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ADVANCED TECHNIQUES FOR MODELING AVIAN NEST SURVIVAL

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Abstract. Estimation of avian nest survival has traditionally involved simple measures of apparent nest survival or Mayfield constant-nest-survival models. However, these methods do not allow researchers to build models that rigorously assess the importance of a wide range of biological factors that affect nest survival. Models that incorporate greater detail, such as temporal variation in nest survival and covariates representative of individual nests represent a substantial improvement over traditional estimation methods. In an attempt to improve nest survival estimation procedures, we introduce the nest survival model now available in the program MARK and demonstrate its use on a nesting study of Mountain Plovers (*Charadrius montanus* Townsend) in Montana, USA. We modeled the daily survival of Mountain Plover nests as a function of the sex of the incubating adult, nest age, year, linear and quadratic time trends, and two weather covariates (maximum daily temperature and daily precipitation) during a six-year study (1995–2000). We found no evidence for yearly differences or an effect of maximum daily temperature on the daily nest survival of Mountain Plovers. Survival rates of nests tended by female and male plovers differed (female rate = 0.33; male rate = 0.49). The estimate of the additive effect for males on nest survival rate was 0.37 (95% confidence limits were 0.03, 0.71) on a logit scale. Daily survival rates of nests increased with nest age; the estimate of daily nest-age change in survival in the best model was 0.06 (95% confidence limits were 0.04, 0.09) on a logit scale. Daily precipitation decreased the probability that the nest would survive to the next day; the estimate of the additive effect of daily precipitation on the nest survival rate was −1.08 (95% confidence limits were −2.12, −0.13) on a logit scale. Our approach to modeling daily nest-survival rates allowed several biological factors of interest to be easily included in nest survival models and allowed us to generate more biologically meaningful estimates of nest survival.

Key words: Charadrius montanus; *Montana; Mountain Plover; nest survival; nesting success; program MARK.*

INTRODUCTION

The study of nest survival is a critical component of the study of the breeding biology of birds. Apparent nest survival, defined as the proportion of successful nests (those where ≥1 egg hatches) in a sample, is often positively biased relative to true nest survival because nest losses early in incubation are underrepresented (Mayfield 1961). For apparent nest survival to accurately reflect true nest survival, a sample of nests must be followed from the day they were initiated (Klett and Johnson 1982). Due to this inherent bias, Mayfield (1961, 1975) developed a method for estimating the daily survival of a sample of nests using exposure days (the cumulative number of days that the nests in the sample were monitored) and the number of known losses. Mayfield estimated daily nest survival as 1 − [(number of nest losses)/(total exposure days)]. Nest survival is then calculated as (daily nest survival)^n where n is the length of the nesting period (incubation or incubation + nestling period, depending on whether the species is precocial or altricial). Because various authors have used different terminology, we define the following terms for this paper: (1) ''daily nest survival rate'' is the probability that a nest will survive a single day, and (2) ''nest survival'' is the probability that a nest will be successful. The latter term has often been called ''nest success'' or ''nesting success'' by other authors, but we prefer the phrase ''nest survival'' because success is more appropriate when referring to an individual bird, not a nest. We prefer to define ''nesting success'' as the probability that an individual brings off a successful nest, even if it takes >1 attempt, equivalent to the term ''hen success'' used elsewhere in the literature (e.g., Cowardin et al. 1985).

Implicit in Mayfield's estimator was the assumption that daily nest survival was constant in time and that the date of a hatch or loss was known exactly. However, field studies often do not collect nest information on a daily basis; rather, nests are checked at regular intervals of one to several days and the timing of a hatch or loss may not be determined exactly. Because the timing of losses between nest checks is often unknown, a com-

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mon procedure has been to use the midpoint of the interval when calculating exposure days (Mayfield 1961). Johnson (1979) showed that the Mayfield estimates generally performed well when compared to maximum likelihood estimates and Mayfield estimates were robust to heterogeneity among nests.

Johnson (1979) and Bart and Robson (1982) expanded Mayfield's model and developed the theory to estimate time-specific nest survival rates, although their models were essentially identical to the one developed by Mayfield. Klett and Johnson (1982) later developed a way to estimate constant daily survival rates for different periods of the nesting cycle, although the choice of these periods can be arbitrary. There have been several recent advances that allow for additional flexibility in modeling nest survival. Bart and Robson (1982) developed a generalized likelihood for estimating daily nest survival rates under assumptions of constant and time-specific survival. Later, techniques were developed to estimate age-specific daily nest survival rates without knowing the age of the nest when found (Pollock and Cornelius 1988). Other recent developments have included models that incorporate random individual nest effects (Natarajan and McCulloch 1999), models to estimate daily nest survival across nest stages (for example, the transition between incubation and nestling stages) where the exact transition date between the stages is unknown (Stanley 2000), and methods for including the effects of nest checks on the daily nest survival rate following a visit (Rotella et al. 2000).

Computer software to estimate daily nest survival rates using these advances is not readily available, so many studies continue to use estimates of constant daily nest survival calculated using the Mayfield method. Such studies often compare Mayfield constant daily nest survival estimates between groups or treatments by simply examining overlap in 95% confidence intervals or by testing for differences in daily nest survival rates using program CONTRAST (Hines and Sauer 1989). Small sample sizes can severely limit the investigator's ability to simultaneously examine multiple covariates when using the traditional Mayfield approach because nesting data must be divided into groups for testing. Many studies also have overlooked the opportunity to explore more interesting biological questions such as temporal variation in daily nest survival, fitting time-trend models to daily nest survival, and modeling daily nest survival as a function of time-specific covariates such as weather or individual covariates specific to each nest being monitored. Incorporating these variables into estimates of daily nest survival will generate more biologically meaningful estimates of nest survival and will allow biologists to rigorously evaluate specific biological questions about variations in nest survival.

In this paper, we introduce a new method for estimating avian nest survival using program MARK (White and Burnham 1999). Program MARK provides a flexible and user-friendly interface that allows the user to build detailed models and rigorously evaluate their support using Akaike's Information Criterion (AIC) model selection (Akaike 1973). We demonstrate the use of this method with nesting data from a study of Mountain Plovers (*Charadrius montanus*) in Montana, USA, in which we modeled the daily survival rates of 432 Mountain Plover nests monitored over six breeding seasons (1995–2000). We used program MARK to test for sex-, year-, and time-specific differences in nest survival and to investigate the importance of two weather covariates (maximum daily temperature and daily precipitation) and nest age on daily nest survival rates. We computed mean nest initiation dates for nests tended by each sex, and then adjusted those dates using a Horvitz-Thompson estimator to compute the adjusted number of nests initiated on a given date. Finally, we estimated the survival of male- and female-tended Mountain Plover nests using the logistic regression equation from our best model with no precipitation effect. Using this approach, we were better able to incorporate specific biological questions into our models, and we were ultimately able to evaluate the importance of those variables and better understand factors that affected the nest survival of this declining bird.

