

STUDY SITES AND FIELD METHODS

Data were collected for two populations of Willow Ptarmigan in northern Canada, separated by 2500 km: La Pérouse Bay, 40 km east of Churchill, Manitoba (58°24′N, 94°24′W) during 1981–1984, and Chilkat Pass in northwestern British Columbia (59°50′N, 136°30′W) during 1985–1988. La Pérouse Bay encompassed 10 km² of subarctic tundra, whereas Chilkat Pass included 4.5 km² of subalpine tundra (Hannon et al. 1988). Nest predators at La Pérouse Bay were predominantly avian (Herring Gulls [*Larus argentatus*] and Parasitic Jaegers [*Stercorarius parasiticus*]), but also included red foxes (*Vulpes vulpes*) and ermines (*Mustela erminea*; Hannon et al. 1988). At Chilkat Pass, red foxes were the primary nest predators (O'Reilly and Hannon 1989). Ptarmigan densities were 7–9 females per km² at La Pérouse Bay and 20–23 females per km² at Chilkat Pass during the study periods (Martin et al. 1989).

At both sites, field methods were similar and work was conducted during late April to early August. More than 90% of birds were captured and color-marked before they began incubation. We classified ptarmigan as yearlings (hatched the previous season) or adults (two or more years of age) based on pigmentation of the 8th and 9th primaries (Bergerud et al. 1963). To determine body condition, we used the residuals of a regression of mass on wing length, with days before the first egg was laid as a covariate at each site (Robb et al. 1992, Hannon et al. 1998).

Ptarmigan females spend only 30–60 min at the nest per day during egg-laying and completely cover the nest with vegetation when they leave. During incubation they spend about 95% of the day on the nest with 3–6 brief recesses (Hannon et al. 1998). We located nests by systematically searching around roosts of males

and using pointing dogs at La Pérouse Bay, and by following radio-marked females at Chilkat Pass. Prior to the onset of breeding at La Pérouse Bay, we randomly selected 40–45 territories (from a potential 75–90 territories) where we monitored females and searched intensively to locate nests during laying or early incubation. Thus, despite different nest finding methods at the two sites, the nests observed were a random subset of all nesting attempts. In both populations, females laid one egg daily and the 22-day incubation period began with laying of the penultimate egg (Hannon et al. 1988). Given different clutch sizes, the duration of a successful first clutch averaged 32 days at La Pérouse Bay (average of 10.8 eggs) and 29 days at Chilkat Pass (average of 8.2 eggs; Sandercock et al. 2005). Most nests were visited 2–4 times per week until hatching or clutch failure (range: 2–20 visits). Eggs from first nests hatched in late June or early July, whereas those from renests hatched from mid-July through early August. Nest survival at both sites was unrelated to investigator disturbance (Hannon et al. 1993). Predation was the principle cause of nest failure in our populations (>90%; SW et al., unpubl. data) and for this analysis we excluded nests that failed due to desertion (eggs in nest cold, no sign of female near the nest on two or more consecutive visits).

From La Pérouse Bay, we used a total of 189 nests from 1981 to 1984 in the analysis, 46% produced by yearlings and 54% by adults. Nests were on average 12.3 ± 7.4 SD days old when found, which was 2–3 days after onset of incubation. Nests were monitored over a 70-day interval (23 May–1 August). We used 336 nests from Chilkat Pass from 1985 to 1988, 50% of which were produced by yearlings. Nests were on average 7.5 ± 5.6 days old when found, which was the first day of incubation, and were monitored over a 65-day interval (24 May–29 July).

NEST ABUNDANCE

For a qualitative evaluation of how the number of active nests may affect daily nest survival within a season, we calculated the number active on each day of the season at each site. This estimate would be biased if not corrected for nests that failed before they were found. Therefore, we first needed to estimate how many of these nests were initiated and then

estimate how long they might have been active before they failed. To estimate how many were initiated, we used the Horvitz-Thompson estimator described by Dinsmore et al. (2002). Using the top nest survival model for each site, we calculated the probability that each nest found survived until the day it was found. We then divided the observed frequency of each nest (i.e., 1) by that probability and used this as the number of nests that were initiated on the same day but failed before they were found (we denote these as 'adjusted' nests for descriptions below). We then summed the frequencies of all found and adjusted nests for each day to generate a distribution of total nest initiations. To estimate how long these adjusted nests were active before they failed, we first assumed that they had a similar daily survival probability and likelihood of being located as nests that were found. We then took all the found nests that were initiated on the same day, calculated the average number of days they were active before being found, and divided this by two as a general estimate of how long the adjusted nests were active before they failed. To calculate the total number of active nests each day, we summed the number of found and adjusted nests for each day of the season. Finally, because of annual differences in the number of nests used to estimate abundance, we scaled the estimated number of active nests each year relative to the total number of known nests for the study area.

