



## EFFECTS OF MATE AND SITE FIDELITY ON NEST SURVIVAL OF WESTERN SANDPIPERS (*CALIDRIS MAURI*)

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**ABSTRACT.**—We examined the effects of mate and site fidelity on Western Sandpiper (*Calidris mauri*) nesting success in a breeding population on the Yukon-Kuskokwim River Delta, Alaska (1998–2005). We estimated return rates (percentage of banded birds that returned to the site in the subsequent season) and mate fidelity among 533 individually marked birds (296 females and 237 males) and monitored 430 nests with sufficient data for nest-survival analyses. Return rates were lower for females (40%) than for males (65%). Annual divorce rates (both members of a pair returned and each mated with a new individual) ranged between 10 and 29%, with 4–26% of pairs reuniting annually. Reuniting pairs initiated clutches earlier than newly formed pairs, and clutches that were initiated early in the season had higher nest-success rates than those initiated later in the season. However, when initiation date was controlled, mate fidelity did not explain significant variation in daily nest survival rate. When we controlled for seasonal variation, nests tended by individuals with prior breeding-site experience had higher daily survival rates than those tended by birds breeding at the site for the first time. This effect was greater for males than for females. We also observed annual and seasonal variation in nest survival, as well as variation associated with nest age. Future study of the proximate causes of temporal variation would add considerably to our understanding of temporal effects on individual behavior, fitness, and population dynamics. Received 27 July 2006, accepted 2 March 2007.

Key words: behavior, *Calidris mauri*, dispersal, divorce, reproduction, shorebird, Western Sandpiper.

### Efectos de la Fidelidad de Pareja y de Sitio sobre la Supervivencia de Nidos en *Calidris mauri*

**RESUMEN.**—Examinamos la fidelidad de pareja y de sitio sobre el éxito de nidificación de *Calidris mauri* en una población reproductiva en el delta del río Yukon-Kuskokwim, Alaska (1998–2005). Estimamos las tasas de retorno (porcentaje de aves marcadas que retornaron al sitio en épocas sucesivas) y fidelidad de pareja entre 533 aves marcadas individualmente (296 hembras y 237 machos) y monitoreamos 430 nidos con datos suficientes para realizar análisis de supervivencia de nidos. Las tasas de retorno fueron menores para las hembras (40%) que para los machos (65%). Las tasas anuales de divorcio (ambos miembros de la pareja retornaron pero cada uno se emparejó con otro individuo diferente) variaron entre el 10 y el 29%, y un 4–26% de las parejas se volvieron a unir anualmente. Las parejas que se volvieron a unir iniciaron las nidadas antes que las parejas que se formaron por primera vez, y las nidadas que se iniciaron tempranamente durante la época reproductiva tuvieron un éxito de nidificación mayor que aquellas que fueron iniciadas más tarde. Sin embargo, al controlar por la fecha de iniciación, la fidelidad de pareja no explicó una variación significativa en la tasa de supervivencia diaria de nidos. Al controlar por la variación estacional, los nidos atendidos por individuos con experiencia previa del sitio de cría tuvieron tasas de supervivencia diaria más altas que aquellos que fueron atendidos por individuos que criaron en el sitio por primera vez. Este efecto fue mayor para los machos que para las hembras. También observamos variación anual y estacional en la supervivencia de nidos, como también variación asociada a la edad del nido. Estudios futuros sobre las causas inmediatas de la variación temporal podrían contribuir considerablemente al entendimiento sobre los efectos temporales sobre el comportamiento de los individuos, la adecuación biológica y las dinámicas poblacionales.

LOW NATAL PHILOPATRY and high adult breeding-site fidelity are typical for many migratory birds (Greenwood 1980, Greenwood and Harvey 1982), including shorebirds (Charadriiformes; Oring and Lank 1984). Interannual breeding dispersal could permit a bird

to breed at a higher-quality site or, during subsequent reproductive efforts, with a higher-quality mate. However, these potential advantages of dispersal are balanced by the risk that a dispersing bird may fail to find a new site, mate, or both, and lose all reproductive

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potential, or that the new site or mate could be of lower quality. Furthermore, reuniting with a prior mate or retaining a territory across seasons may be beneficial because breeding at a familiar site or with a familiar mate may have reproductive advantages (Oring and Lank 1982, 1984; Schieck and Hannon 1989). Breeding-site fidelity often differs between the sexes in birds (Clarke et al. 1997). With some exceptions (e.g., Anseriformes; Oring and Saylor 1992), males are generally more likely than females to return to the site where they bred the previous year (Greenwood and Harvey 1982, Drilling and Thompson 1988, Payne and Payne 1993). Male-biased site fidelity suggests that the costs of dispersal should be greater or the benefits of site fidelity greater, or both, for males (Ward and Weatherhead 2005). Knowing the location of resources (food, nest sites) and predators may make a familiar site more valuable than an unfamiliar site (Pärt 1994). Consequently, females should also benefit from site familiarity. However, monogamous females do not appear to compete for resources as much as males in many bird species (Lightbody and Weatherhead 1987), which may reduce the benefits of site familiarity for females compared with males (Ward and Weatherhead 2005). Male site familiarity may be especially advantageous in species where males have to compete for territories to attract mates (Paton and Edwards 1996, Schjorring et al. 2000), because dispersing individuals forfeit resident advantage (Davies 1978; Greenwood 1980, 1984; Krebs 1982; Desrochers and Hannon 1989).