Nest Survival Model

The nest survival model available in program MARK (White and Burnham 1999) is an extension of the model described by Bart and Robson (1982) and allows increased flexibility in modeling daily nest survival, including the use of individual and group- and time-specific covariates. Here, the survival of a nest refers to the probability that a nest survives a specified time interval, typically one day. The assumptions of the nest survival model are: (1) nests can be correctly aged when they are first found; (2) nest fates are correctly determined; (3) nest discovery and subsequent nest checks do not influence survival; (4) nest fates are independent; and (5) homogeneity of daily nest survival rates.

Minimally, the nest survival model requires five pieces of information for each nest j out of a total of n nests. These five pieces of information are: (1) the day the nest was found (k); (2) the last day the nest was checked alive (l); (3) the last day the nest was checked (m); (4) the fate of the nest (0 = successful, 1 = depredated) (f); and (5) the number of nests with this encounter history.

In MARK, these pieces of information are used to generate an encounter history for each nest in live/dead (LDLD. . .) format. There are eight possible ways to code the triplet involving k, l, and m (where $k \leq l \leq m$) and the fate (f) in the input file as shown in the following examples (the values used for k, l, and m are examples only):

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1) $k = 1$, $l = 3$, $m = 5$, and $f = 1$ returns a probability of $S_1S_2[1 - S_3S_4]$;
2) $k = 1$, $l = 3$, $m = 5$, and $f = 0$ is invalid and should be coded as $k = 1$, $l = 5$, $m = 5$;
3) $k = 1$, $l = 3$, $m = 3$, and $f = 1$ is invalid and should be coded as $k = 1$, $l = 1$, $m = 3$;
4) $k = 1$, $l = 3$, $m = 3$, and $f = 0$ returns a probability of S_1S_2;
5) $k = 1$, $l = 1$, $m = 3$, and $f = 1$ returns a probability of $1 - S_1S_2$;
6) $k = 1$, $l = 1$, $m = 3$, and $f = 0$ is invalid;
7) $k = 1$, $l = 1$, $m = 1$, and $f = 1$ is invalid; or
8) $k = 1$, $l = 1$, $m = 1$, and $f = 0$ is invalid.

In example 2, a nest that is successful on day 5 must be coded as last checked alive on that day ($l = 5$) because assumption 2 implies that the exact hatch date is known. In example 3, the nest cannot be observed both alive and destroyed on the same day. In example 6, the nest is observed alive only on a single day; thus there is no information to estimate daily survival. In examples 7 and 8, there is also no information to estimate daily survival since the nest is only under observation for a single day. The encounter history for each nest is automatically coded in MARK. As an example, a nest with $k = 1$, $l = 3$, and $m = 5$ has an encounter history of 10 10 10 00 01 with cell probability $S_1S_2[1 - S_3S_4]$. In MARK, all encounters up to day l are automatically recorded as ''10,'' but an encounter history of 10 00 10 00 01, under the same scenario given above ($k = 1$, $l = 3$, and $m = 5$), would generate the same cell probability.

Nests are assigned to groups (in our study, groups were male- and female-tended nests in each of the six years) using the following lines in the input file in program MARK:

Nest survival group = 1; /*	k	l	m	f	number */
/*GGOO, 1995-076*/	53	59	63	1	1;
/*OGDD, 1995-047*/	18	36	36	0	1;
/*WGDD, 1995-003*/	6	20	20	0	1;
/*OGDY, 1995-032*/	14	24	24	0	1;
etc.					

where individual nests within the group followed each group label; the comment (text between /* and */) at the beginning of each encounter history includes the color band combination and the nest identification number and is followed by values for k, l, m, fate, and the number of nests with this history.

The likelihood (L) for the daily survival (S_i) from day i to day $i + 1$ for a sample of n nests is:

$$L(S_i \mid k_j, l_j, m_j, f_j) \propto \prod_{j=1}^{n} \left[\left(\prod_{\substack{i=k \\ (k<l)}}^{l-1} S_i \right) \left(1 - \prod_{i=l}^{m-1} S_i \right)^{f} \left(\prod_{i=l}^{m-1} S_i \right)^{1-f} \right].$$

To illustrate the model, suppose that a nest is found on day 3 is next checked alive on day 6 and has been depredated by the next check on day 10. The fate of this nest is coded as 1 ($f = 1$, a failure):

Day							
3	4	5	6	7	8	9	10
↑			↑				↑
Found (k)			First check (l)				Last check (m).

This nest is known to have survived until day 6. The probability of surviving the first interval (from day 3 to day 6) is then

$$\prod_{\substack{i=k \\ (k<l)}}^{l-1} S_i = S_3S_4S_5.$$

The nest was lost sometime between day 6 and day 10. The four possible outcomes explaining this loss are: the nest was lost between days 6 and 7 $[(1 - S_6)]$, the nest survived until day 7 and was lost between days 7 and 8 $[S_6(1 - S_7)]$, the nest survived until day 8 and was lost between days 8 and 9 $[S_6S_7(1 - S_8)]$, or the nest survived until day 9 and was lost between days 9 and 10 $[S_6S_7S_8(1 - S_9)]$. The probability of being lost anytime during the interval between day 6 and day 10 is simply one minus the probability of surviving this interval, which can be written as

$$\left(1 - \prod_{i=l}^{m-1} S_i \right)^{f} = 1 - S_6S_7S_8S_9$$

where $f = 1$ in this example. The third term in the model likelihood has a value of one. Thus, the overall probability of observing this encounter history is $S_3S_4S_5[1 - S_6S_7S_8S_9]$.

In program MARK, individual covariates can be easily incorporated into the nest survival model with the use of the logit or another link function. Models incorporating an individual or time-specific covariate used a logit link function; all other models that had a one-to-one correspondence between $\hat{\beta}_i$ and S_i used a sine link function. Formulas for the two link functions are

$$\text{logit}(\hat{S}_i) = \ln\left(\frac{\hat{S}_i}{1 - \hat{S}_i} \right) = \hat{\beta}_0 + \hat{\beta}_1(X) \qquad \sin(\hat{S}_i) = \hat{\beta}_i$$

where X represents some variable of interest such as the daily age of the nest. Back transformation is then used to generate real parameter estimates. For example, a model with an intercept (β_1), an additive linear trend on survival (β_2), and an additive effect of nest age at time i (β_3) can be expressed in the form

$$\text{logit}(\hat{S}_i) = \hat{\beta}_1 + \hat{\beta}_2(\text{trend}) + \hat{\beta}_3(\text{nest age}_i)$$

and the estimate of survival (S_i) is obtained by back transformation, where

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$$\hat{S}_i = \frac{1}{1 + \exp\{-[\hat{\beta}_1 + \hat{\beta}_2(\text{trend}) + \hat{\beta}_3(\text{nest age}_i)]\}}.$$

