

**Demography and Behavior of Western Sandpipers (*Calidris mauri*)
Breeding on the Yukon-Kuskokwim River Delta, Alaska**

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Demography and Behavior of Western Sandpipers (*Calidris mauri*)
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Abstract

I conducted demographic and behavioral studies of Western Sandpipers (*Calidris mauri*) breeding on the Yukon-Kuskokwim River Delta, Alaska (1998–2005). In chapter one, I estimated apparent annual survival (product of true survival and site fidelity) while correcting for the probability of encounter for 237 males and 296 females. Overall return rates (individual returned to the site in a subsequent season) were lower for females (40%) than males (65%), as was apparent annual survival (\pm SE, females = 0.65 ± 0.05 , males = 0.78 ± 0.03), and encounter rate (females = 0.51 ± 0.07 , males = 0.74 ± 0.04). In chapter two, I examined the effects of mate and site fidelity on nesting success (N = 430 nests). Annual divorce rate ranged between 37–83%, with 17–63% 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 compared to late-season nests. When I controlled for clutch-initiation date, nests tended by individuals with prior breeding-site experience had higher daily survival rates compared to birds breeding at the site for the first time. The effect of site experience was greater for males than females. In chapter 3, I reported that Western Sandpipers exhibited aggregated breeding behavior on a 36 ha plot. Breeding aggregations occurred when dominant and/or older individuals excluded younger, subordinate individuals from preferred habitat. The pattern of habitat occupancy conformed to an ideal despotic distribution with aggregated nesting birds in

less preferred habitat experiencing lower reproductive success. In chapter 4, I described and demonstrated the form and function of parent-chick communication in the Western Sandpiper. Through experimental playback of adult vocalizations to chicks in the field, I demonstrated: (1) chicks respond to the alarm call by vocalizing relatively less often and moving away from the signal source, (2) chicks respond to the gather call by vocalizing relatively more often and moving toward the signal source, (3) and chicks respond to the freeze call by vocalizing relatively less often and crouching motionless on the substrate for extended periods of time. I also describe two distinct chick vocalizations (chick-contact and chick-alarm calls).

Attributions

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Harold Bailey Professor, Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 24061. Dr. Walters served as the chair of my doctoral committee and provided constructive comments on all aspects of my research. He is a coauthor on all four chapters of my dissertation.

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Chapter 1: Apparent survival of breeding Western Sandpipers on the Yukon-Kuskokwim River Delta, Alaska

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Abstract

The Western Sandpiper (*Calidris mauri*) is considered a species of high concern despite being one of the most abundant shorebirds in the western hemisphere (U.S. Shorebird Conservation Plan, 2001). We used eight years of live recapture data (1998–2005) to estimate apparent annual survival while correcting for the probability of encounter for male ($n = 237$) and female ($n = 296$) Western Sandpipers breeding on a 36 ha plot on the Yukon-Kuskokwim River Delta, western Alaska. Apparent annual survival (Φ) is the product of true survival and site fidelity. Overall return rates (individual returned to the study site in a subsequent season) were lower for females (40%) than males (65%), as was Φ (\pm SE, females = 0.65 ± 0.05 , males = 0.78 ± 0.03), and encounter rate (females = 0.51 ± 0.07 , males = 0.74 ± 0.04). However, model selection did not indicate that Φ varied during the course of this study for either sex. Results differed from previous estimates of Φ for this species in that our estimates of Φ were higher for both sexes compared to estimates from a breeding site and two nonbreeding locations. Further, annual variation in Φ has been reported in other studies of the Western Sandpiper that were of considerably shorter duration. Disparity among Φ estimates from the breeding and nonbreeding grounds highlights the need to delineate site-specific factors, throughout the annual cycle, that influence population dynamics in the Western Sandpiper. Reported decline in numbers at staging sites might be caused by a variety of factors (e.g., shifts in migration patterns, Ydenberg et al. 2004) besides a decreasing population and not impact demographic rates. As further study is needed to clarify the conservation status of the species, our estimates of apparent survival will be useful in assessing population viability for Western Sandpipers.

Keywords: *Calidris mauri*, demography, shorebird, mark-recapture

Introduction

Robust demographic parameter estimation is central to understanding population dynamics of avian species (Eberhardt 1985, Lande 1988, Clobert and Lebreton 1991, Warnock et al. 1997, Lieske et al. 2000). Estimation of survival rate is particularly important because the stability of any animal population is at least partially the result of a balance between the recruitment of new breeders to the population via reproduction and immigration and the emigration and mortality of established breeders (Lebreton et al. 1993, Lieske et al. 2000). Estimation of these parameters and identification of ecological factors that affect avian populations requires long-term studies of marked individuals (Lebreton and North 1993).

Twenty one percent of the world's 155 shorebird species are listed as species of conservation concern by Birdlife International (Piersma et al. 1997, Johnson and Oring 2002, Sandercock 2003). Several long-term studies have revealed population declines among migratory shorebirds (Charadriiformes) in Europe (Tucker and Heath 1994, Hagemeyer and Blair 1997), North America (Howe et al. 1989, Morrison et al. 2001, Haig et al. 2005), and Asia (Rose and Scott 1997). The life history of migratory shorebirds is generally characterized by delayed maturity, low productivity, and relatively high adult survivorship (Evans and Pienkowski 1984, Piersma and Baker 2000). A better understanding of shorebird demography would facilitate conservation efforts; however, population models have been developed for only a few shorebird species. Sensitivity analyses have found that adult survival often has the highest elasticity value and potentially the greatest impact on population growth rates (Hill and Carter 1991, Hitchcock and Gratto-Trevor 1997, Reed et al. 1998, Plissner and Haig 2000, Larson et al. 2002, Sandercock 2003). Although effective conservation of migratory shorebirds requires

reliable estimates of annual survival rates, such estimates have only been produced for < 10% of shorebird species worldwide (Sandercock 2003).