STATISTICAL ANALYSES

We examined patterns of nest predation by modeling daily nest survival rates using program MARK. Dates were scaled so that day 1 was the date the earliest nest was found within each population. We began with a simple model that included a single daily nest survival estimate for each population separately. To test for annual patterns of nest survival, we added year to the model. We then considered models that allowed nest survival to vary over the breeding season in a linear and a curvilinear (quadratic) pattern. At each site, we also included interactions between seasonal trends and year to test whether seasonal patterns varied annually. Constructing models with all possible combinations of constant, linear, and curvilinear trends across years would greatly increase the number of models. Therefore, we only considered interaction terms using the best seasonal trend from the additive models at each site. To test whether temporal change in nest survival might be related to nest age, we also compared models with a linear and quadratic effect of nest age. Separating time of season and nest age effects can be difficult because nests at the start and end of the season will primarily be in the laying and late incubation stages, respectively. However, females began breeding over a two-week period at the start of the season and those that failed typically made one to three renesting attempts. Therefore, for most days of the breeding season, there were adequate samples of females in different stages of the nesting period to allow us to consider separate effects of nest age and time of season on daily nest survival. Finally, we added female age class (yearling or adult) and body condition to the top models at this point. Because we did not expect nest visibility, female behavior, or individual characteristics to vary considerably from year to year, we did not include interaction terms with year and nest age, female age, or condition. Data on body condition were available for 85% of nesting attempts at Chilkat Pass and 64% at La Pérouse Bay. Missing covariate values are a problem because the parameter values for those individuals with missing data are also missing; thus, they cannot contribute to the likelihood. One solution is to replace missing cells with the population average and then standardize the covariate (Cooch and White 2005). We believed too many estimates of condition were missing to use this method for La Pérouse Bay, but used this approach for Chilkat Pass by including the mean body condition for adults and yearlings, as determined by equations in Robb et al. (1992). Because our measure of condition was based on the residuals of a regression of mass on wing corrected for days before laying, the mean value was near 0. Thus, individuals assigned the mean had little influence on the estimate and we did not further standardize the covariate. For body condition, the range of the residuals was 201 ± 33 g (SD), indicating considerable individual variation. In total, we considered 17 candidate models for La Pérouse Bay and 16 for Chilkat Pass.

We used Akaike's information criterion for small samples (AIC_c) for model selection, and ΔAIC_c and Akaike weights (w_i) to infer support for different models in the candidate model set (Akaike 1973, Burnham and Anderson 2002).

We report results from the top model but acknowledge model uncertainty by also considering results that would be generated from other supported models. While model averaging is a useful way to account for model uncertainty, we chose not to use model averaging across models with linear and quadratic terms, as the averaged beta estimates may not reflect the hypotheses under consideration (Burnham and Anderson 2002, Blums et al. 2005). We identified a confidence set on the models by including those that were within 6 AIC_c units of the top model, which typically represent a combined weight (w_i) of >0.95 (Burnham and Anderson 2002). For our analyses, a sine link function was used for the constant survival model, while a logit link function was used for all other models. There is currently no suitable goodness-of-fit test for nest survival models (Dinsmore et al. 2002, Rotella 2005), thus we have not used one here.

RESULTS

TEMPORAL VARIATION IN NEST ABUNDANCE

At both sites and in most years, the number of active nests increased in late May and remained high until around the end of the third week in June, after which it began to decline steadily toward the end of July (Fig. 1a, 1b). At La Pérouse Bay in 1983, the onset of egg-laying was delayed by about 10 days, leading to a temporal shift in the number of active nests relative to the other three years.