Our choice of a link function was not critical to our analysis because we modeled a covariate value for each day, and used the back-transformed daily survival rate in the likelihood. Thus, our approach provided nearly the same estimates of daily nest survival regardless of the link function used. In contrast, other nest survival estimation methods typically use data grouped across time, and use a covariate appropriate to each interval. Thus, their analyses depend critically on the link function used, because the link function determines how the covariate must be pooled to obtain the appropriate relationship with daily survival. Other nest survival estimation methods have typically used a log link because that is the link function that allows covariate values to be summed across time to obtain a value appropriate for the time interval being modeled. For example, to compute the probability of nest survival over a three-day interval, say $S_1S_2S_3$, and with a time-varying covariate such as temperature (45, 50, 55°F for the three days) they assume a linear model with a log link: $\beta_1(3) + \beta_2 (45 + 50 + 55)$, where β_1 scales the interval length for three days, and β_2 is the temperature effect. In contrast, our approach uses the inverse link function, regardless of what it is, to estimate S_1 with $\beta_1 + \beta_2 (45)$, S_2 with $\beta_1 + \beta_2 (50)$, and S_3 with $\beta_1 + \beta_2 (55)$, and then these values of S_1, S_2, and S_3 are used in the likelihood directly, and not as just the product. The flexibility to choose a link function in program MARK also increases the probability that nest survival models will converge, a problem often encountered when only using the log link function.

Once a set of candidate models is built using the program MARK, model selection by Akaike's Information Criterion (AIC; Akaike 1973) is used to choose a model or models for inference (Burnham and Anderson 1998). The set of R candidate models is ranked using AIC_c (Burnham and Anderson 1998), which is defined as

$$\text{AIC}_c = -2 \log L + 2K\left(\frac{n}{n - K - 1}\right)$$

where $\log L$ is the natural logarithm of the likelihood function evaluated at the maximum likelihood estimates, K is the number of estimable parameters, and n is the sample size. The second term in the above equation includes a correction for small sample size. In our example below, the sample size is the total number of days all nests were monitored, where each day corresponds to an independent Bernoulli trial.

There is currently no method for estimating extra-binomial variation in the nest survival model in program MARK. Extra-binomial variation (overdispersion) results from more variation in nest survival than is accounted for (modeled) with the binomial distribution. Biological reasons for extra-binomial variation include individual heterogeneity of nest survival rates, and/or lack of independence of nests in the sample. However, extra-binomial variation cannot be detected reliably in these data. The deviance : degrees of freedom ratio has been suggested as a measure of overdispersion, but this approach requires that deviance be distributed according to a chi-square distribution. With asymptotic sample sizes, deviance is known to be chi-square distributed. But with finite sample sizes, deviance is not well approximated with a chi-square distribution. As a result, the deviance:degrees of freedom ratio is biased high, suggesting more overdispersion than actually occurs (McCullagh and Nelder 1989:118–119). However, the chi-square approximation is usually quite accurate for differences in deviances even though it is inaccurate for the deviances themselves (McCullagh and Nelder 1989:119).

As a result of the lack of a chi-square distribution for deviance, other approaches are required for estimating the degree of overdispersion in nest survival data. But with the global model where a time-specific nest survival rate is estimated for each day, any overdispersion is masked because only one binomial variate is observed for each day. In theory, the data could be split into multiple groups and the variance of the estimated deviance across the groups estimated to obtain a measure of the overdispersion. But such a procedure is inefficient, and impractical with typical sample sizes. Methods based on a parametric bootstrap don't appear to work well (White 2002). With typical sample sizes, no additional analyses are possible to estimate the degree of overdispersion in nest survival data.

Once AIC_c values are computed for each model, the R models are ranked relative to the model with the minimum AIC_c value. The relative distances (ΔAIC_c) between the best approximating model ($\text{AIC}_{c_{\min}}$) and each competing model (AIC_{c_i}) are calculated as

$$\Delta\text{AIC}_{c_i} = \text{AIC}_{c_i} - \text{AIC}_{c_{\min}}.$$

Normalized Akaike weights (w_i) are then computed (see Burnham and Anderson 1998) for each of the R models as

$$w_i = \frac{\exp\left[-\left\{\frac{\Delta\text{AIC}_{c_i}}{2}\right\}\right]}{\sum_{r=1}^{R} \exp\left[-\left\{\frac{\Delta\text{AIC}_{c_i}}{2}\right\}\right]}.$$

These normalized weights evaluate the strength of evidence for each model and can be used to estimate model selection uncertainty (Burnham and Anderson 1998). As with other models in program MARK, a wide range of modeling options is available including a full variance–covariance matrix of the β and S_i estimates and model averaging (Burnham and Anderson 1998).

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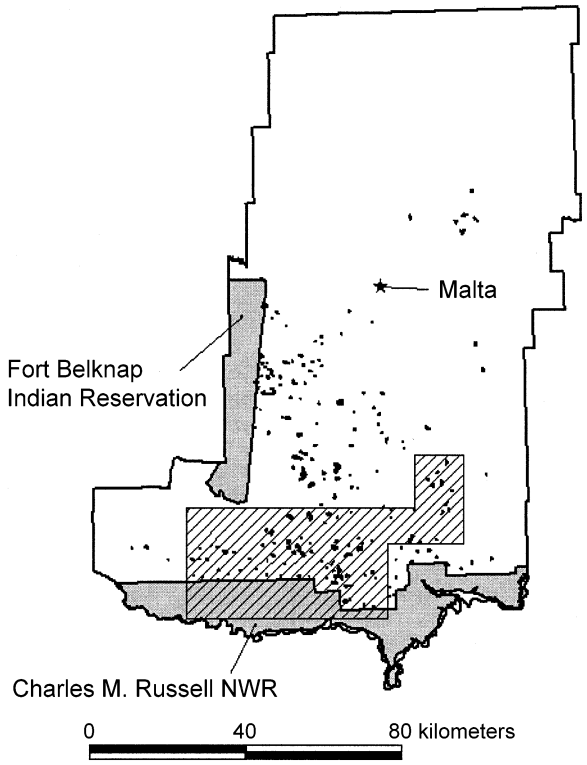

FIG. 1. Map of Phillips County, Montana, USA, showing the 2000 distribution of black-tailed prairie-dog colonies (in black) at the Charles M. Russell National Wildlife Refuge, and Fort Belknap Indian Reservation. The hatched region represents the study area.

CASE STUDY USING MOUNTAIN PLOVERS

Study area

We studied Mountain Plovers on a 3000 km^2 area in southern Phillips County in north-central Montana (47°40′ N–47°55′ N, 107°35′ W–108°30′ W; Fig. 1). The study area is bounded by the Missouri River to the south, the Sun Prairie and Content Roads to the east, Beaver Creek to the north, and Highway 191 to the west. Approximately 2250 km^2 of the study area is in public ownership with the Bureau of Land Management (BLM, Malta Field Office) and the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge). This area is a mixed-grass prairie with sagebrush flats bordering the southwestern edge of the Prairie Pothole Region (Knowles et al. 1982, Olson and Edge 1985). We studied Mountain Plovers exclusively on or adjacent to active black-tailed prairie dog colonies within this area because previous work had shown that Mountain Plovers in Montana preferentially used such sites (Knowles et al. 1982, Knowles and Knowles 1984). Active black-tailed prairie dog (*Cynomys ludovicianus*) colonies contained variable amounts of bare ground interspersed with sparse vegetation that included fringed sagewort (*Artemisia frigida*), plains prickly pear (*Opuntia polycantha*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), and Sandberg bluegrass (*Poa secunda*), with fewer grasses generally present on the older colonies. Mean annual precipitation near the center of the study area was 33 cm, most of which fell from May to July (D. Veseth, *personal communication*). Mean elevation was ~930 m.