Studies of avian mate fidelity and breeding-site fidelity typically examine whether individuals divorce or disperse more often after reproductive failure than after a successful reproductive effort (Martin 1974, Darley et al. 1977, Brooke 1978, Oring and Lank 1982). Numerous studies have shown that breeding-site fidelity is positively correlated with previous reproductive performance (Nolan 1978, Harvey et al. 1979, Newton and Marquiss 1982, Dow and Fredga 1983, Weatherhead and Boak 1986), and a causal link between breeding success and return rates has been demonstrated in a few species (Haas 1998, Hoover 2003). Consistent with this approach, hypotheses explaining breeding-site fidelity in birds (reviewed by Greenwood 1980) generally predict that birds return or disperse using a decision rule based on previous breeding experience (Darley et al. 1977, Gavin and Bollinger 1988, Bollinger and Gavin 1989). However, this approach may miss important benefits of mate and site fidelity, because the effects of prior breeding success on dispersal and mate and site fidelity are confounded with mortality and individual age. Most field studies are based on small spatial scales in relation to bird movement patterns. Thus, dispersing birds are not tracked, dispersal is not distinguished from mortality, and postdispersal fitness is not determined. Therefore, the proportion of birds returning to a particular study site and mate may reflect the cumulative decision of birds to remain faithful to a site or mate as opposed to dispersing to a new area or searching for a new mate, or may merely be indicative of mortality pattern, with low-quality individuals being more likely to perish (Askenmo 1979, Weatherhead and Boak 1986, Nol and Smith 1987). Furthermore, studies relating dispersal to prior nesting success cannot differentiate between the effects of nesting success, mate fidelity, and site fidelity on dispersal probability because of intercorrelations between these variables (Greenwood and Harvey 1982, Cézilly et al. 2000, Beheler et al. 2003). Nest failure may result from a low-quality territory or mate (Goodburn 1991), which, in

turn, may affect mate fidelity (Choudhury 1995, Dubois and Cézilly 2002) and site fidelity (Catlin et al. 2005). Further, disentangling the effects of site experience versus bird age can be difficult, because they are often confounded, and it is not possible to age many species after their first year. Young birds, with less breeding-site experience, commonly nest later in the season than older, more experienced conspecifics (Sæther 1990, Forslund and Pärt 1995, Martin 1995), and nest survival often decreases across the nesting season (Perrins 1970, Daan et al. 1988). As a result of all these difficulties, benefits of mate and site experience have seldom been quantified or even demonstrated. Disentangling the effects of mate fidelity versus site fidelity on nesting success generally requires long-term data from marked populations, because any benefit of reuniting is confounded with prior site experience.

Here, we used eight years of nest-survival data from a marked population to contrast nest-survival rates between individuals that were site-faithful and recent immigrants to the population, and modeled the effects of mate fidelity and site fidelity on Western Sandpiper (*Calidris mauri*) nest survival while controlling for temporal variation in clutch initiation. The Western Sandpiper is a long-distance migratory shorebird (Charadriiformes) that primarily breeds in western Alaska and exhibits male-biased breeding-site fidelity (Holmes 1971, 1973; Sandercock et al. 2000). The species has been studied previously in northern Alaska by Sandercock and colleagues (Sandercock 1998; Sandercock et al. 1999, 2000). We report results that contrast with those of Sandercock et al. (2000) and discuss reasons for these differences.

## METHODS

*Study species, site, and general methodology.*—We studied Western Sandpipers during 1998–2005 at the Yukon Delta National Wildlife Refuge's Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta (YKD), Alaska (61°22'N, 165°07'W). On the YKD, Western Sandpipers inhabit upland tundra habitat that is typically a mosaic of patches, some of which contain graminoid species and some of which do not, with intermingled wet, low-lying areas (lowland moist low-scrub community; Jorgenson and Ely 2001, Johnson and McCaffery 2004). Western Sandpipers are socially and genetically monogamous and exhibit biparental care of eggs and young (Holmes 1971, 1973; Blomqvist et al. 2002). After arriving on the breeding grounds, males establish territories on upland tundra habitat and advertise for mates (Brown 1962, Holmes 1971, Lanctot et al. 2000). Both parents share incubation of their four-egg clutches for 27 days (Holmes 1971, 1973; Sandercock 1997). In 1998 and 2002, data were gathered primarily on a 16-ha plot (1998: 43 nests monitored, 53 adults banded; 2002: 58 nests monitored, 28 adults banded). During the other six years of study, data were collected on an additional 20 ha surrounding the original plot (36 ha total; mean  $\pm$  SD number of nests monitored per year =  $113 \pm 25$ , mean  $\pm$  SD number of adults banded per year =  $89 \pm 16$ ).

During all years, two to four observers surveyed daily from early May through late July for banded birds, nests, and broods. Adults and chicks were marked with a federal identification band as well as with unique combinations of UV-stable color bands at the nest (chicks marked with color bands only from 2003 to 2005).

Adults were sexed by culmen length during banding (>93% of all birds; Page and Fearis 1971, Cartar 1984). When culmen length was inconclusive (24–25 mm), birds were sexed via behavior (courtship displays, copulation position) and size comparison with their mate (females larger than males; Sandercock et al. 2000). Nest locations were mapped, and nests were checked every one to four days through hatch, predation, or abandonment. Nest age was determined by backdating incomplete clutches (1.5 days per egg, based on known-age nests at the site; M. Johnson and J. R. Walters unpubl. data) or by floating eggs (Sandercock 1998). Nests hatching  $\geq 1$  egg were considered successful. For analyses, we considered only a pair's initial nesting attempt in a season. Pairing events in different years were considered to be independent, because the sexes spend the nonbreeding season at different locations and mate choice occurs annually (Sandercock et al. 2000). The terms "divorced" and "reunited" refer to pairs in which both members returned but each mated with a different or the same individual, respectively.

*Clutch initiation date.*—We used SAS PROC MIXED to compare mean clutch initiation date between pairs that previously nested together and pairs breeding together for the first time (analysis of variance [ANOVA]; Littell et al. 2002). Clutch initiation date was the dependent variable in the model, and prior mate experience was a two-level fixed-factor independent variable (1 = yes, 0 = no). We also used SAS PROC MIXED to compare mean clutch initiation date among pairs in four site-experience classes (0, 1, 2, and >3 years of prior site experience). Although some of these pairs had previously bred at the site, they had not bred with each other. Initiation date was the dependent variable in this model, and number of years prior site experience was a four-level fixed-factor independent variable (female site experience = male site experience, first to fourth year at the site). We also included year as a random factor in both models to partially control for annual variation. For the model that contrasted reuniting pairs with pairs breeding together for the first time, we compared mean initiation date using least-square means. For the model comparing pairs with zero through three years of site experience, we compared mean initiation date using the step-down Bonferroni adjustment. After a square-root transformation, residuals from both models were normally distributed (Shapiro-Wilk tests,  $P > 0.10$ ) and had homogeneous variance.