TEMPORAL VARIATION IN DAILY NEST SURVIVAL

The top model at La Pérouse Bay contained a linear seasonal trend and a quadratic effect of nest age, although a model with a quadratic seasonal trend also had strong support (Table 1a). A positive parameter estimate for the linear time trend indicated higher daily nest survival as the season progressed (Table 2a, Fig. 2). The quadratic effect of nest age indicated that on any given day of the season, nests during the laying stage and late in incubation had higher daily nest survival rates than nests early in incubation (Fig. 2). Parameter estimates for the linear and quadratic time terms in the second-best model were time: -0.040 ± 0.069 (mean $\pm$ SE) and time^2: 0.001 ± 0.001. This model indicated a slight initial

decrease in daily nest survival rate over the first two weeks followed by an increase to the end of the season (Fig. 2). Models with year effects were within 2 AIC_c of the top model without year effects, despite the addition of three extra parameters. This suggests annual variation was present at La Pérouse Bay. To examine this further, we estimated the annual process variance using the variance components option and an intercept-only model (Burnham and White 2002). Estimates of annual process variation (σ) were 0.004. Adding two standard deviations ($2\sigma = 0.008$) to the average daily nest survival rate (0.971) produced a range from 0.963 to 0.979. These values raised to the power of 32 (average nest cycle for an 11-egg clutch) give an expected range of annual nest survival at La Pérouse Bay from 0.30 to 0.51 (average from constant model = 0.42).

All models with support at Chilkat Pass contained an interaction with year and a quadratic seasonal trend (Table 1b). Models with a linear seasonal trend or constant survival over time received little support. These results indicate that daily nest survival followed a curvilinear seasonal pattern in which survival was high early in the season, decreased to a low midseason, and increased again toward the end of the breeding season (Table 2b, Fig. 3). The year by time^2 interaction indicates there was some annual variation in the timing and extent of the decrease in survival. Overall, the pattern of low nest survival tended to coincide with periods of higher nest abundance midseason (Fig. 1, 3). Unlike results from La Pérouse Bay, nest age did not appear to influence daily nest survival, since the inclusion of linear or quadratic nest age terms did not improve model fit (β with 95% CI: nest age = 0.008 [-0.022, 0.038], nest age^2 = 0.038 [-0.077, 0.152], -0.001 [-0.005, 0.003]; Table 1b). The estimate of yearly process variance for Chilkat Pass was 0.023 (σ). Adding two standard deviations to the average daily nest survival rate (0.965) gives a range of annual daily nest survival from 0.919 to 1.00, which, when raised to the power of 29 (nest cycle based on mean clutch of 8 eggs), gives an expected annual variation in nest survival of 0.08 to 1.00 (average from constant model = 0.34). By comparison, the estimated range from the year-specific estimates from this study (without seasonal covariates) was 0.933 (1987) to 0.990 (1986), which gives a range of nest
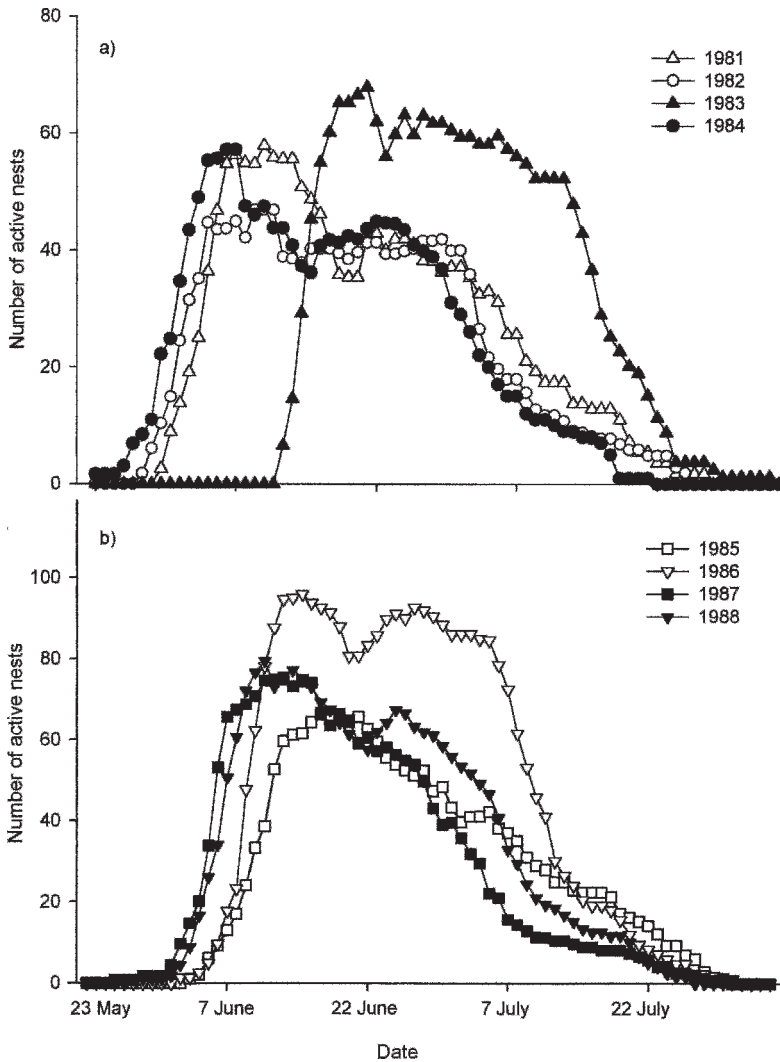
FIGURE 1.   Number of active Willow Ptarmigan nests across the breeding season at a) La Pérouse Bay, Manitoba, and b) Chilkat Pass, British Columbia. Daily nest survival estimates from the top model at each site were used to correct for the number of nests that were likely active but failed prior to being found. The approximate size of the study area was 10 km^2 for La Pérouse Bay and 4.5 km^2 for Chilkat Pass. Note the different scales on the y-axes.