The Western Sandpiper (*Calidris mauri*) is considered a species of high concern despite being one of the most abundant shorebirds in the western hemisphere (U.S. Shorebird Conservation Plan, Brown et al. 2001; global population size estimated at 3–3.5 million birds, Bishop et al. 2000, Morrison et al. 2000). Declining numbers during spring (Butler and Lemon 2001) and fall (Neil 1992, Butler and Lemon 2001) migration surveys at key staging areas in British Columbia and Texas coupled with a limited breeding distribution and threats to nonbreeding habitat has led to this conservation assessment (Brown et al. 2001, Fernández et al. 2006). Western Sandpipers breed along the coasts of western Alaska and eastern Siberia and winter primarily along the Pacific coast from California to Peru, and the Atlantic coast from New Jersey to Surinam (Wilson 1994). Male Western Sandpipers spend the nonbreeding season at more northerly latitudes compared to females (Page et al. 1972, Harrington and Haase 1994, Buenrostro et al. 1999, Nebel et al. 2002), and males generally precede females north during spring migration (Holmes 1971, Senner et al. 1981, Butler et al. 1987) with the opposite trend during fall migration (Butler et al. 1987, Ydenberg et al. 2005). Comparative studies along their nonbreeding distribution have revealed divergent life history strategies (O’Hara et al. 2005). Juveniles from the southern portion of the nonbreeding range (i.e., females) are more likely to remain at nonbreeding sites during their first breeding season compared to northerly counterparts (males). This suggests that Western Sandpiper life history varies between sexes with first year females favoring increased survival and first year males emphasizing initial breeding opportunities (O’Hara et al. 2005). Thus, as in other migratory shorebirds, Western Sandpiper survival probability may be correlated with migration length and breeding success (Piersma

1994, Boyd and Piersma 2001, Brochard et al. 2002). Subsequently, Western Sandpipers may have age- and sex-specific differences in annual survival.

The objective of this study was to produce robust estimates of apparent annual survival for Western Sandpipers at a breeding site in western Alaska. Survival estimates are needed to clarify the species' conservation status, because a decline in numbers at staging sites might be caused by a variety of factors (e.g., shifts in migration patterns) besides a decreasing population and not impact demographic rates (Ydenberg et al. 2004). We used eight years of live recapture data to determine whether apparent annual survival rate varied between the sexes at our study site and whether survival varied significantly during the course of this study.

Methods

Study area and field methods

We studied breeding Western Sandpipers at the Yukon Delta National Wildlife Refuge's Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (61°22' N, 165°07' W). Our 36 ha study plot is situated in dry upland tundra habitat along the Kuyungsik River (lowland moist low scrub community, Jorgenson and Ely 2001), and supports an average of 80 breeding pairs annually (Johnson et al. 2005). From 1998–2005, two to four observers searched this study plot daily from early May through late July for banded birds, nests, and broods. We banded each adult with a U.S. Fish and Wildlife Service identification band and unique color combinations at the nest (3 UV-stable color bands/bird). A few birds (10 males, 4 females) lost a color band or their bands became stained; and as a result, we were not able to conclusively identify them during subsequent years. In all such cases, we recaptured the individual, identified it by its U.S. Fish and Wildlife Service identification band and re-banded the individual with new color bands.

Adults were sexed by culmen length during banding (Page and Fearis 1971, Carter 1984), and we recorded the location and behavior of banded birds daily. Based on plumage characteristics, it is possible to differentiate first-year Western Sandpipers (birds that hatched in the previous breeding season) from birds that are ≥ 2 years old (Sandercock et al 1999). However, our sample of first year birds was limited (24% of females and 17% of males were banded as first-year birds), and previous attempts to estimate apparent survival in this population revealed unacceptable overdispersion when fitting age-specific models to the dataset ($\hat{c} > 8$, unpublished data). As our objective was to produce robust estimates of apparent annual survival, we did not attempt to partition survival between age classes (first-year and ≥ 2 year old birds); rather, we estimated apparent survival for all breeding adults.

Statistical analyses

We used mark-recapture methods to estimate apparent annual survival (Φ) while correcting for the probability of encounter (p). Apparent survival rate was the probability that a bird alive in breeding season i survived until the following breeding season ($i + 1$) and returned to our study plot. Encounter probability was the probability that we detected a bird given that it was alive. Losses from the breeding population may have been the result of permanent emigration or mortality, and are the complement of apparent survival. We constructed encounter histories for individual sandpipers from live encounter data where 0 = not detected and 1 = captured or resighted during the breeding season. Following methodologies outlined by Burnham and Anderson (1998), we conducted mark-recapture analysis using program MARK (version 4.2, Cooch and White 2004).

We incorporated sex (*sex*) and time-dependence (*t*) as variables in our global model of Φ and p because both parameters are known to vary between the sexes and across years in many bird species (Sandercock 2003). Several nonexclusive factors may lead to lower apparent survival rates during the first interval after initial capture in many bird populations (Sandercock and Jaramillo 2002). We therefore modeled Φ for the interval following initial capture (Φ^1) and all subsequent intervals (Φ^{2+}) separately within each sex (time-since-marking, or two age-class model). Because we did not expect p to vary between first and subsequent time intervals, we modeled p as a function of *sex* and *t*. Thus, our starting global model was $\Phi^1_{sex*t} * \Phi^{2+}_{sex*t}, p_{sex*t}$.