*Parameter and model selection.*—We used a priori hypotheses to develop specific models to explain variation in the nest survival of Western Sandpipers. We modeled daily survival of Western Sandpiper nests primarily to better understand the effects of mate and site experience on daily nest survival, and secondarily to obtain an estimate of nest survival. We estimated nest survival as the product of daily nest-survival rates across the 27-day incubation period using MARK (Dinsmore et al. 2002, Cooch and White 2007). To examine the effect of site experience on Western Sandpiper nest success, we considered the first two seasons of data (1998–1999) as baseline data, and modeled nest survival using the remaining six years of data (2000–2005). By doing so, we effectively established an individually marked population with known breeding histories. In 2000 and thereafter, we considered all unbanded birds to be first-time breeders at the site (no site experience). Because of our low sample size for birds breeding at the site for more than four years (22 males and 17 females),

we considered all birds breeding at the site for more than four years to have three years prior site experience in analyses. We also assumed that immigrants did not have prior mate experience with any individuals in the study population.

We incorporated six sources of variation into our nest survival models.

1. Year: We observed an apparent decline in nest success during the study (M. Johnson and J. R. Walters unpubl. data); therefore, we modeled the effect of year to account for annual variation.
2. Temporal variation within seasons: We fit a constant nest-survival model to our data, as well as two time-trend models, to evaluate temporal variation in the daily survival rate of nests across the nesting season. A linear time trend was modeled initially, because daily nest survival often decreases across the nesting season (Perrins 1970, Daan et al. 1988). We also fit a quadratic time-trend model that allowed daily nest survival to follow a curvilinear pattern (Dinsmore et al. 2002).
3. Nest age: Among precocial species, daily survival rate of nests may be higher for older nests because nests in locations most at risk will be depredated early (Klett and Johnson 1982). To reduce potential confounding of nest age effects and temporal variation in daily nest survival rates, we created individual covariates that were each nest's age on each day of the nesting season using the add function in the design matrix of MARK (Cooch and White 2007).
4. Mate experience: We hypothesized that pairs that bred together in a previous season would have higher daily nest-survival rates in the current season compared with birds that were pairing for the first time. We modeled prior mate experience as a binomial covariate (no prior pair experience, nested together in the previous breeding season).
5. Female experience at site: We hypothesized that mated pairs in which the female had site experience would have higher daily nest-survival rates than pairs in which the female was breeding at the site for the first time. We modeled female site experience as a continuous variable, indicating the number of years an individual was observed breeding at the site (first year, second year, third year, fourth year).
6. Male experience at site: We hypothesized that mated pairs in which the male had site experience would have higher daily nest-survival rates than pairs in which the male was breeding at the site for the first time. We modeled male site experience as a continuous variable, indicating the number of years an individual was observed breeding at the site (first year, second year, third year, fourth year).

The effects of female and male site experience on Western Sandpiper nest survival are confounded with age. On the basis of plumage characteristics, we differentiated first-year Western Sandpipers (birds that hatched in the previous breeding season) from birds that are two years old and older (Sandercock et al. 1999). Our sample of first-year birds is limited (24% of females and 17% of males were banded as first-year birds), and only 1% of natal birds returned to the site (1999–2005; M. Johnson and R. J. Walters unpubl. data). Thus, we do not have an estimate of age for most individuals, but we have robust estimates of breeding-site experience. We therefore refer to the combined effects of

bird age and breeding-site experience as breeding-site experience, but consider possible roles of both age and site experience in interpreting our results.

We used a two-phase approach to model daily nest survival, following Dinsmore et al. (2002). We first constructed a base model that included the effects of year, seasonal variation, and nest age on daily survival rate. We then added mate- and site-fidelity covariates to the best base model(s). Mate fidelity and site fidelity should have the same general effect on any particular model controlling for temporal variation (annual and seasonal) and nest age, so we added these covariates only to the best model(s) to see whether their addition improved on the best model(s) (Dinsmore et al. 2002). During phase I, we limited our analysis to 11 *a priori* models (Table 1). Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ) was computed for each model to compare model ranks and weights in determining the likelihood of each model, given the data (Burnham and Anderson 1998, Anderson et al. 2000). We then used model selection results from phase I to test *a priori* hypotheses that mate and site experience positively affect nest survival of Western Sandpipers. During phase II of model construction, we considered all base models from phase I that were within two  $AIC_c$  units from the best-fit model. We added three covariates (prior mate experience, female site experience, and male site experience) to the top-performing model(s) from phase I. These covariates were added to the top-performing model(s) individually, with male and female site experience paired, male or female site experience paired with mate experience, and the additive effects of site experience for each sex and prior mate experience (Table 1). Models examining the effects of mate and site experience were ranked using  $AIC_c$ , and model weights ( $w_i$ ) were used to determine the likelihood of each model given the data (Burnham and Anderson 1998, Anderson et al. 2000).

**Contrasting model estimates.**—We computed estimates of nest survival for all possible dates of clutch initiation during our study (thirty-two 27-day incubation intervals in a 59-day nesting season). Nest survival was calculated using the logistic regression equation from the best model, in which the nest began at age 1 on day  $x$  and aged throughout the 27-day incubation period (Dinsmore et al. 2002). Each estimate of nest survival was the product of 27 daily nest-survival rates. Computing variance associated with these nest-survival probabilities is possible through the delta method (Seber 1982), but because the underlying model was nonlinear, and model parameters were correlated, this is a poor estimator of precision (Dinsmore et al. 2002). We therefore evaluated experience effects by examining the slope estimates for mate and site experience in our best model(s).

## RESULTS

We individually marked 533 breeding sandpipers (296 females and 237 males) from 1998 through 2004. Return rate (percentage of banded birds that returned to the site in the subsequent season) was lower for females (40%) than for males (65%). We monitored 660 Western Sandpiper nests between 11 May and 17 July, 2000–2005. Of these, 512 were initial nesting attempts and, of those, 39 had insufficient data for nest-survival analyses and 43 were experimentally manipulated and not included in

TABLE 1. Hypothesis-driven *a priori* models of daily nest survival in Western Sandpipers at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005. Model construction occurred in two phases. During phase I, we constructed a base model that included the effects of year, seasonal variation, and nest age on nest daily survival rate (11 models). During phase II, we used the best model(s) from phase I of model construction to test the hypotheses that mate and breeding-site experience affect nest survival of Western Sandpipers.