Locating nests

We studied Mountain Plovers during six nesting seasons (1995–2000). Each year, fieldwork began on 19 or 20 May and continued until the last nest had hatched, usually in late July or early August. Active prairie-dog colonies within the study area were systematically searched for Mountain Plover nests ≥3 times each year. We slowly drove a vehicle across each colony and periodically stopped to scan for plovers. Individual adult plovers were watched from a distance until they returned to a nest. Hereafter, a nest is defined as a nest structure containing ≥1 egg. Once we found a nest, we marked it with small rockpiles or dried cattle droppings; these ''natural'' markers were used to minimize the possibility that a predator would cue in on the nest. On larger prairie-dog colonies with multiple plover nests we sometimes placed a small orange flag 25 m from the nest.

We trapped adult plovers immediately with a walk-in wire-mesh trap placed over the nest. Juveniles, many of which returned to nest in subsequent years, were captured as chicks, usually ≥10 d of age. Both juvenile and adult plovers were banded with a unique combination of four colored leg bands and an aluminum size 3A U.S. Geological Survey numbered leg band (U.S. Bird Banding laboratory, Laurel, Maryland, USA). Beginning in 1996, we collected a feather sample from every plover for gender determination; we collected only a limited number of feather samples in 1995. Sex of Mountain Plovers cannot be reliably determined either in the hand or in the field, unless courtship is seen. Thus, the sex of each plover could only be determined using molecular techniques (Griffiths et al. 1998, Kahn et al. 1998, Fridolfsson and Ellegren 1999). Frozen feather samples taken from adult and juvenile plovers were analyzed by the Quinn lab at Denver University in Denver, Colorado, USA, and by AvianBiotech International in Jacksonville, Florida, USA. Sex determination followed the procedures outlined in Kahn et al. (1998). DNA was extracted following the protocol of the Wizard Genomic DNA Purification System (Promega, Madison, Wisconsin, USA). This technique examined a highly conserved gene (CHD) that is linked to the sex chromosome in birds. When electrophoresed, the PCR amplifications showed two bands for females (one each for the W and Z chromosomes) and a single band for males (for the Z chromosome). Overall success in determining the sex of plovers was 85% (487 of 576 samples).

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TABLE 1. Nest ages of Mountain Plover nests in southern Phillips County, Montana, USA, as determined by egg floatation.

Nest age (d)	Mean age (d)	Description
1–3	2	egg lying flat on bottom
2–6	4	large end of egg beginning to float
6–18	12	egg standing upright on bottom
16–18	17	egg about to float to surface
16–20	18	egg floating, top barely breaking water surface
20–26	23	egg floating high with >25% above water surface
26–28	27	egg floating with noticeable tilt; young often pipping
29–32	29	eggs hatching (young leave nest within a few hours)

Note: Ranges for each incubation stage were determined from 31 nests that were followed from nest initiation to hatch.

Once found, nests were checked every 3–7 d until the eggs hatched or failed. The incubation period for Mountain Plovers is 29 d, defined as the time the last egg is laid until hatch. Mountain Plovers do not begin incubation until the clutch is complete (Stephen J. Dinsmore, *personal observation*), so we were unable to evaluate daily nest survival during the egg laying period. A nest was considered successful if ≥1 egg hatched, regardless of the size of the clutch. Nest age was determined by floating the eggs (Table 1). Nest age could be accurately determined to within 1–2 d for most nests, especially for nests early or late in incubation and for nests with ≥3 nest checks. A small number of nests failed between the date they were found and the first nest check; for these nests we assigned them the mean age of their incubation stage when they were found (see Table 1). Most incubation stages covered an interval of only a few days and introduced little bias into daily nest survival estimates. However, one of the intermediate incubation stages covered 13 d and the use of the midpoint might have introduced a slight bias into the estimates of daily nest survival. We used eggshell evidence to infer hatching (Mabee 1997), although most (>90%) of the broods were seen post-hatch because they always remained on the same prairie-dog colony and were relatively easy to relocate. Hatch dates were determined using egg floatation (Table 1), the presence of eggshell fragments in the nest lining, or finding young in or near the nest. We could not accurately determine the hatch date for five nests that we were certain were successful. For these nests, we used the last nest check as the hatch date to avoid positively biasing the number of exposure days.

The Colorado State University Animal Care and Use Committee approved the field methods used in this study (Protocol 98-134A-01).

A priori hypotheses and predictions

We developed a set of a priori biological hypotheses that we used to develop specific models to explain variation in the nest survival of Mountain Plovers. Below, we outline our hypotheses about the six sources of variation we incorporated into our nest survival models:

1) Year. Annual variation is a common source of variation in nest survival rates, and can result from factors such as changes in regional weather patterns, fluctuations in predator numbers, and many other factors. By modeling year effects, we hoped to account for annual variation that was not specifically addressed in any other sources of variation (see following list items).

2) Sex of the incubating adult. Mountain Plovers have a rapid multi-clutch mating system (Graul 1973) in which male and female plovers incubate separate nests, the first nest being tended by the male (Stephen J. Dinsmore, *personal observation*). We hypothesized that male plovers would have an earlier mean nest initiation date, and thus higher nest survival (see Ainley and Schlatter 1972), simply because of the ordering of clutches by sex. Few birds have mating systems where both sexes incubate nests (Oring 1982), and we were not aware of any studies that had addressed sex-specific differences in nest survival.

3) Nest age. In most precocial bird species, older nests are expected to have higher survival because nests in locations most at risk will be depredated early (Klett and Johnson 1982). This is contrasted to altricial species, where the adults make more nest visits as the nest ages (e.g., to feed young) and nest survival is expected to decrease in the oldest nests. We hoped to reduce potential confounding of nest age effects and temporal variation in daily nest survival rates by monitoring nests of varying ages across the entire nesting season, although we suspected this would be hard to accomplish early and late in the nesting season.

4) Temporal variation within seasons. The assumption of constant within-season daily nest survival rates seemed unrealistic. To evaluate temporal variation, we fit a simple constant nest survival model to our data, and then added two additional time trend models that we hoped would better illustrate the pattern in daily nest survival. The first time trend was linear, under which we hypothesized that daily nest survival would decrease across the nesting season because early nesters are generally the most successful (Ainley and Schlatter 1972). However, a simple linear time trend could not reflect a bimodal pattern of nest survival,

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which might result if there were substantial numbers of plovers re-nesting in midsummer. To evaluate this possibility, we also fit a quadratic time trend model that allowed daily nest survival to follow a curvilinear pattern. We did not consider more complex time trend models for fear of over-fitting the data.