We used two methods to assess the fit of our global model to the sandpiper survival data; a parametric bootstrap goodness-of-fit test and the median \hat{c} procedure in program MARK (Cooch and White 2004). During the parametric bootstrap goodness-of-fit procedure, we generated a bootstrap distribution of expected deviances through simulation ($n = 1000$ replicates) and calculated a variance inflation factor (\hat{c}) as the observed deviance divided by the mean expected deviance from the bootstrap distribution (Burnham and Anderson 1998). In the median \hat{c} procedure, we simulated sandpiper survival data with a range of deviances ($n = 1000$ replicates), obtained \hat{c} values for each of the simulated data sets, and performed a logistic regression to estimate the median \hat{c} value of the simulated data (Cooch and White 2004). Moderate amounts of overdispersion are common in mark-recapture analyses with \hat{c} values of 1–3 indicating an acceptable global model fit (Lebreton et al. 1992).

After examining the fit of our starting global model, we fit reduced models with fewer parameters to the sandpiper dataset. We began the model selection process by first modeling encounter probabilities followed by survival probabilities (Doherty et al. 2002, Nicolai et al.

2005). After modeling p , we contrasted models with one and two age classes (Φ vs. $\Phi^{1*} \Phi^{2+}$). We modeled all probabilities (Φ and p) by initially dropping parameters from a factorial model to create an additive model, and finally examined single factor and constant models. We assessed model fit with quasi-Akaike's Information Criterion, adjusted for small sample sizes (QAIC_c, Burnham and Anderson 1998). Models where ΔQAIC_c was < 2 from the best fit model ($\Delta\text{QAIC}_c = 0$) were considered equally parsimonious, and Akaike weights (w_i) were used to determine the relative likelihood of a model within the set of candidate models. The ratio of QAIC_c weights between two candidate models was used to quantify the relative degree that a particular model was supported by the data relative to other models (Burnham and Anderson 1998). We used the variance components procedure in Program MARK to obtain overall estimates of apparent survival and encounter probability. We used the model averaging procedure in program MARK to obtain annual estimates of apparent survival. We report means \pm SE.

Results

We individually marked 533 breeding sandpipers (296 females and 237 males) in the first 7 of 8 years of study. Overall return rates (individual returned to the study site in a subsequent season) were lower for females (40%) than male (65%). Both goodness-of-fit methods detected minor overdispersion when we fit our global model to the sandpiper survival data set (parametric bootstrap goodness-of-fit procedure $\hat{c} = 2.9$; median \hat{c} procedure $\hat{c} = 1.4$). Although these two estimates vary, both indicated that our global model was a satisfactory starting point ($\hat{c} \leq 3.0$), so we chose the more conservative estimate of overdispersion ($\hat{c} = 2.9$) and continued with model selection. Further, after completing model selection, we systematically varied \hat{c} between the two

estimates and found no differences among the top performing models, regardless of which \hat{c} value was used.

Model selection based on QAIC_c indicated that the best-fit model (Φ_{sex}, p_{sex}) was one where survival and encounter probabilities varied between the sexes but were constant over time (Table 1.1). Apparent survival rate of females (0.65 ± 0.05) was lower than that of males (0.78 ± 0.03) as was encounter rate (females = 0.51 ± 0.07 , males = 0.74 ± 0.04). Model selection also revealed support for a time since marking (two age-class) model with variation between the sexes ($\Phi^1_{sex} \Phi^{2+}_{sex}, p_{sex}$; $\Delta QAIC_c = 1.6$; Φ^1 , females = 0.57 ± 0.08 , males 0.72 ± 0.06 ; Φ^{2+} , females = 0.69 ± 0.06 , males 0.81 ± 0.04), but the best-fit model (Φ_{sex}, p_{sex}) had > 2 times the support of this model. Model selection did not support annual variation in survival rates ($\Delta QAIC_c > 7.3$); however, we did examine the point estimates of annual apparent survival from our global model ($\Phi^1_{sex*t} \Phi^{2+}_{sex*t}, p_{sex*t}$) because time dependence is often not supported in sparse datasets (Burnham and Anderson 1998). In the interval after first capture (Φ^1) and later intervals (Φ^{2+}), female apparent survival was lower in 2001 compared to other years (Fig. 1.1).

Discussion

We used mark-recapture statistics to estimate apparent annual survival in a breeding population of Western Sandpipers on the Yukon-Kuskokwim River Delta, Alaska. Apparent survival was lower for females compared to males, and hierarchical model selection results did not indicate that survival varied annually. Previous estimates of apparent survival for Western Sandpipers breeding near Nome, Alaska, that also were based upon mark-recapture techniques for live encounter data were higher for males than females, but our estimates were higher for both sexes compared to the Nome study (Table 1.2). Our estimates of encounter probability also varied

between the sexes, and, especially for females (0.51), were lower than previous estimates (males 0.81–0.82, females 0.80, Sandercock et al. 2000). The only other comparable data for Western Sandpipers from the breeding grounds are return rates, which underestimates both true and apparent survival because they are the product of Φ and p . These rates were 0.58 for males and 0.49 for females breeding on the Yukon-Kuskokwim River Delta approximately 30 km northwest of our study site (1966–1969, Holmes 1971). Two studies have used mark-recapture techniques to estimate apparent annual survival rates on the nonbreeding grounds for this species. Juvenile and adult males in Baja California had relatively low apparent annual survival, and females had higher apparent annual survival rates compared to males in Chitré, Panama (Table 1.2). Return rates to a nonbreeding site were higher among juveniles (0.61) compared to adults (0.54) in Cabo Rojo, Puerto Rico (Rice 1995).