Model parameters	Notation
Phase I: Base models	
Single estimate of daily survival	$S_{\text{CONSTANT}}$
Effect of year only	$S_{\text{YEAR}}$
Effect of nest age only	$S_{\text{AGE}}$
Linear seasonal trend	$S_{\text{T}}$
Quadratic seasonal trend	$S_{\text{TT}}$
Linear seasonal trend plus year	$S_{\text{T+YEAR}}$
Linear seasonal trend plus nest age	$S_{\text{T+AGE}}$
Linear seasonal trend plus year and nest age	$S_{\text{T+AGE+YEAR}}$
Quadratic seasonal trend plus year	$S_{\text{TT+YEAR}}$
Quadratic seasonal trend plus nest age	$S_{\text{TT+AGE}}$
Quadratic seasonal trend plus year and nest age	$S_{\text{TT+AGE+YEAR}}$
Phase II: Mate and site experience models	
Base model(s) from phase one of model construction	$S_{\text{BM}}$
BM + effect of mate experience	$S_{\text{BM+MATE}}$
BM + effect of female site experience	$S_{\text{BM+FEMALE}}$
BM + effect of male site experience	$S_{\text{BM+MALE}}$
BM + effect of female + male site experience	$S_{\text{BM+FEMALE+MALE}}$
BM + effect of mate experience + female site experience	$S_{\text{BM+MATE+FEMALE}}$
BM + effect of mate experience + male site experience	$S_{\text{BM+MATE+MALE}}$
BM + effect of mate experience + female + male site experience	$S_{\text{BM+MATE+FEMALE+MALE}}$

TABLE 2. Pairing of Western Sandpipers in relation to number of years of breeding experience at Kanaryarmiut Field Station, Yukon-Kuskokwim Delta, Alaska (number of pairs, 2000–2005,  $n_{\text{nests}} = 430$ ).

Male experience (years)	Female experience (years)			
	1	2	3	4
1	39	34	5	5
2	44	81	10	10
3	22	24	16	5
4	33	46	21	35

analyses. This resulted in a sample of 430 nests to estimate Western Sandpiper nest survival over a 59-day nesting season (11 May to 9 July; Table 2). Seventy-five percent of these nests failed to hatch at least one egg ( $n = 324$ ). Predation was the primary cause of nest failure (96% of failed nests), with 4% of nests being abandoned before hatch. We observed Long-tailed Jaeger (*Stercorarius longicaudus*), Glaucous Gull (*Larus hyperboreus*), Mink (*Mustela vison*), Arctic Fox (*Alopex lagopus*), and Red Fox (*Vulpes vulpes*) depredating nests and preying on young at the site. However, we have no data on the relative influence of these predators on Western Sandpiper nesting success.

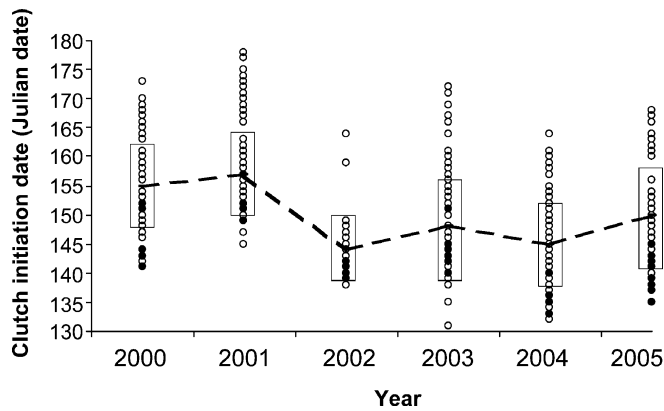


FIG. 1. Clutch initiation dates for Western Sandpipers at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005 ( $n = 430$ ). Open circles represent pairs attempting reproduction together for the first time, and closed circles represent pairs that bred together during the previous season. Dashed line indicates mean annual clutch initiation date (open rectangles indicate mean  $\pm$  SD).

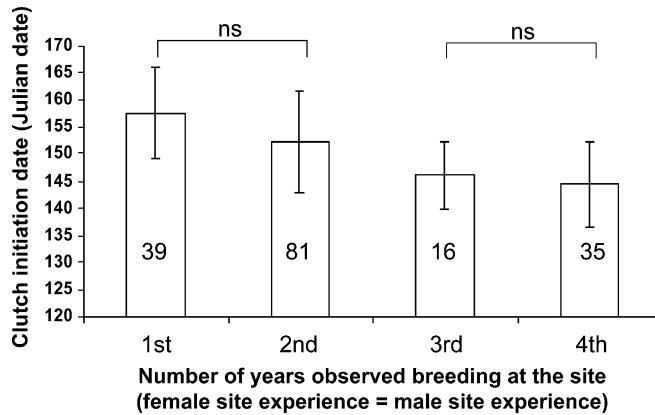


FIG. 2. Clutch initiation dates (mean  $\pm$  SD) for Western Sandpiper pairs with no prior mate experience and zero to three years site experience at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005 ( $n = 171$ ). Numbers within bars indicate number of pairs in each experience class. All mean comparisons are statistically different, except as indicated; all  $P < 0.001$ .

Most nests were located before clutch completion (mean  $\pm$  SD number of days post-initiation that nests were discovered =  $2.6 \pm 3.0$ ). Mean clutch-initiation date varied annually ( $F = 27.3$ ,  $df = 5$  and  $424$ ,  $P < 0.001$ ), and individuals that bred with a prior mate initiated clutches earlier than pairs breeding together for the first time ( $F = 27.3$ ,  $df = 1$  and  $423$ ,  $P < 0.001$ ; Fig. 1). Among individuals breeding together for the first time, birds with more years of experience at the site tended to initiate clutches earlier ( $F = 11.8$ ,  $df = 3$  and  $162$ ,  $P < 0.001$ ; Fig. 2). Annual divorce rate (both members of a pair returned and each mated with a new individual) ranged between 10 and 29%, with 4–26% of pairs reuniting annually (Table 3).

TABLE 3. Interannual mate-fidelity rates of Western Sandpipers at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 1998–2005.

Year	Number of pairs	One returned <sup>a</sup> (%)	Both returned and divorced <sup>b</sup> (%)	Both returned and reunited <sup>c</sup> (%)	Uncertain status <sup>d</sup> (%)
1998–1999	24	54.2	20.8	4.2	20.8
1999–2000	33	42.4	12.1	15.2	30.3
2000–2001	58	20.7	25.9	25.9	27.5
2001–2002	42	40.5	9.5	11.9	38.1
2002–2003	55	36.4	20.0	18.1	25.5
2003–2004	55	43.6	29.1	12.7	14.6
2004–2005	53	50.9	11.3	18.9	18.9
Total	320	39.7	19.1	16.6	24.6

<sup>a</sup>One bird returned and mated with a new individual.