5) Maximum daily temperature. Mountain Plover eggshells are unusually thick and susceptible to heat (Knopf 1996) and we surmised that extreme temperatures (e.g., maximum daily temperature) would reduce daily nest survival rates.

6) Daily precipitation. We hypothesized that daily nest survival rates decrease following precipitation events because one of the primary nest predators, the bull snake (*Pituophis melanoleucus*), shows increased activity immediately following such events (Gibbons and Semlitsch 1987).

Modeling the nest survival of mountain plovers

We used program MARK to model the daily survival of Mountain Plover nests primarily to better understand the effects of several biological factors on their daily nest survival, and secondarily to obtain an estimate of nest survival. Here, we used the product of daily nest survival rates across the 29-d incubation period as an estimate of nest survival. For our data, we standardized 19 May as day 1 and numbered all nest check dates sequentially thereafter. For each nest, we summarized the five pieces of information required by the nest survival model in program MARK. Year and sex were combined and modeled as groups, resulting in 12 groups for our analyses (two sex groups in each of six years). For each nest we also included 78 individual covariates. Measures of maximum daily temperature and daily precipitation were obtained from a weather station at the center of the study area. During our study, plover nests were active from 19 May to 3 August (77 d), regardless of year, which resulted in 76 estimates of daily nest survival. The remaining 76 individual covariates accounted for the daily age of the nest on each of the 76 d preceding an estimate of S_i. Beginning on the day the nest was found, we entered the nest age (in days) sequentially until it hatched at 29 d; all other values were zero. Thus, the nest age covariates took on values from 0 to 29. We always included covariates up to age 29 even if a nest was lost before reaching that age; once a nest was lost it contributed no additional information on survival and thus the age of the nest had no effect. We labeled these covariates Age1, Age2, . . . , Age76. We modeled daily nest age as a single parameter in MARK. As an example, we coded the encounter history for a single nest as

```
/*GGOO, 1995-076*/ 53 59 63 1 1 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 4 5 6 7 8 9 10 11 12
13 14 15 16 17 18 19 20 21 22 23 24 25 26 27;
```

where the first part was a comment section showing the bird and nest identification, followed by values of *k, l, m,* and *f* and the number of birds with this encounter history (always one in our example), and finally the 76 covariates for daily nest age.

Normally, individual covariates in MARK are standardized with a mean of zero and a range of $\pm$ ~3 standard deviations to increase the feasibility of the numerical parameter estimation. We did not standardize individual covariates for nest age in MARK because we would have had to standardize across all 76 individual covariates, and because the unstandardized range of these covariates did not hamper numerical optimization of the likelihood. MARK will usually identify problems encountered during numerical optimization, but a good strategy to verify numerical solutions is to re-run models with different initial values (using the Provide Initial Parameter Estimates option in MARK) to make sure the parameter estimates remain the same on successive model runs.

We limited our analyses to a small set of 12 a priori models that examined the effects of year, the sex of the incubating adult, daily nest age, time trends, and two weather covariates on the daily nest survival of Mountain Plovers. Our simplest model (Model 1; see list below), in which only a single daily nest survival rate was estimated, was analogous to the model described by Johnson (1979) and Bart and Robson (1982), except that we used a logit link instead of a log link (with the link function not making a difference in this model). We then modeled the main effects of year and sex separately (Models 2 and 3). For each of these two main effects models (year and sex), we fit two additional additive models, one with a linear and one with a quadratic time trend on daily nest survival (Models 4–7). Next, we added nest age effects to the set of three models containing the best main effect (sex, in our case; Models 8–10). Finally, we modeled the two weather covariates (maximum daily temperature and daily precipitation) by adding each one separately to the best model from the set of 10 models we had run thus far (Models 11 and 12). We reasoned that the weather covariates would have the same general effect on any particular model, so we chose to add them only to the best model to see if the addition of either weather covariate improved on the best model. Specifically, we considered the following 12 models in our analyses:

Model	Notation
1) Single estimate of daily survival	$S_{(.)}$
2) Effect of year only	S_{year}
3) Effect of sex only	S_{sex}
4) Effect of year plus a linear trend	$S_{\text{year}+T}$
5) Effect of year plus a quadratic trend	$S_{\text{year}+TT}$
6) Effect of sex plus a linear trend	$S_{\text{sex}+T}$
7) Effect of sex plus a quadratic trend	$S_{\text{sex}+TT}$
8) Effect of sex plus nest age	$S_{\text{sex}+\text{age}}$
9) Effect of sex plus a linear trend and nest age	$S_{\text{sex}+T+\text{age}}$

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Model (continued)	Notation
10) Effect of sex plus a quadratic trend and nest age	$S_{\text{sex}+TT+\text{age}}$
11) Best model plus maximum daily temperature effect	$S_{\text{sex}+TT+\text{age}+\text{temp}}$
12) Best model plus daily precipitation effect	$S_{\text{sex}+TT+\text{age}+\text{precip}}$

Estimating the survival of female- and male-tended nests

To estimate the probability that female- and male-tended Mountain Plover nests would survive the 29-d incubation period, we needed to account for possible sex-specific differences in nesting phenology. We assumed that differences in mean sex-specific nest initiation dates were not the result of changes in nest detection probabilities: our ability to detect nests was extremely high both within and between years. We first computed the weighted mean nest initiation date for birds of each sex based on observed nest data. We suspected observed nest initiation dates might have been biased relative to true nest initiation dates in our sample because of the ordering of clutches by sex and possible differential nest survival by sex. To address this possible source of bias, we adjusted the mean observed nest initiation dates for each sex using a Horvitz–Thompson estimator (Horvitz and Thompson 1952). To adjust for the number of nests that were initiated by each sex, we used the logistic regression equation from the best nest survival model to compute the probability that each nest had survived up to the date we actually found the nest. We then divided the observed frequency for each nest (always 1) by the probability that it survived until we found it and called the result the adjusted number of nests that would have been found had they survived, and that were initiated on the same day that the found nest was initiated. We then summed the frequencies of the adjusted number of nests by sex and calculated an adjusted mean nest initiation date for each sex. The use of this method provided an unbiased estimate of the number of nests that were initiated by each sex. As a best estimate of sex-specific nest survival, we used the adjusted mean nest initiation date for each sex and the logistic regression equation from the best model to compute nest survival (the product of 29 consecutive daily nest survival rates, beginning on the adjusted mean nest initiation date), ignoring the effects of daily precipitation.