Our results are similar to those for other *Calidris* species when mark-recapture techniques were used to estimate apparent annual survival rates on the breeding grounds. Male Semipalmated Sandpipers (*C. pusilla*) near Nome, Alaska, had higher apparent survival rates than females (Table 1.2) and both rates were close to our estimates for Western Sandpipers. Male Semipalmated Sandpipers breeding at La Pérouse Bay, Manitoba, Canada had higher apparent survival rates than females (Table 1.2). These estimates were lower than ours for Western Sandpipers; however, there was considerable annual variation in that study (1980–1987, males 0.53–0.74, females 0.43–0.71, Sandercock and Gratto-Trevor 1997). Apparent annual survival rate for Purple Sandpipers (*C. maritima*) breeding in Scotland was similar to our estimate for male Western Sandpipers, but there was no variation between the sexes in the Purple Sandpiper study (Table 1.2).

Differences between our estimates of apparent survival and those from Nome could be the result of differing methodologies. We constructed encounter histories using all detected individuals (captured and resighted birds); however, the Nome study constructed encounter histories using only individuals captured on a nest. Thus, the probability of a bird being counted as present in Nome was the product of true survival, site fidelity rate, probability of breeding, probability of a nest being found, and the probability of capture (Sandercock et al. 2000). Whereas in our study, the probability of a bird being counted as present in a given year was the product of true survival, encounter probability, and site fidelity rate. However, it is unlikely that methodological differences resulted in the observed variation in survival estimates between the two studies as encounter probabilities were approximately 0.80 in Nome for both sexes and much lower, at least for females, during this study. An alternative explanation is that permanent emigration rates may vary between these two localities. If sandpipers breeding near Nome exhibit lower site fidelity rates compared to the population we studied on the Yukon-Kuskokwim River Delta, then true survival could be similar between the two populations, yet apparent survival rates would differ.

Whether lower apparent annual survival among female Western Sandpipers represents variation in true survival or sexual variation in breeding site fidelity is unknown because we are not able to differentiate the relative influence of mortality versus permanent emigration in our estimation of apparent annual survival. Among sandpipers, males generally exhibit greater breeding site fidelity than females (Oring and Lank 1982, Piersma et al. 1996). Therefore, we can not conclude that female annual survivorship is lower than that of males in our study population because females may merely exhibit lower breeding site fidelity than males. Local permanent emigration was not common at our study site. As part of an unrelated study, we

surveyed 29 plots (8.3-ha/plot) annually within a 29-km² area surrounding our study site (15–31 May, 2004–2005). We made considerable effort to detect any banded birds while traversing this area, but failed to detect any color-marked birds during 50 hours of observation. Additionally, no banded birds that went undetected in our surveys were encountered by concurrent research projects being conducted in the surrounding area (2003–2005). Encounter probabilities were lower for females during this study, which may indicate temporary emigration (i.e. attempting reproduction at another location for one or more intervening years) is more common among females, or that there are behavioral differences that result in lower detection rates for females. Males are the more conspicuous sex early in the breeding season because they engage in conspicuous epigamic displays daily, whereas females are more cryptic spending greater amounts of time in concealed locations, such as wet meadows (Lanctot et al. 2000). Female encounter rates also may be lower if only a portion of those individuals that permanently emigrate still pass through our study site before settling at other locales, or if some individuals pass through quickly and avoid detection.

Model selection results did not indicate that apparent annual survival varied during the course of our study (Table 1.1). We were surprised by these results because annual variation in apparent survival has been reported in other studies of the Western Sandpiper that were of considerably shorter duration (Sandercock et al. 2000, 1993–1996; Fernández et al. 2003, 1994–1997). However, examination of point estimates from our global model did reveal that female survival was lower in 2001 compared to other years (Fig. 1.1). We are not able to account this variation, but lower female survival in 2001 may partially explain why overall estimates of apparent survival were lower for females compared to males.

Reported decline in numbers at staging sites might be caused by a variety of factors (e.g., shifts in migration patterns, Ydenberg et al 2004) besides a decreasing population and not impact demographic rates. The closely related Semipalmated Sandpiper is likely to have comparable population demographics to the Western Sandpiper (Fernández et al. 2003). Western Sandpiper apparent annual survival estimates are similar to true annual survival rates required to sustain a breeding population of Semipalmated Sandpipers (Hitchcock and Gratto-Trevor 1997). If Western Sandpiper numbers are declining, annual survival does not appear to be the dominant contributing factor. However, disparity among apparent survival estimates from the breeding and nonbreeding grounds highlights the need to delineate site-specific factors, throughout the annual cycle, that influence population dynamics in the Western Sandpiper. As further study is needed to clarify the conservation status of the species, our estimates of apparent survival will be useful in assessing population viability for Western Sandpipers.

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Table 1.1. Mark-recapture modeling to estimate apparent annual survival of adult Western Sandpipers breeding near Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (1998–2004).

Model structure ^b	Model statistics ^a			
	<i>K</i>	Deviance	ΔQAIC_c	w_i
Φ_{sex}, p_{sex}	4	122.6	0.0	0.489
$\Phi^1_{sex} \Phi^{2+}_{sex}, p_{sex}$	6	120.2	1.6	0.217
$\Phi^1_{sex} \Phi^{2+}_c, p_{sex}$	5	123.1	2.5	0.142
Φ_c, p_{sex}	3	127.6	3.0	0.110
Φ_{sex}, p_c	3	130.8	6.2	0.046
Φ_{sex+t}, p_{sex}	10	117.7	7.3	0.013
$\Phi^1_{sex+t} \Phi^{2+}_{sex+t}, p_{sex}$	15	110.9	10.7	0.002
Φ_{sex*t}, p_{sex*t}	26	105.3	28.1	<0.001
$\Phi^1_{sex*t} * \Phi^{2+}_{sex*t}, p_{sex*t}$	36	97.2	43.5	<0.001

^a We described model fit by the number of parameters (*K*), deviance, and the difference in quasi-Akaike's Information Criterion (ΔQAIC_c) from the best-fit model. QAIC_c values were calculated using a variance inflation factor of 2.9. We present models with moderate support (Akaike weight $w_i \geq 0.01$) in order of relative fit to the best-fit model (i.e. $\Delta\text{QAIC}_c = 0$), followed by a two age-class (time-since-marking) model with additive effects of sex and time, a standard Cormack-Jolly-Seber model that did not control for time since marking, and the starting global model which did.