<sup>b</sup>Both members of a pair returned, and each mated with a new individual.

<sup>c</sup>Both members of a pair returned and reunited.

<sup>d</sup>Prior or current pairing status not confirmed.

Phase I model-selection results indicated that the daily survival of Western Sandpiper nests exhibited nonlinear temporal variation within seasons, given that the top four models (less than two  $AIC_c$  units from the top model) all contained a quadratic time trend (Table 4). Year and nest age also had strong support in two of the four top models; however, none of the four top models was weighted exceptionally high compared with the others ( $w_i$  of top models: 0.17–0.33; Table 4), and all were within two  $AIC_c$  units of the best-fit model. Therefore, we used all four models as our base model during phase II of model selection and added the seven *a priori* models to each of these four base models.

TABLE 4. Summary of model selection results for a model of Western Sandpiper daily nest survival that included the effects of year, seasonal variation, and nest age (Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005,  $n_{\text{nests}} = 430$ ).

Model structure <sup>b</sup>	Model statistics <sup>a</sup>			
	$K$	Deviance	$\Delta AIC_c$	$w_i$
$S_{TT}$	3	1,749	0.0	0.33
$S_{TT+YEAR}$	4	1,747	0.4	0.27
$S_{TT+AGE}$	4	1,748	1.1	0.19
$S_{TT+AGE+YEAR}$	5	1,746	1.3	0.17
$S_{T+AGE+YEAR}$	4	1,754	7.6	<0.01
$S_{T+AGE}$	3	1,756	7.8	<0.01
$S_T$	2	1,759	8.0	<0.01
$S_{T+YEAR}$	3	1,757	8.01	<0.01
$S_{AGE}$	2	1,770	19.3	<0.01
$S_{YEAR}$	2	1,785	34.0	<0.01
$S_{CONSTANT}$	1	1,788	34.9	<0.01

<sup>a</sup>Model fit by the number of parameters ( $K$ ), deviance, model weight ( $w_i$ ), and the difference in Akaike's Information Criterion ( $\Delta AIC_c$ ) from the best-fit model.

<sup>b</sup>Model factors included YEAR, daily nest age (AGE), linear seasonal trend (T), quadratic seasonal trend (TT), and a model with constant daily nest survival (CONSTANT).

TABLE 5. Summary of model-selection results for a model of daily nest survival in Western Sandpipers that included the effects of annual and seasonal variation and nest age, as well as mate- and site-experience effects (Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005,  $n_{\text{ests}} = 430$ ).

Model structure <sup>b</sup>	Model statistics <sup>a</sup>			
	<i>K</i>	Deviance	$\Delta\text{AIC}_c$	$w_i$
$S_{\text{TT+AGE+YEAR+FEMALE+MALE}}$	7	1,728	0.0	0.42
$S_{\text{TT+AGE+YEAR+FEMALE+MALE+MATE}}$	8	1,728	1.9	0.16
$S_{\text{TT+AGE+YEAR+MALE}}$	6	1,732	2.6	0.11
$S_{\text{TT+YEAR+FEMALE+MALE}}$	6	1,734	3.9	0.06
$S_{\text{TT+AGE+YEAR+MALE+MATE}}$	7	1,732	4.1	0.05
$S_{\text{TT+AGE+FEMALE+MALE}}$	6	1,735	4.9	0.04
$S_{\text{TT+YEAR+MALE}}$	5	1,737	5.1	0.03
$S_{\text{TT+YEAR+FEMALE+MALE+MATE}}$	7	1,733	5.7	0.02
$S_{\text{TT+AGE+MALE}}$	5	1,738	6.2	0.02
$S_{\text{TT+YEAR+MALE+MATE}}$	6	1,737	6.8	0.01
$S_{\text{TT+FEMALE+MALE}}$	5	1,739	6.9	0.01
$S_{\text{TT+AGE+FEMALE+MALE+MATE}}$	7	1,735	6.9	0.01

<sup>a</sup>We described model fit by the number of parameters (*K*), deviance, model weight ( $w_i$ ), and the difference in Akaike's Information Criterion ( $\Delta\text{AIC}_c$ ) from the best-fit model.

<sup>b</sup>Model factors included YEAR, daily nest age (AGE), a quadratic time-trend (TT), number of years female observed breeding at site (FEMALE), number of years male observed breeding at site (MALE), and prior mate experience (MATE).

Phase II model-selection results indicated that the daily survival of Western Sandpiper nests was a function of female and male site experience, nest age, and year, in addition to the seasonal effect (Table 5). Nests tended by parents with prior site experience had higher daily survival rates than nests tended by parents breeding at the site for the first time. The estimates from the best model for the additive effect on survival of nests tended by females and males with site experience were  $\hat{\beta}_{\text{female}} = 0.45$  (SE = 0.21) and  $\hat{\beta}_{\text{male}} = 0.59$  (SE = 0.17), and these coefficients were always positive in models with site-experience effects. Models incorporating the daily age of the nest received substantial support in the best model,  $\hat{\beta}_{\text{age}} = -0.03$  (SE = 0.01), and this coefficient was always negative in models with age effects, indicating that nest survival declined with nest age, contrary to our expectation. Daily survival of nests declined over the course of the study,  $\hat{\beta}_{\text{year}} = -0.09$  (SE = 0.03); and models with quadratic trends on nest survival during the breeding season received strong support; linear trends received less support (Tables 4–5). Model-selection results did not indicate that prior mate experience explained significant variation in Western Sandpiper nest survival. Prior mate experience was a factor in the second best-performing model but not in the best; otherwise, the models were identical (Table 5). Exclusion of prior mate experience improved the model substantially (an increase of 1.9  $\text{AIC}_c$  units), with support  $>2\times$  that received when prior mate experience was included (Table 5). Further, inclusion of prior mate experience did not reduce model deviance (Table 5), slope estimates for prior mate experience were inconsistent among models in which the variable appeared (range:  $-0.004$  to  $0.15$ ), and slope estimates were not significantly different than zero in any model. Therefore, we concluded that the logistic regression equation for the best model was (with standard error [SE] for each