To illustrate temporal patterns in sex-specific nest survival, we computed all possible estimates of nest survival during our study ($n = 48$; the maximum number of 29-d intervals in our 76-d nesting season). For each estimate, we started the nest at age 1 on day 1 and calculated successive daily nest survival rates using the logistic regression equation from the best model. Each estimate of nest survival was then the product of 29 daily nest survival rates. We tried computing the variances of these nest survival probabilities using the delta method (Seber 1982), but because these parameters were highly correlated and the underlying model was nonlinear, the delta method provided a poor estimate of precision. Therefore, we did not estimate precision for sex-specific nest survival estimates, but instead evaluated sex-specific differences by looking at the slope estimate for sex in our best model.

TABLE 2. Number of nests by sex and apparent nesting success for Mountain Plovers in southern Phillips County, Montana, USA, 1995–2000.

Year	Female-tended	Male-tended	Unknown	Total	Nesting success (%)
1995	10	13	46	69	57
1996	23	29	21	73	53
1997	26	40	21	87	57
1998	35	55	22	112	64
1999	50	50	13	113	45
2000	48	53	29	130	72
Total	192	240	152	584	58†

† 1 Standard error = 9.2.

RESULTS

We monitored 641 Mountain Plover nests during this study. Of this total, 57 had insufficient data for nest survival analyses and 152 were tended by birds whose sex was not determined, resulting in a sample of 432 nests to estimate nest survival (Table 2). We monitored these nests for a total of 5542 exposure days across a 77-d interval (19 May–3 August) during the six-year study. After removing 15 renesting efforts, the sex ratio of plovers observed on nests was 230 males (55%) and 187 females (45%). Males ($n = 10$) renested more often than females ($n = 5$), although the sample size was small. The mean age of nests when they were found was 11.9 d (± 7.50; 1 SD).

Observed mean initiation dates for nests tended by female and male Mountain Plovers did not differ (females, mean = 31 May ± 2.0 d, 1 SE; males, mean = 2 June ± 3.2 d; Fig. 2). When we adjusted these estimates for the time interval before they were found, the adjusted mean nest initiation dates still did not differ between sexes (females, mean = 27 May ± 6.2 d, 1 SE; males: mean = 26 May ± 8.4 d).

Estimates of nest survival

The daily survival of Mountain Plover nests was a function of both the sex of the incubating adult and nest age (Table 3). Nests tended by male Mountain Plovers had higher daily survival than those tended by females (Fig. 3). The estimate from the best model for the additive effect on survival of nests tended by males compared to females was $\hat{\beta}_{\text{male}} = 0.37$ (1 SE = 0.17, 95% CL = 0.03, 0.71) on a logit scale and this coefficient was always positive in models with sex effects. Models incorporating the daily age of the nest received

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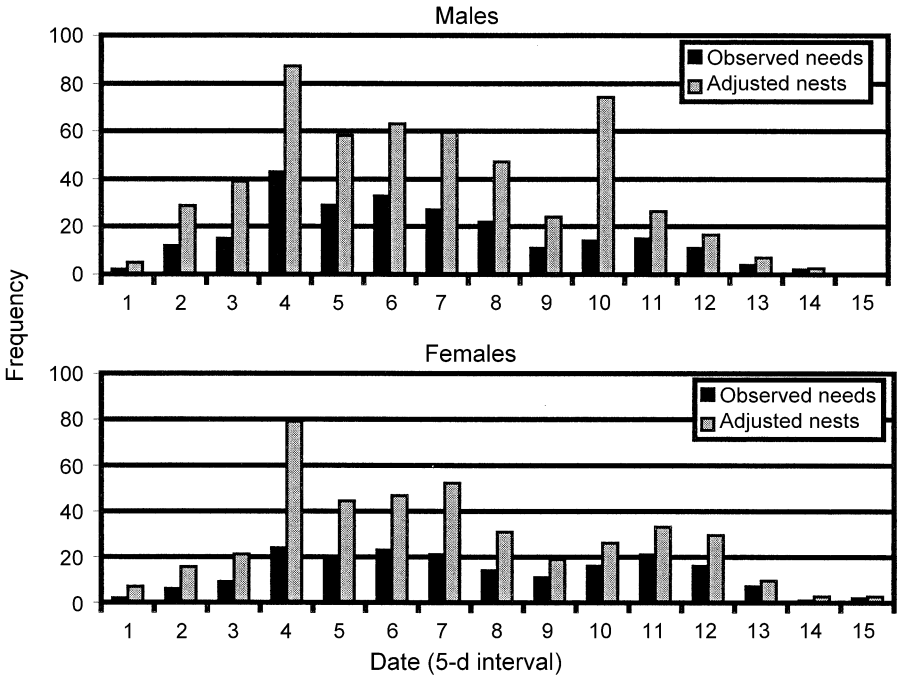

FIG. 2. Observed and adjusted initiation dates for female- and male-tended Mountain Plover nests in southern Phillips County, Montana, USA, 1995–2000. A Horvitz-Thompson estimator was used to calculate the adjusted number of nests that were initiated on the same day that the found nest was initiated and that would have been found had they survived. This information was then used to calculate a mean adjusted nest initiation date that adjusted for sex-specific nest survival rates. Date is shown by 15 five-day intervals beginning on 26 April and ending on 6 July (72 d; the last interval is only two days). Mean nest initiation dates did not differ by sex (observed: 31 May for females and 2 June for males; adjusted: 27 May for females and 26 May for males).

substantial support; in the best model, $\hat{\beta}_{age} = 0.06$ (1 SE = 0.01, 95% CL = 0.04, 0.09) on a logit scale and this effect was always positive in models with age effects. Models with quadratic trends on nest survival received strong support; linear trends received less support. The confidence intervals for the coefficients of both the linear and quadratic trends included zero. There was no evidence of direct year effects on nest survival.

TABLE 3. Summary of model selection results for the nest survival of Mountain Plovers in southern Phillips County, Montana, USA, 1995–2000.

Model	Deviance	K	AIC_c	ΔAIC_c	w_i
$S_{sex+age+TT+precip}$	858.29	6	870.39	0.00	0.56
$S_{sex+age+TT}$	862.09	5	872.15	1.76	0.23
$S_{sex+age}$	868.12	3	874.14	3.75	0.09
$S_{sex+age+TT+temp}$	862.06	6	874.16	3.76	0.09
$S_{sex+age+T}$	868.05	4	876.10	5.71	0.03
S_{sex+TT}	888.92	4	896.97	26.58	0.00
$S_{year+TT}$	885.07	8	901.25	30.85	0.00
S_{sex+T}	895.61	3	901.64	31.25	0.00
S_{sex}	897.76	2	901.77	31.38	0.00
$S_{(\cdot)}$	902.29	1	904.29	33.90	0.00
S_{year}	893.30	6	905.40	35.01	0.00
S_{year+T}	891.54	7	905.68	35.29	0.00

Notes: Models are ranked by ascending ΔAIC_c; w_i is the model weight and K is the number of parameters. Factors in models included year, sex, daily nest age (age), daily precipitation (precip), maximum daily temperature (temp), a linear time trend (T), a quadratic time trend (TT), and a model with constant daily nest survival ($\cdot$). Deviance is computed as $-2[\log_e(L(\theta)) - 2\log_e(L_s(\theta))]$ where θ represents a maximum likelihood estimate whose log-likelihood is evaluated for the model in question $[L(\theta)]$ and for the saturated model $[L_s(\theta)]$.