^b Model factors included: Φ^1 = apparent survival during the first year post banding, Φ^{2+} = apparent survival during subsequent years, Φ = annual apparent survival in models lacking age structure, *c* = constant, *sex*, *t* = time or annual variation, * = a factorial model, and + = an additive model.

Table 1.2. Apparent annual survival estimates for *Calidris* sandpipers from studies that used mark-recapture statistics.

Species		Range ¹	Age ²	Sex ³	Apparent survival ⁴	No. birds	No. years ⁵	Reference
Western Sandpiper	<i>C. mauri</i>	B	A	F/M	0.57	236	4	Sandercock et al. 2000
		NB	J	M	0.49	139	4	Fernández et al. 2003
			A	M	0.45	117		
		NB	J/A	F	0.62	1990	3	Fernández et al. 2004
				M	0.54	1383		
		B	J/A	F	0.65	296	8	Johnson et al. 2006
M	0.78			237				
Dunlin	<i>C. alpina</i>	NB	A	F/M	0.74	1051	4	Warnock et al. 1997
Red Knot	<i>C. canutus</i>	NB	A	F/M	0.84	1603	4	Brochard et al. 2002
Purple Sandpiper	<i>C. maritima</i>	NB	A	F/M	0.79	94	6	Summers et al. 2001
Semipalmated Sandpiper	<i>C. pusilla</i>	B	A	F	0.56	249	8	Sandercock & Gratto-Trevor 1997
				M	0.61	237		
		B	A	F	0.59	122	4	Sandercock et al. 2000
				M	0.73	108		

¹Range: B = breeding site, NB = nonbreeding site.

²Age: J= juveniles \leq 1 year of age, A = adults \geq 1 year of age.

³Sex: F = females, M = males.

⁴Apparent survival: estimate from best-fit model, or average of annual estimates (i.e., Sandercock & Gratto-Trevor 1997).

⁵No. years: duration of study in years.

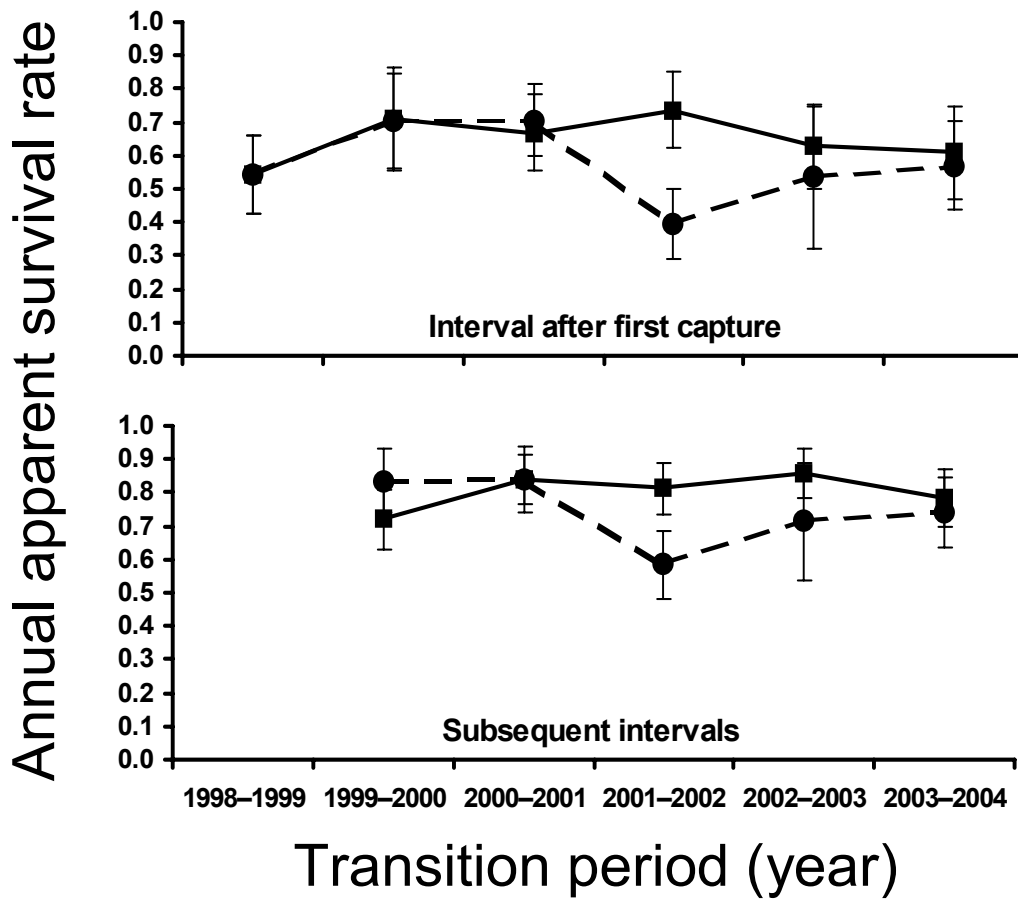


Figure 1.1. Annual apparent survival rates (mean \pm SE) of adult Western Sandpipers (296 females, 237 males) breeding near Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (1998–2004) in the interval after first capture and subsequent intervals (males = squares connected with solid lines, females = circles connected with broken lines).