$\hat{\beta}$  given below in parentheses)

$$\text{Logit}(\hat{S}_i) = 4.06 - 0.08 \text{ T} + 0.01 \text{ TT} - 0.03 (\text{nest age}) - \\ (0.40) (0.03) (0.006) (0.01) \\ 0.09 (\text{year}) + 0.59 (\text{male}) + 0.45 (\text{female}) \\ (0.03) (0.17) (0.21)$$

We plotted curves showing these effects for selected values of each variable in the above equation (Fig. 3) to evaluate the effects of male and female site experience and daily nest age on Western Sandpiper nest survival. For nests early (nest age = 1) and late (nest age = 27) in incubation, we plotted the daily nest survival for breeding pairs composed of birds with 0–3 years breeding experience at the site (first, second, third, or fourth year observed at the site). Daily nest-survival rates of Western Sandpiper nests gradually declined until just past midseason and rose slightly during the last part of the breeding season (Fig. 3). The seasonal drop in daily survival rate was less pronounced for younger nests. Nests tended by pairs with three to four years of site experience showed less seasonal variability than nests tended by pairs breeding at the site for the first time (Fig. 3). When nest age and date were held constant, nests tended by pairs with three to four years of site experience had higher daily nest survival than nests tended by pairs breeding at the site for the first time

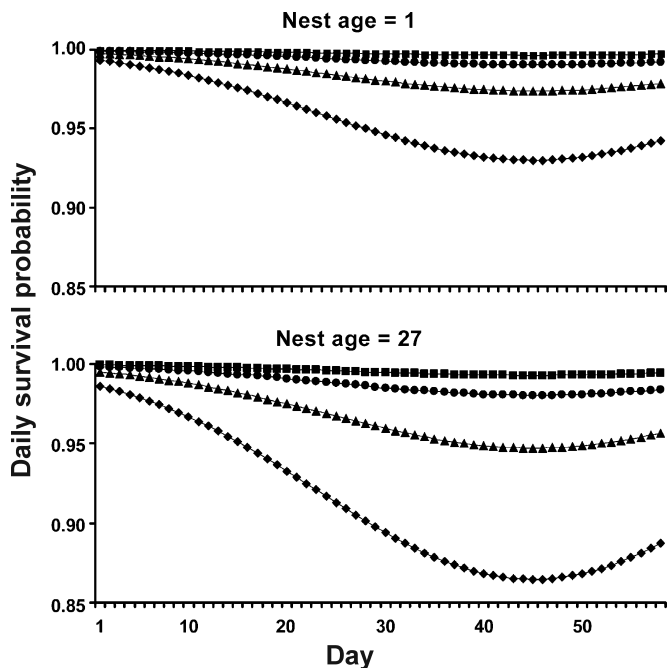


FIG. 3. Effects of nest age (1- and 27-day-old nests) and site fidelity (first to fourth year observed breeding at the site) on daily survival rates of Western Sandpiper nests at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005, as a function of time of season (Day). Female site experience = male site experience; number of years observed breeding at the site: diamonds = first, triangles = second, circles = third, and squares = fourth. Day 1 corresponds to 11 May, and day 59 corresponds to 8 July.

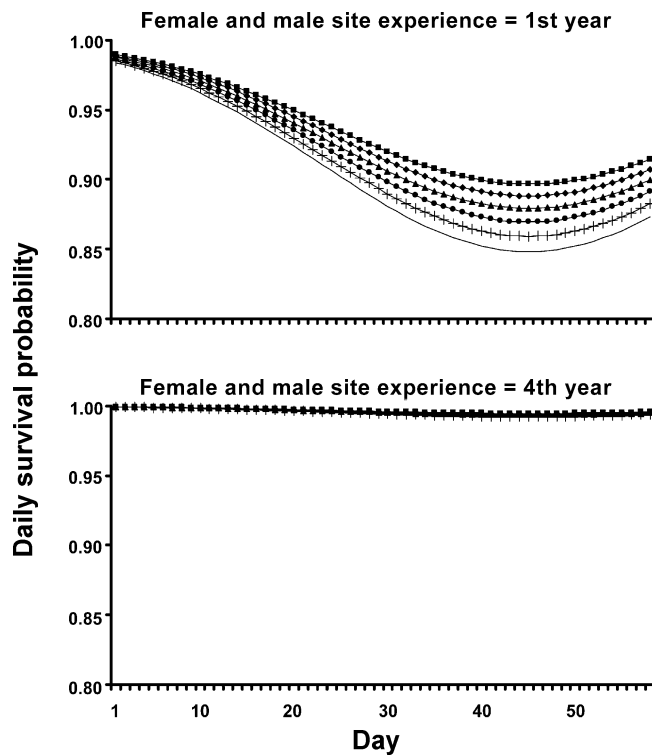


FIG. 4. Effects of site fidelity (first and fourth year observed breeding at the site) and year on the daily survival rates of Western Sandpiper nests at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005, as a function of time of season (Day). Female site experience = male site experience (first or fourth year observed breeding at the site), squares = 2000, diamonds = 2001, triangles = 2002, circles = 2003, crosses = 2004, and plain line = 2005. Day 1 corresponds to 11 May, and day 59 corresponds to 8 July.

(Fig. 3). Annual variation in daily survival probability for Western Sandpiper nests also was most apparent among pairs breeding at the site for the first time and less pronounced among pairs with site experience (Fig. 4).

In general, nest survival of Western Sandpipers varied temporally and followed the pattern of daily nest-survival rates increasing with the number of years of site experience (Fig. 5). We first used the mean initiation date for all 430 nests (2 June) to compute survival for nests tended by parents with varying site experience (small rectangles in Fig. 5). The probability of Western Sandpiper nests tended by parents with two or three years of site experience surviving the 27-day incubation period was 0.71 and 0.88, respectively. The probability of nests tended by parents with one year or no site experience surviving the incubation period was considerably lower (0.38 and 0.08, respectively). These estimates differ significantly, because the logistic regression equation used to predict them contained the same seven regression coefficients with only site experience differing ( $\hat{\beta}_{\text{female}} = \hat{\beta}_{\text{male}} = 1\text{--}4\text{ years}$ ), and because nest survival was measured across the same interval for each level of site experience (Dinsmore et al. 2002). Thus, nest-survival rates increased with the number of years of experience