When maximum daily precipitation was added to the best model, it improved that model substantially (an increase of 1.76 ΔAIC_c units). The slope estimate for daily precipitation was negative ($\hat{\beta}_{precip} = -1.08$, 1 SE = 0.48, 95% CL = −2.02, −0.13) on a logit scale. Adding maximum daily temperature to the best model did not result in an improvement (2.00 ΔAIC_c units below the best model with the addition of a single parameter); the confidence interval for the effect of maximum daily temperature on a logit scale included zero ($\hat{\beta}_{temp} = 0.01$, 1 SE = 0.01, 95% CL = −0.02, 0.03).

The logistic regression equation (one standard error for each, β_i are shown below in parentheses) for the best model was

$$\text{logit}(\hat{S}_i) = \underset{(0.61)}{3.23} + \underset{(0.17)}{0.37}(\text{sex}) + \underset{(0.01)}{0.06}(\text{nest age}) - \underset{(0.04)}{0.06}T + \underset{(0.0007)}{0.001}TT - \underset{(0.48)}{1.08}(\text{precip})$$

To evaluate the effects of sex, precipitation, and daily nest age on the daily survival of Mountain Plover nests,

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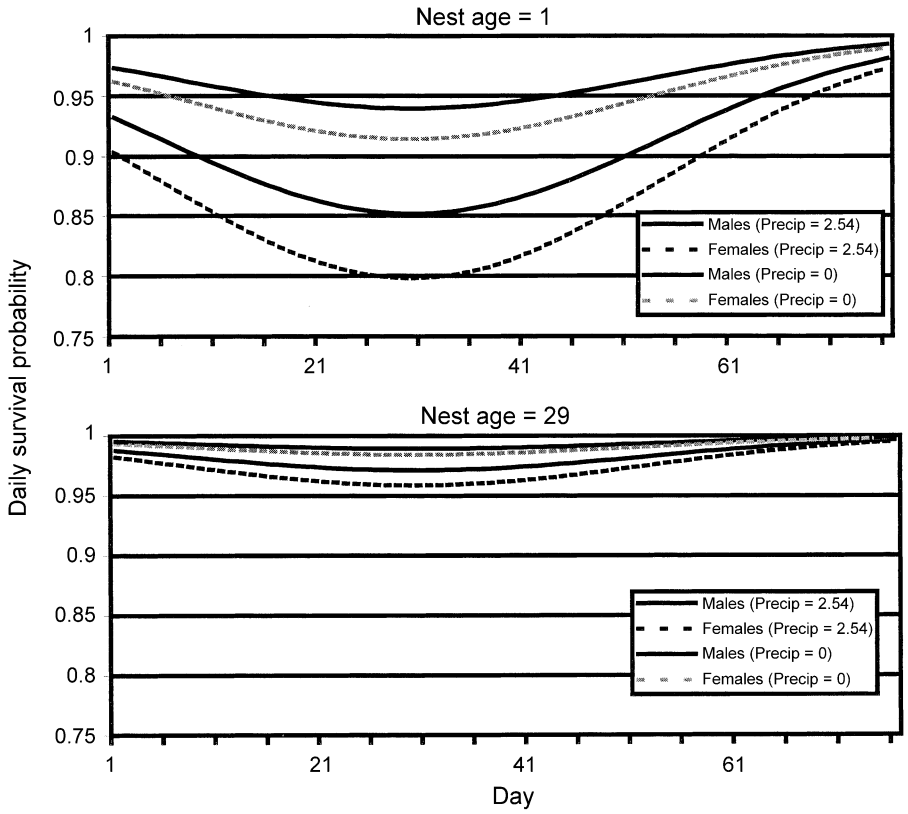

FIG. 3. The effects of nest age (1- and 29-d-old nests), sex, and daily precipitation (0 or 2.54 cm) on the daily survival rates of Mountain Plover nests in southern Phillips County, Montana, USA, 1995–2000. Day 1 corresponds to 19 May, and day 77 corresponds to 3 August.

we plotted curves showing these effects for selected values of each variable in the above equation. For nests early (nest age = 1) and late (nest age = 29) in incubation, we plotted the daily nest survival of female- (sex = 0) and male- (sex = 1) tended nests at levels of low (precip = 0 cm) and high (precip = 2.54 cm) precipitation. Daily nest survival rates of Mountain Plover nests gradually declined until midseason, and then gradually rose to a peak at the end of the nesting season (Fig. 3). When nest age was held constant at 1, nests tended by males had higher daily nest survival than nests tended by females, and daily nest survival was higher for both sexes when there was no precipitation (Fig. 3). Younger nests (age = 1) had low daily survival rates in mid-June. The daily survival of older nests (age = 29) showed a similar seasonal pattern, although the drop in mid-June was less pronounced.

Daily survival rates of nests of both sexes varied temporally. To illustrate seasonal patterns in daily nest survival rates and their precision, we plotted the predicted daily survival rate of three nests (one early season, one midseason, one late season) spread across the nesting season (Fig. 4). We generated estimates of the daily nest survival rate by substituting the appropriate values (sex of the incubating adult, daily nest age, linear and quadratic time trend coefficients, and daily precipitation) into the logistic regression equation for the best model, ignoring whether or not the nest actually survived. The pattern for each nest is similar to the patterns in Fig. 3 with daily survival increasing as the nest aged. The midseason nest had the lowest overall survival while the late nest had the highest survival. Precipitation events resulted in sharp drops in daily nest survival on some dates.

Success of female- and male-tended nests

The nest survival of Mountain Plovers varied temporally and followed the general pattern of daily nest survival rates with male-tended nests having much higher nest survival (Fig. 5). Because mean initiation dates did not differ between male- and female-tended nests, we used 26 May (the mean nest initiation date for males) to compute nest survival for both sexes. Using the logistic regression equation from the best model, the probability of a Mountain Plover nest surviving the 29-d incubation period beginning on 26 May was 0.33 for females and 0.49 for males. These estimates differ significantly because the logistic regression equation used to predict them contained the same six regression coefficients for each sex, with only the sex effect ($\hat{\beta}_{male}$) differing significantly between the

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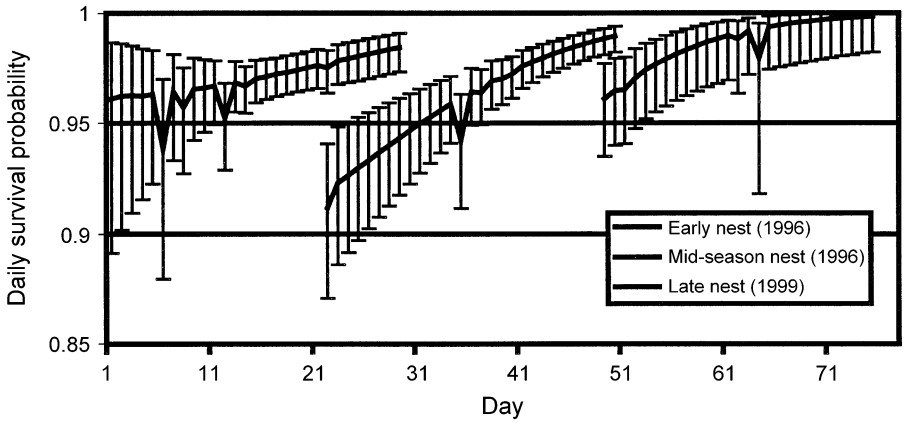