Chapter 2: Mate and site fidelity effects on Western Sandpiper nest survival

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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 adults 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 rate was lower for females (40%) compared to males (65%). Among pairs where at least one member returned, annual divorce rate ranged 10–29% with 4–25% of pairs reuniting annually. When we restricted our analysis to pairs where both members returned to the site in the following year, annual divorce rate ranged between 37–83%, with 17–63% 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 compared to late-season nests. However, mate-fidelity did not explain significant variation in daily nest survival rate when we controlled for initiation date. To examine the effect of breeding-site experience on Western Sandpiper nest success, we contrasted daily nest survival rates between individuals that were site faithful and recent immigrants to the population. Nests tended by individuals with prior breeding-site experience had higher daily survival rates compared to birds breeding at the site for the first time. This effect was greater for males than females. It is unclear whether our results indicate site experience or age-specific effects on nest survival, or their interaction. 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.

KEY WORDS: *Calidris mauri*, shorebird, divorce, dispersal, reproduction, behavior

Introduction

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). Inter-annual breeding dispersal may or may not result in a bird breeding at a higher quality site, or with a higher quality mate, during subsequent reproductive efforts. Many studies have reported increased breeding dispersal following reproductive failure (Wiklund 1996, Gowaty and Plissner 1997, Haas 1998). However, these potential advantages of dispersal are balanced by the risk that a dispersing bird may fail to find a new site and/or mate and lose all reproductive potential, or the new site/mate could be of lower quality. Furthermore, reuniting with a prior mate or retaining a territory across seasons may be beneficial because familiar pairs may have higher reproductive success than unfamiliar pairs (Oring and Lank 1982, 1984, Schieck and Hannon 1989).

The proportion of birds returning to a particular study site may reflect the cumulative decision of birds to remain site-faithful as opposed to disperse to a new area or may merely be indicative of a mortality pattern with low-quality individuals being more likely to perish (Askenmo 1979, Weatherhead and Boak 1986, Nol and Smith 1987). 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, Haas 1998, Hoover 2003). Numerous studies have shown that breeding-site fidelity is positively correlated with previous reproductive performance (Nolan 1978, Harvey et al. 1979, Dow and Fredga 1983, Newton and Marquiss 1982, Weatherhead and Boak 1986, Gavin and Bollinger 1988, Bollinger and Gavin 1989, Murphy 1996, Paton and Edwards 1996, Doligez et al. 1999), and a causal link between breeding success and return rates has been demonstrated in a few species (Haas 1998, Hoover 2003).

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, Lemon et al. 1996, Murphy 1996, Clarke et al. 1997). Consequently, male-biased site fidelity suggest that the costs of dispersal should be greater and/or the benefits of site fidelity greater for males (Ward and Weatherhead 2005).

Although males are generally the more site faithful sex among monogamous avian species, the relationship between previous breeding performance and return rate is often stronger in females (Newton and Marquiss 1982, Drilling and Thompson 1988, Murphy 1996, Paton and Edwards 1996). Sex-specific differences in site fidelity may result from sex-specific benefits associated with site familiarity (Hinde 1956, Greenwood 1980, Bensch and Hasselquist 1991). While the relationship between site fidelity and site dominance is uncertain (Shutler and Weatherhead 1992, Searcy and Yasukawa 1995, Veiga et al. 2001), males that return to their previous breeding territory are generally successful in acquiring it again (Rohwer 1982, Lanyon and Thompson 1986, Shutler and Weatherhead 1992). Male site familiarity would be especially advantageous in species where males have to compete for territories to attract mates (Paton and Edwards 1996, Schjorring et al. 2000). Thus, site fidelity should be favored in territorial males because dispersing individuals forfeit resident advantage (Davies 1978; Greenwood 1980, 1984; Krebs 1982; Desrochers and Hannon 1989; Paton and Edwards 1996; Schjorring et al. 2000; 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). Females should therefore also benefit from site familiarity; however, monogamous females do not appear to compete for resources in many bird species (Lightbody and Weatherhead 1987), or at least competition is considerably

less than among males. Thus, the relative benefits of site familiarity may be lower for females compared to males (Ward and Weatherhead 2005). Further, females have the flexibility to move and find the best mate or territory, whereas the opportunity for male reconnaissance is limited as a result of territoriality (Johnson 2002). If a male attempts reproduction, he must acquire and defend a territory and advertise for mates, all time consuming activities that would limit time available for reconnaissance.

Hypotheses accounting for variation in mate fidelity rates propose that individuals do not reunite after an unsuccessful reproductive attempt because: divorcing pairs were not well matched for each other (Coulson 1972), individuals disperse and find a site or mate of higher quality (Ens et al. 1993), habitat preference (Haig and Oring 1988, Cézilly and Johnson 1995), aspects of migration (Dhondt and Adriaesen 1994, Rees et al. 1996), or are related to mortality rate (McNamara and Forslund 1996). Alternately, divorce may result from dispersal following breeding failure (Oring and Lank 1984, Ens et al. 1996).

In most field studies based in single study sites, dispersing birds are not tracked and, thus, dispersal is often not distinguished from mortality and post-dispersal fitness is not determined. Differentiating between the effects of nesting success, mate fidelity, and site fidelity also is difficult because of inter-correlations 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 as they are often confounded, and it is not possible to age many species after their first year.

We investigated the effects of mate and site fidelity on reproductive success in a breeding population of Western Sandpipers (*Calidris mauri*). 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). Previous studies did not report a positive effect of mate fidelity on nesting success in Western Sandpipers (Sandercock et al. 2000). We reexamined the effect of mate fidelity, and explored the effects of site fidelity on Western Sandpiper nest survival.