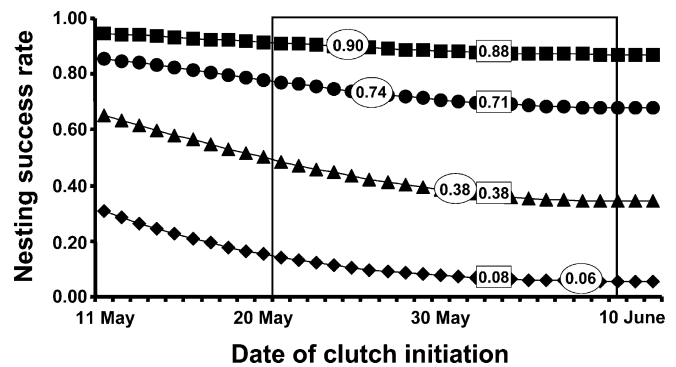


FIG. 5. Predicted nest-survival rates (i.e., the probability that a nest survives the 27-day incubation period beginning on day  $x$ ) for Western Sandpipers with varying breeding experience at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005. Nest survival was calculated using the logistic regression equation from the best model, in which the nest began at age 1 on day  $x$  and continued to age throughout the 27-day incubation period. This calculation was possible from 11 May to 11 June. Nest-survival estimates for pairs with none, one-, two-, and three-years site experience are given for nests initiated on the overall mean initiation date for the population in small rectangles (2 June; large open rectangular area =  $\pm$  SD), and for nests initiated on the mean initiation date for each experience class in small ovals (0 years = 7 June, 1 year = 1 June, 2 years = 26 May, 3 years = 25 May). Female site experience = male site experience; number of years observed breeding at the site: diamonds = first, triangles = second, circles = third, and squares = fourth.

at the site, independent of seasonal patterns in nest survival and variation associated with nest age. However, the effect of prior site experience on Western Sandpiper nesting success was even more pronounced when we incorporated both seasonal and nonseasonal effects (small ovals in Fig. 5). Nonseasonal differences in nesting success rate associated with prior site experience (small rectangles in Fig. 5) were amplified by incorporating variation in clutch initiation date associated with prior site experience (small ovals in Fig. 5). The overall mean initiation date for the population, regardless of prior site experience, was used to calculate nest survival rates given in the small rectangles in Figure 5, whereas the estimates given within small ovals in Figure 5 were calculated based on the mean initiation date for each experience class (0 years = 7 June, 1 year = 1 June, 2 years = 26 May, 3 years = 25 May).

We also used the logistic regression equation from the best model to examine the relative effect of site experience for each sex. We computed survival by systematically varying site experience for one member of the pair (first to fourth year at the site) while holding site experience constant at one and four years for the other member of the pair. For individuals breeding at the site for the first time (site experience = 1), females paired with more experienced males had higher nest survival than males pairing with more experienced females (Fig. 6). Among individuals with the most site experience (four years), variation in nest survival was greater among females (Fig. 6). Experienced males paired with inexperienced females had higher nest survival than experienced females paired with inexperienced males (Fig. 6).

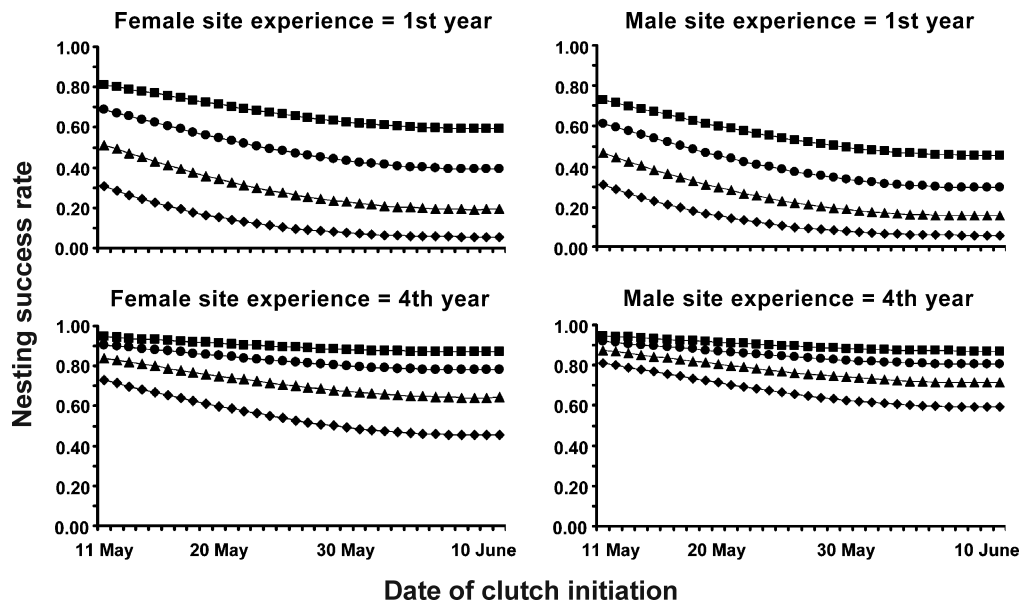


FIG. 6. Predicted nest-survival rates (i.e., the probability that a nest survives the 27-day incubation period beginning on day  $x$ ) for Western Sandpiper pairs with varying breeding experience at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005. Nest survival was calculated using the logistic regression equation from the best model, in which the nest began at age 1 on day  $x$  and continued to age throughout the 27-day incubation period. This calculation was possible from 11 May to 11 June. Female and male site experience (number of years observed breeding at the site) were held constant at one and four years while varying mate site experience between one and four years (number of years mate bred at site: diamonds = first, triangles = second, circles = third, squares = fourth).

## DISCUSSION

Roughly half of all Western Sandpipers banded at our site exhibited breeding-site fidelity, and males generally returned in greater numbers than females. This result is consistent with previous studies of Western Sandpipers (Holmes 1971, 1973; Sandercock et al. 2000), other monogamous shorebird species (Soikkeli 1967, Oring and Lank 1982, Gratto et al. 1985, Haig and Oring 1988, Flynn et al. 1999), and birds in general (Clarke et al. 1997). Male and female Western Sandpipers that were site-faithful had higher nesting-success rates than recent immigrants when we controlled for seasonal trends, but prior mate experience (mate fidelity) did not directly affect nesting success. Instead, reuniting pairs initiated clutches earlier than newly formed pairs, and clutches that were initiated early in the season had higher nest-success rates than those initiated later in the season. Western Sandpiper nesting success also exhibited annual declines from 2000 to 2005, and older nests had lower daily survival rates than younger nests.