survival from 0.13 to 0.75 over the course of this study. However, due to the strong seasonal effects, we would expect variation about these values depending on when the nest was initiated.

EFFECT OF FEMALE AGE AND CONDITION ON NEST SURVIVAL

At La Pérouse Bay, addition of female age as a covariate did not considerably improve model support, suggesting age has little influence on

nest survival (β estimate with 95% CI = -0.141 [-0.632, 0.350]). We had insufficient data to include condition as a covariate at La Pérouse Bay. At Chilkat Pass, addition of female age and condition as covariates also did not improve model support (β with 95% CI: female age = 0.113 [-0.205, 0.430], condition = -0.0004 [-0.005, 0.004]; Table 1b). Thus, characteristics of breeding females had little influence on daily nest survival in both populations.

TABLE 1. Confidence set of nest survival models for Willow Ptarmigan at a) La Pérouse Bay, Manitoba, 1981–1984, and b) Chilkat Pass, British Columbia, 1985–1988. Deviance is the difference in the -2 log-likelihood between each model and the saturated model, AIC_c = Akaike's information criterion for small samples and ΔAIC_c = adjusted AIC_c relative to the top model, w_i = Akaike weight, a measure of the relative support for each model, and K = number of parameters in the model. TIME = linear time trend, TIME^2 = quadratic time trend, NAGE = linear nest age effect, NAGE^2 = quadratic nest age effect, YEAR = categorical year effect, FAGE = female age, CONDITION = female body condition. A "+" indicates an additive effect of the variable, while a "*" indicates an interaction between the two variables. The confidence set for each site includes those models within 6 AIC_c units of the top model.

Model	Deviance	K	ΔAIC_c	w_i
a) La Pérouse Bay				
TIME + NAGE^2	496.96	4	0.00	0.28
TIME^2 + NAGE^2	495.76	5	0.81	0.19
TIME + NAGE^2 + YEAR	492.42	7	1.49	0.13
TIME + NAGE^2 + FAGE	496.64	5	1.69	0.12
TIME^2 + NAGE^2 + FAGE	495.53	6	2.59	0.08
TIME^2 + NAGE^2 + YEAR	491.65	8	2.74	0.07
NAGE^2	502.72	3	3.75	0.04
TIME^2	503.96	3	5.00	0.02
TIME	506.24	2	5.27	0.02
b) Chilkat Pass				
YEAR*TIME^2	987.22	12	0.00	0.41
YEAR*TIME^2 + FAGE	986.74	13	1.53	0.19
YEAR*TIME^2 + NAGE	986.93	13	1.72	0.17
YEAR*TIME^2 + CONDITION	987.20	13	2.00	0.15
YEAR*TIME^2 + NAGE^2	986.67	14	3.47	0.07

TABLE 2. Parameter estimates and standard errors for the top logistic regression model of daily nest survival at a) La Pérouse Bay, Manitoba, 1981–1984, and b) Chilkat Pass, British Columbia, 1985–1988. Abbreviations are as in Table 1. Years 1 to 4 refer to estimates for years 1985 to 1988.