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 (i.e., extra-pair paternity is rare) 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). Both parents share incubation of their four-egg clutches for 27 d (Holmes 1971, 1973; Sandercock 1997). In 1998 and 2002, data were primarily gathered 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 at this site, data were collected on an additional 20 ha surrounding the original plot (36 ha total; mean \pm SD number of nests monitored per yr = 113 ± 25 , mean \pm SD number of adults banded per yr = 89 ± 16).

During all years, two to four observers surveyed for banded birds, nests, and broods daily from early May through late July. Adults and chicks were marked with a U.S. Fish and Wildlife Service identification band as well as with unique combinations of UV-stable color bands at the

nest (chicks only marked with color bands from 2003–2005). Adults were sexed by culmen length during banding (Page and Fearis 1971, Carter 1984). Nest locations were mapped and nests were checked every 1–4 d through hatch, predation, or abandonment. Nest age was determined by backdating incomplete clutches (1.5 d per egg, based on known age nests at the site, unpublished data) or floating complete clutches (Sandercock 1998). Nests hatching ≥ 1 egg were considered successful, and we only considered a pairs' initial nesting attempt in a season in analyses.

Mate fidelity rate

We examined mate fidelity in mated pairs of marked Western Sandpipers where at least one member of the pair returned to breed at the study site in the following year. After Sandercock et al. (2000), we use the term mate change to indicate that one member of a pair returned and mated with a new individual. Mate change may result from the absence of a mate due to mortality, dispersal, or undetected divorce (mate returned but we failed to resight it). Divorced and reunited refer to pairs where both members returned but each mated with different or the same individual, respectively. We considered pairing events in different years to be independent because the sexes spend the nonbreeding season at different locations and consider mate choice annually (Sandercock et al. 2000).

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 (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 with 0–3 years of prior site

experience. Although 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, 1st–4th 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 0–3 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 27d incubation period using program MARK (Dinsmore et al. 2002, Cooch and White 2005). 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). 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 this study (unpublished data), we therefore 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, as daily nest survival often decreases across the nesting season (Ainley and Schlatter 1972). We also fit a quadratic time trend model that allowed daily nest survival to follow a curvilinear pattern (Dinsmore et al. 2000); (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 program MARK (Cooch and White 2005); (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 to 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 mated pairs where the female had site experience would have higher daily nest survival rates compared to pairs with a female that 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 (1st year, 2nd year, 3rd year, ≥ 4 years). (6) Male experience at site – We hypothesized that mated pairs where the male had site experience would have higher daily nest survival rates compared to pairs with a male that 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 (1st year, 2nd year, 3rd year, ≥ 4 years).

The effect of female and male site experience on Western Sandpiper nest survival is confounded with age. Based on plumage characteristics, it is possible to differentiate first-year Western Sandpipers (birds that hatched in the previous breeding season) from birds that are ≥ 2 years old (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 (1999–2004, unpublished data). Thus we do not have an estimate of age for most individuals, but we do 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. We first constructed a base model that included the effects of year, seasonal variation, and nest age on daily survival rate. During phase I, we limited our analysis to 11 *a priori* models (Table 2.1). Akaike's Information Criterion (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 affects 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 2.1). Models examining the effects of mate and site experience were ranked using AIC_c , and model weights 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 all possible estimates of nest survival during our study ($N = 32$; the maximum number of 27d incubation intervals in our 59d nesting season). 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 27d 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 this is a poor estimator of precision because the underlying model was nonlinear, and model parameters were correlated (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%) compared to 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 analyses. This resulted in a sample of 430 nests to estimate Western Sandpiper nest survival over a 59d nesting season (11 May – 9 July, Table 2.2). Most nests were located prior to clutch completion (mean \pm SD number of days post initiation that nests were discovered = 2.6 ± 3.0). Mean clutch initiation date varied annually ($F_{5,424} = 27.3, p < 0.001$), and individuals that bred with a prior mate initiated clutches earlier compared to pairs breeding together for the first time ($F_{1,423} = 27.3, p < 0.001$, Fig. 2.1). Among individuals breeding together for the first time, birds with more years of experience at the site tended to initiate clutches earlier (Fig. 2.2; $F_{3,162} = 11.8, p < 0.001$). For pairs where at least one

member returned in the following season, 10–29% of birds changed mates and 4–25% of pairs reunited annually (Table 2.3). Among pairs where both members returned to the site in the following year, annual divorce rate ranged between 37–83% with 17–63% of pairs reuniting annually (Table 2.3). From 1998–2005, females and males that hatched chicks returned to the site in a subsequent season at a higher rate compared to individuals that tended nests that failed [% returned \pm SD (N); hatched chicks, females = 0.55 ± 0.20 (139), males = 0.66 ± 0.09 (149); nests failed, females = 0.23 ± 0.05 (272), males = 0.60 ± 0.11 (311)].

Phase I model selection results indicated that the daily survival of Western Sandpiper nests exhibited nonlinear temporal variation within seasons, as the top four models (< 2 AIC_c units from the top model) all contained a quadratic time trend (Table 2.4). Year and nest age also had strong support in two of the four top models; however, none of the four top models were weighted exceptionally high compared to the others (Table 2.4, range w_i top models = 0.17–0.33), and all were within two AIC_c units of the best-fit model. We therefore 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.