Studies of avian mate and breeding-site fidelity typically examine whether individuals divorce or disperse more often after reproductive failure than after a successful reproductive effort (Martin 1974, Darley et al. 1977, Brooke 1978, Harvey et al. 1979, Oring and Lank 1982, Oring et al. 1983); instead, we contrasted nest daily survival rates between individuals that were site-faithful and recent immigrants to the population. Both methods are flawed, because the effects of prior breeding success on dispersal and site fidelity are confounded with mortality and individual age. Neither approach revealed a direct positive effect of mate fidelity on nesting success for Western Sandpipers. Nest success in the previous

season was higher among divorcing pairs (91% of nests hatched) than among reuniting pairs (63% of nests hatched); and clutch size, volume, and initiation date did not differ between divorcing and reuniting pairs near Nome, Alaska (Sandercock et al. 2000). Further, adult mortality and factors associated with migration (synchrony of arrival and clutch initiation) were not correlated with mate fidelity (Sandercock et al. 2000). In our study, prior mate experience also did not directly affect Western Sandpiper nesting success; rather, mate fidelity had positive effects on reproductive success via the timing of reproduction. Clutch initiation date was less variable near Nome (34-day range, 80% of nests initiated within a two-week period; Sandercock et al. 1999, 2000) than on our study site (48-day range, 60% of nests initiated within a two-week period), and variation in breeding-season length is likely the result of latitudinal differences between the two sites (Nome = 64°N, Kanaryarmiut Field Station = 61°N). Thus, differences in the timing of reproduction between reuniting and newly formed pairs of Western Sandpipers that we observed may not be feasible for birds breeding farther north because of the truncated breeding season near Nome.

Among pairs breeding together for the first time, prior site experience directly affected nesting success, because nests tended by parents with two or three years of site experience survived to hatch at a significantly higher rate than nests tended by parents with one year or no site experience when we controlled for variation in clutch initiation date. Direct effects of prior site experience on nesting success were indirectly exaggerated by the negative correlation between clutch initiation date and number of years of breeding experience at the site. Both of these patterns may have



resulted from variation associated with individual age rather than prior site experience, because our measure of breeding-site fidelity is confounded by bird age. Younger, less experienced individuals may be more likely to disperse than older individuals (Bollinger and Gavin 1989, Newton 1993, Daniels and Walters 2000), which could have biased our sample of site-faithful birds toward older individuals. However, given that >75% of immigrants to the population were two years old and older, and that nesting success rate continued to increase with number of years of prior experience at the site (i.e., nest success rate did not level off after one to two years of site experience), there is likely some effect of site experience on nesting success in Western Sandpipers.

Sex-specific benefits associated with site familiarity are correlated with variation in breeding-site fidelity in several avian species (Hinde 1956, Greenwood 1980, Bensch and Hasselquist 1991). Contrary to our findings, however, previous studies reported that female site experience, not male site experience or mate fidelity, affected male display rate and clutch initiation date in Western Sandpipers near Nome, Alaska, and neither male nor female site experience significantly affected nesting success (Sandercock et al. 1999, Lanctot et al. 2000). Site-faithful male Western Sandpipers may use prior site knowledge to select high-quality habitat, and prior experience also may facilitate territory acquisition and defense. Males that spend less time defending their territory can spend more time soliciting females (Holmes 1973, Lanctot et al. 2000), potentially attracting a higher-quality or better-matched mate (Coulson 1972). Further, site experience may improve female foraging efficiency and expedite both mate choice and the onset of fertility if site-faithful females have prior knowledge of resources such as food and high-quality nest sites (Pärt 1994). We suspect that in the shorter breeding season near Nome, nest-site selection by females is paramount; whereas at our study site, male territory acquisition is more important. Regardless, prior site experience by both members of a pair may accelerate pair formation that could explain the negative correlation we observed between clutch initiation date and number of years of breeding experience at the site. Nonseasonal differences in nesting success rate associated with prior site experience were amplified by variation in clutch initiation date, but male detection–arrival date did not vary with prior site experience (M. Johnson and J. R. Walters unpubl. data). However, we could not accurately quantify arrival and pairing date for recent emigrants, because they were not individually marked before incubation, and estimating female arrival date is problematic because birds regularly forage in areas not surveyed and, as a result, they are not necessarily detected upon arrival (many females are not detected until paired with a male or even after clutch initiation).

In contrast to altricial birds, where nests farther along in the nest cycle may be more conspicuous to predators as a result of increased nest visitation rate by provisioning parents (Gill 1995), older nests are expected to have higher daily survival rates among precocial birds, because nests located in areas most at risk are generally depredated early (Klett and Johnson 1982, Dinsmore et al. 2002). However, older Western Sandpiper nests had lower daily survival rates than younger nests. The effect of nest age on nest survival was greatest for birds breeding at the site for the first or second time, whereas nest survival among birds with more than two years of site experience varied little with nest

age. Similar to the effects of nest age, annual variation in nest survival was more pronounced in birds breeding at the site for the first time. Increases in nest survival with site experience may be attributable, in part, to nest-site reuse by experienced birds. Western Sandpipers reuse nest cups across years, or use nest cups previously occupied by heterospecifics and conspecifics, or both (Holmes 1971, Sandercock et al. 2000). Nesting success may increase with site experience as birds discover, reuse, and take over safe microsites on the tundra. Similarly, a negative relationship between daily nest-survival rate and nest age that varies with experience may be a function of the need for coordination of biparental care during incubation. Western Sandpipers exhibit obligate biparental care during incubation; experimental removal of either member of the pair always resulted in nest abandonment (Erckmann 1983). Incubation is energetically costly for several shorebird species, and incubation bout length increases with clutch age (Ashkenazie and Safriel 1979; Safriel 1980; Cresswell et al. 2003, 2004). Thus, inexperienced pairs may have difficulty maintaining energy balance and coordinating joint incubation that could result in increased probability of nest failure. Regardless, our nest-survival model controlled for underlying variation associated with nest age as well as seasonal and annual variation in Western Sandpiper daily nest survival rate, so observed effects of mate and breeding-site fidelity are likely robust. Future study of the proximate causes of annual and seasonal variation in nest survival, as well as variation associated with nest age, would add considerably to our understanding of temporal effects on individual behavior, fitness, and population dynamics.

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