Parameter	Estimate ± SE
a) La Pérouse Bay	
Intercept	4.205 ± 0.802
TIME	0.031 ± 0.013
NAGE	−0.254 ± 0.100
NAGE^2	0.008 ± 0.003
b) Chilkat Pass	
YEAR 1	16.788 ± 4.612
TIME (Year 1)	−0.929 ± 0.293
TIME^2 (Year 1)	0.015 ± 0.005
YEAR 2	6.593 ± 5.534
TIME (Year 2)	−0.287 ± 0.395
TIME^2 (Year 2)	0.007 ± 0.007
YEAR 3	6.218 ± 1.227
TIME (Year 3)	−0.227 ± 0.082
TIME^2 (Year 3)	0.003 ± 0.001
YEAR 4	5.475 ± 1.802
TIME (Year 4)	−0.140 ± 0.114
TIME^2 (Year 4)	0.002 ± 0.002

DISCUSSION

SITE AND ANNUAL VARIATION IN NEST SURVIVAL

Average nest survival rates were about 8% higher at La Pérouse Bay than at Chilkat Pass, but this difference was small compared to the expected annual variation at each site. Annual variation in nest survival was considerably higher at Chilkat Pass. Yearly differences in nest survival could be due to fluctuations in the density of ptarmigan, predators, or alternative prey, or variation in weather (Kurki et al. 1997, Bêty et al. 2002, Morrison and Bolger 2002). There was little evidence that changes in breeding density affected nest survival at either site. Densities at Chilkat Pass increased from 1985 to 1987, and declined in 1988, but only ranged from 20 to 23 pairs per km^2 during this time. These changes are slight compared to the differences in annual nest survival, particularly between 1986 and 1987. Breeding densities were lower at La Pérouse Bay and only varied from approximately nine pairs per km^2 in 1981 to
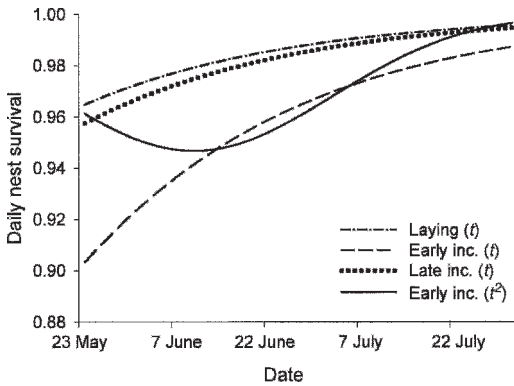
FIGURE 2. Predicted daily nest survival rates for Willow Ptarmigan in relation to time of season and nest age at La Pérouse Bay, Manitoba. Estimates were generated using the logistic regression equation from the top model (Table 1a, 2a). Nest observations began on 23 May. For nest age, we used the equation to predict average survival of a nest during laying (days 1–7), early incubation (days 12–18), and late incubation (days 24–30). The solid black line shows daily survival estimates for a nest during early incubation using the second-best model with a quadratic time (t^2) trend. Average mean date of clutch initiation was 3 June, mean onset of incubation was 11 June, and mean hatching date was 3 July. Sample sizes for this analysis were: 1981 = 32, 1982 = 54, 1983 = 54, and 1984 = 49.

seven in 1982–1984 (Martin et al. 1989). Because >90% of nest losses were due to predation at both sites, we also suspect variation in weather had little direct influence on nest survival, although it is possible that weather and predators interact in a more complex manner (Morrison and Bolger 2002). Changes in the abundance of predators or alternative prey may be the most likely explanation for annual variation in daily nest survival and for the differences between the two sites. Increases in alternative prey species may alleviate predation pressure on other species because of predator satiation or selectivity (Abrams and Matsuda 1996). For instance, avian nest success in some regions is positively related to annual fluctuations in the densities of small mammals, because predators turn to nests when small mammals decline (Angelstam et al. 1984, Bêty et al. 2002). La Pérouse Bay has a more diverse community than Chilkat Pass and fluctuations in the abundance of any one species may have less of an effect on another. Chilkat Pass is also located close to the boreal forest, where the abundance of many species is connected to cycles in either snowshoe hares or voles and mice (Krebs et al. 2001). Foxes are the main nest predators at Chilkat Pass, but it is not clear whether functional or numerical responses in foxes are tied to these cycles (Krebs et al. 2001). We also note that with only four years of data, it is difficult to identify the full range of annual variation in nest survival at a site, thus longer studies are needed to determine if these patterns are consistent.