FIG. 4. Predicted daily survival rates and 95% confidence intervals for three Mountain Plover nests in southern Phillips County, Montana, USA, 1995–2000. Estimates and confidence intervals were generated using the logistic regression equation from the best model. These three nests span the entire nesting season with an early-season nest (19 May–16 June 1996; days 1–29), a midseason nest (9 June–7 July 1996; days 22–50), and a late-season nest (6 July–1 August 1999; days 49–75). Day 1 corresponds to 19 May, and day 77 corresponds to 3 August. The sharp downward spikes in each graph represent the effects of precipitation.

sexes, and because nest survival was measured across the same time interval for each sex.

DISCUSSION

Modeling avian nest survival

Avian nesting studies often report a measure of nest survival. Whether nest survival is reported for altricial (success during the incubation and nestling stages) or precocial (success during the incubation stage only) species, this measure is an important component of nesting ecology and the manner in which it is estimated is of critical importance.

We have introduced an improved method for estimating avian nesting success, as illustrated in our study of Mountain Plovers. In this study, we posed several specific hypotheses to explain variation in the daily nest survival of this species, and then rigorously addressed those hypotheses using the new nest survival model in program MARK. Our modeling results revealed that plover nest survival was best explained by a variety of factors including the sex of the incubating adult, nest age, a quadratic time trend, and daily precipitation. Our set of models allowed us to assess the importance of each of these variables relative to our original hypotheses, and to then generate daily nest survival estimates that reflected this variation. These findings are a substantial improvement over simple Mayfield constant-nest-survival estimates and permitted a more thorough exploration of the factors influencing nest survival in this species. This approach also removed the necessity to divide nest samples into discrete groups in order to test hypotheses about nest survival (e.g., program CONTRAST). In the next subsection, we discuss the interpretation of our results regarding the general modeling technique and then show how this approach will benefit others interested in estimating avian nest survival.

Interpretation of results and confounded effects

As with any model, a careful consideration of the assumptions is necessary before making inferences. Of the five assumptions listed in the *Methods* section, one (assumption 2) was not a problem in this study. The assumption that all nests could be aged when found (assumption 1) was violated because a small number of nests in the third incubation stage could not be aged and were assigned the mean age of that stage (13 d). This probably strengthened the age effect we found because the majority of these nests were <13 d old. The assumption of no observer impact on nest survival (assumption 3) was carefully considered and we at-

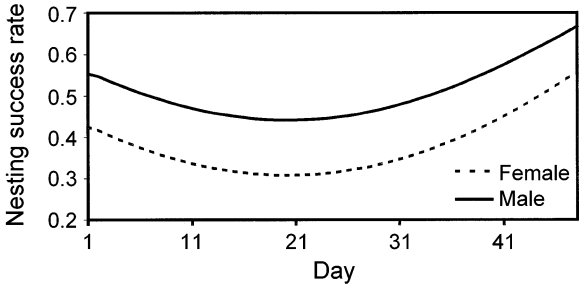

FIG. 5. Predicted sex-specific nest survival rates (the probability that a nest survives the 29-d incubation period, beginning on day x) for Mountain Plovers in southern Phillips County, Montana, USA, 1995–2000. Nest survival was calculated using the logistic regression equation from the best model, where the nest began at age 1 on day x and continued to age throughout the 29-d incubation period. This calculation was possible from 19 May to 5 July (days 1 to 48), where day refers to the starting date for each nest survival calculation.

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tempted to minimize disturbances during nest checks, marked the nests in an inconspicuous manner, and avoided harassing the incubating adult. As modeling techniques improve, it may soon be possible to rigorously examine observer effects on daily nest survival in program MARK (see Rotella et al. 2000). We cannot thoroughly address assumption 4 (independent fates of nests), although we believe this was not a problem because nests were widely dispersed on the landscape and we had no a priori reason to believe fates were dependent.

Several potentially confounded effects that could affect interpretation of the results merit additional discussion. We found strong evidence for differences in nest survival as a function of the age of the nest. Nest survival increased for older nests, supporting our initial hypothesis and the results of others (see Klett and Johnson 1982). Nest age, however, may be confounded with both temporal variation and individual heterogeneity. Temporal variation in nest survival was probably not a serious problem because our sample of nests spanned the entire nesting season with adequate samples of nests of differing ages throughout that time span (see Fig. 2). Differences due to individual heterogeneity cannot be dismissed so easily. If individual nests differed inherently in their survival, then models incorporating heterogeneity might be appropriate. Nest age differences may have resulted because the most vulnerable nests were lost early in incubation; nests that were actually found tended to be those that had survived longer. If this were occurring, then modeling nest age effects as we did is one method of approximating this situation, which could perhaps be more thoroughly addressed using mixture models or models with full random effects (Burnham and Rexstad 1993, Natarajan and McCulloch 1999, Link et al. 2002). However, we agree with Klett and Johnson (1982) that confounding with heterogeneity may not be a serious problem, and in our example the nest age differences appeared real. We modeled nest age in an attempt to reduce the bias in nest survival estimates resulting from heterogeneity, but we cannot be certain that the nest age effect we detected was due to nest age alone, or was due to a combination of nest age, temporal variation, and individual heterogeneity.

Implications to future studies of nest survival

The techniques outlined here will have broad application to nesting studies of birds. Using the nest survival model in program MARK, researchers can now explore complicated nest survival models that were beyond consideration using the traditional Mayfield approach, and incorporate meaningful covariates into future analyses of nest survival. Some covariates to consider include measures of the body condition of the incubating adult (mass, percentage body fat, etc.), habitat characteristics of the nest site, measures of individual heterogeneity such as nest attentiveness, an individual bird's prior experience, observer effects on survival following nest checks (Rotella et al. 2000), and possibly others such as the use of random-effects models (Natarajan and McCulloch 1999) that might explain additional variation not accounted for by individual covariates. The flexibility to model nest survival in the presence of these covariates will promote a better general understanding of nest survival.

Our recommendations for future studies of nest survival include (1) obtaining sufficiently large samples of nests to generate estimates of daily nest survival with reasonable precision, (2) conducting nest checks at regular intervals that are spaced to obtain adequate encounter histories while avoiding undue disturbance, (3) incorporating group effects such as age and sex of the incubating adult into estimates of nest survival, and (4) using meaningful individual covariates such as nest age, body condition of the incubating adult, and habitat features of the nest site.

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