SEASONAL VARIATION IN NEST SURVIVAL

At Chilkat Pass, we observed a curvilinear seasonal trend: daily nest survival was high early in the season (23 May–11 June), decreased to a low midseason (early June to early July), then increased again to the end of the season (early August). The pattern at La Pérouse Bay also revealed increasing survival from the middle to the end of the season, but there was uncertainty as to the trend during the first third of the season. The top model suggested a linear increase, but the second-best model with similar support suggested a slight initial decrease in survival over the first couple of weeks followed by a steady increase. This uncertainty may reflect the smaller sample sizes at La Pérouse Bay, as well as potential problems in separating effects of nest age and time of season when few nests are active and most are in the laying stage. Despite these issues, the seasonal fluctuations in nest survival appeared to be stronger at Chilkat Pass overall.

Seasonal patterns of nest survival could be influenced by several factors. It may not be profitable for predators to search for nests when few birds are nesting, and our observation that periods of low nest survival tended to coincide with higher nest abundance, particularly at Chilkat Pass, suggests predators may cue in to nests when they are most abundant. Few studies have examined the relationship between survival and abundance of nests within a season, partly because methods to examine continuous temporal change in survival have only recently become available. Studies that have compared nest survival among patches differing in nest density have found evidence for density-dependent nest predation in some cases (Niemuth and Boyce 1995, Larivière and Messier 1998), but not others (Andrén 1991, Ackerman et al. 2004). In simpler communities
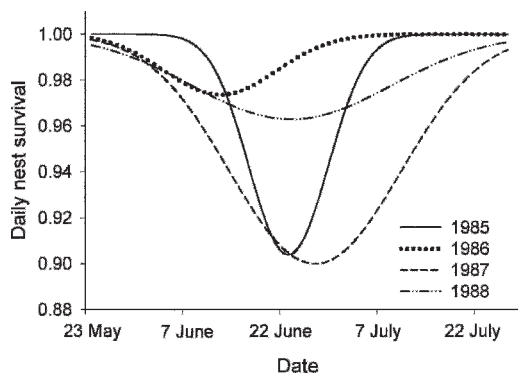
FIGURE 3. Predicted daily nest survival rates for Willow Ptarmigan nests at Chilkat Pass, British Columbia, in relation to year and time of season. Estimates were generated using the logistic regression equation from the top model (Table 1b, 2b). Nest observations began on 24 May. For all first clutches averaged across the four years, mean date of clutch initiation was 5 June, mean onset of incubation was 11 June, and mean hatching date was 4 July. Sample sizes for this analysis were: 1985 = 60, 1986 = 82, 1987 = 97, and 1988 = 97.

such as those at Chilkat Pass, predators may exhibit a stronger functional response to a change in the abundance of primary resources (Gilg et al. 2006). The prey community at La Pérouse Bay is far more complex, with abundant waterfowl and shorebirds, and ptarmigan are relatively less common. Thus, predators may still respond to changes in ptarmigan nest availability at La Pérouse Bay, but perhaps less so than at Chilkat Pass (Hannon et al. 1998). Seasonal variation in nest survival may also depend on when other types of prey become available. At both sites, resources are likely limited early in the season, requiring predators to primarily focus on nests. By July, a number of alternative resources are available, including chicks of ptarmigan and shorebirds (and waterfowl at La Pérouse Bay), passerine fledglings, and juvenile arctic ground squirrels (*Spermophilus parryi*), all of which may be easier to locate than nests.

It is also possible that higher nest survival at both sites during the last third of the nesting season is related to changes in vegetation cover at the nest (Sullivan and Dinsmore 1990). Ptarmigan initiated egg-laying well before the onset of vegetation growth, but by approximately mid-June new growth of willow leaves

(*Salix* spp.) would provide additional nest concealment. However, a previous study at Chilkat Pass found that nest cover had little effect on probability of nest predation (Schieck and Hannon 1993). Studies of Spruce Grouse (*Falcipennis canadensis*; Deon 1997) and Rock Ptarmigan (*Lagopus muta*; Scherini et al. 2003) found that cover did not influence nest survival, while greater cover led to higher nest survival in White-tailed Ptarmigan (*L. leucura*; Wiebe and Martin 1998a) and White-winged Scoters (*Melanitta fusca*; Traylor et al. 2004). Thus, it is unclear whether the seasonal increase in vegetation cover influenced nest survival at our sites.

EFFECTS OF NEST AGE ON SURVIVAL

Differences among populations and species in the effects of nest age on daily nest survival may be due to factors such as the visibility of a nest, changes in female activity over the nesting period, or the type of predator community (Klett and Johnson 1982, Cresswell 1997, Traylor et al. 2004, Grant et al. 2005). Studies on precocial birds have produced mixed results; daily nest survival was not influenced by nest age for scaup (*Aythya* spp.; Walker et al. 2005), increased from laying to incubation and then did not vary until hatching for White-winged Scoters (Traylor et al. 2004), and increased linearly throughout the season for Mountain Plovers (*Charadrius montanus*; Dinsmore et al. 2002). Among altricial species, daily nest survival increased from laying to hatching in some cases (Cresswell 1997, Grant et al. 2005), but declined over the season in others (Burhans et al. 2002, Jehle et al. 2004).

We also observed variation in our two study populations; daily nest survival was more or less constant with nest age at Chilkat Pass, but was higher during laying and late incubation at La Pérouse Bay. Females likely have similar nest behaviors and activities between the two sites, but environmental characteristics may interact with behavior to affect daily nest survival. The predominantly avian predator community (visual hunters) at La Pérouse Bay may be more likely to cue in to female activity to locate nests, especially since this site has more open vegetation (Hannon et al. 1988). At Chilkat Pass, where the predator community is primarily mammalian (olfactory hunters), changes in nest visibility or female activity with

nest age may have less effect on survival. We are uncertain why nests at La Pérouse Bay had higher survival at the end of the incubation period. Vulnerable nests may fail early while more secure nests survive longer, giving the appearance of increasing daily nest survival with age. However, if this were the case here, we should have observed the pattern at both sites (Klett and Johnson 1982, Dinsmore et al. 2002). Our finding that nest age effects appear stronger in a community where avian predators are more common could be tested further by comparing the relationship between nest age and nest survival across study sites that differ in the composition of mammalian and avian predators. Alternatively, it could also be examined within a site by identifying mammalian and avian nest predators, and testing how predation patterns vary for each group as a function of nest age.

INDIVIDUAL CHARACTERISTICS AND NEST SURVIVAL

Individuals may be able to influence the likelihood of predation through nest placement, incubation behavior, or nest defense (Schieck and Hannon 1993, Martin et al. 2000, Traylor et al. 2004, Remeš 2005). While these behaviors may have differed among individuals in our study due to age or condition, we found no evidence that they influenced nest survival. These results are consistent with an earlier study at Chilkat Pass (Hannon and Smith 1984), other studies of ptarmigan (Myrberget 1988, Wiebe and Martin 1998b) and waterfowl (Hepp and Kennamer 1993), and birds in general (Sæther 1990). Previous studies in these two populations have shown that other aspects of reproduction are influenced by age and condition. Older females tend to breed earlier, produce larger clutches, and are more likely to renest following failure (Wiebe and Martin 1998b). Females in better condition also produce heavier chicks (Robb et al. 1992). If nest survival is determined more by ecological features such as predator behavior or the abundance of alternative prey, females may have little control over nest survival and all individuals may be equally susceptible. Altering breeding date or, in particular, the likelihood of renesting following failure, may be a means by which individuals can offset losses due to nest predation (Martin et al. 1989).

Overall, our results suggest that nest survival in these two Willow Ptarmigan populations is determined more by environmental features than by individual characteristics of females. While the influence of individual characteristics was similar between the two populations, there were differences between sites in the extent of annual and seasonal variation, and in whether survival varied in relation to the age of the nest. We suggest these differences might be related to the type of predator community (mammalian versus avian) and to the complexity of the prey community.

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