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 2.5). Nests tended by parents with prior site experience had higher daily survival rates compared to nests tended by parents breeding at the site for the first time (Fig. 2.3). The estimates from the best model for the additive effect on survival of nests tended by females and males with site experience were $\hat{\beta}_{\text{female}} = 0.45$ (1 SE = 0.21) and $\hat{\beta}_{\text{male}} = 0.59$ (1 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, $\hat{\beta}_{\text{age}} = -0.03$ (1 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 (Fig. 2.3). Daily survival of nests declined over the course of this study (Fig. 2.4; $\hat{\beta}_{\text{year}} = -0.09$, 1 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 the best; otherwise the models were identical (Table 2.5). Exclusion of prior mate experience improved the model substantially (an increase of 1.9 AIC_c units), and had > 2 times the support than when prior mate experience was included (Table 2.5). The logistic regression equation for the best model was (1SE for each $\hat{\beta}$ is given below in parentheses)

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

$$(0.40) \quad (0.03) \quad (0.006) \quad (0.01) \quad (0.03) \quad (0.17) \quad (0.21)$$

We plotted curves showing these effects for selected values of each variable in the above equation (Fig. 2.3) 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 day) and late (nest age = 27 days) in incubation, we plotted the daily nest survival for breeding pairs composed of birds with 0–3yrs breeding experience at the site (1st, 2nd, 3rd, or 4th 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. 2.3). 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. 2.3). 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. 2.3). 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. 2.4).

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. 2.5). We used the mean initiation date for all 430 nests (2 June) to compute survival for nests tended by parents with varying site experience. Using the logistic regression equation from the best model, the probability that Western Sandpiper nests tended by parents with two or three years of site experience surviving the 27d incubation period was 0.71 and 0.88, respectively (Fig. 2.5). 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, Fig. 2.5). These estimates differ significantly because the logistic regression equation used to predict them contained the same seven regression coefficients with only site experience differing ($\hat{\beta}_{\text{female}} = \hat{\beta}_{\text{male}} = 1-4$ years), and because nest survival was measured across the same time interval for each level of site experience (Dinsmore et al. 2000).

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 (1st-4th 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 compared to males pairing with more experienced females (Fig. 2.6). Among individuals with the most site experience (4 years), variation in nest survival was greater among females (Fig. 2.6). Experienced males paired with inexperienced females had higher nest survival compared to experienced females paired with inexperienced males (Fig. 2.6).

Discussion

Male and female Western Sandpipers that were site faithful had higher nesting success rates compared to recent immigrants; but prior mate experience (mate fidelity) did not directly affect nesting success when we controlled for seasonal trends. Rather, reuniting pairs initiated clutches earlier than newly formed pairs, and clutches that were initiated early in the season had higher nest success rates compared to late-season nests. Western Sandpiper nesting success also exhibited annual declines from 2000–2005, and older nests had higher daily survival rates compared to younger nests.

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 other shorebird species (Soikkeli 1967, Oring and Lank 1982, Gratto et al. 1985, Haig 1987, Flynn et al. 1999), previous study of Western Sandpipers (Holmes 1971, 1973; Sandercock et al. 2000), and birds in general (Clarke et al. 1997). 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 (e.g., Martin 1974, Darley et al. 1977, Brooke 1978, Harvey et al. 1979, Oring and Lank 1982, Oring et al. 1983); whereas, we contrasted nest daily survival rates between individuals that were site faithful and recent immigrants to the population. Both methods are flawed as the effects of prior breeding success on dispersal and site fidelity are confounded with mortality and individual age. Neither approach revealed a 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) compared to 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 (e.g., synchrony of arrival and clutch initiation) were not correlated with mate fidelity (Sandercock et al. 2000). Prior mate experience also did not directly affect

Western Sandpiper nesting success in our study; rather, mate fidelity had positive effects on reproductive success via the timing of reproduction.

We found that nesting success increased with the number of years breeding experience an individual had at the site. Further, clutch initiation date was negatively correlated with number of years breeding experience at the site. Both of these patterns may have resulted from variation associated with individual age rather than prior site experience, as our measure of breeding-site fidelity is confounded by bird age. Younger, less experienced individuals may be more likely to disperse compared to 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, as over 75% of immigrants to the population were ≥ 2 years old, and nesting success rate continued to increase with number of years prior experience at the site (i.e., nest success rate did not level-off after 1–2 years site experience), there is likely some effect of site experience on Western Sandpiper nesting success.

Male habitat use is correlated with age, and nesting success varies among habitat patches in this population (Johnson and Walters, submitted). Habitat did explain slight variation in nest survival, but the addition of a habitat variable to our model did not substantially improve model fit, or alter results (unpublished data). Regardless of whether differences in nesting success were the result of individual age, habitat use, or factors associated with site experience, the overall effect was greater among males.

In several species, sex-specific benefits associated with site familiarity are correlated with variation in breeding-site fidelity (Hinde 1956, Greenwood 1980, Bensch and Hasselquist 1991). In species such as the Western Sandpiper where males must defend a territory to attract a mate, the benefits of site fidelity often are greater for males because familiarity with the previous year's territory gives them an advantage over intruding males (Davies 1978, Greenwood 1980, 1984, Krebs 1982, Desrochers and Hannon 1989, Paton and Edwards 1996, Schjorring et al.

2000). Western Sandpipers that spend less time defending their territory are able to spend more time soliciting a mate (Holmes 1973). Site faithful males also may use prior site knowledge to select high quality habitat.

In contrast to altricial birds, where nests further 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 compare to 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 > 2 years 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. We are not able to account for underlying variation associated with nest age as well as seasonal and annual variation in Western Sandpiper daily nest survival rate. However, our nest survival model did control for such variation, so observed affects of mate and breeding-site fidelity are likely robust.

Conclusions

Reuniting pairs of Western Sandpipers initiate clutches earlier compared to pairs breeding together for the first time, and nests initiated early in the season have higher nest success compared to late-season nests. However, mate fidelity did not explain significant variation in daily nest survival rates when we controlled for initiation date. We also observed that nests tended by individuals with prior breeding experience at the site had higher daily survival rates compared to birds breeding at the site for the first time, and this effect was greater for males than females. Whether our results indicate experience or age-specific effects on nest survival, or their interaction, remains unclear. We also observed annual and seasonal variation in nest survival, as

well as variation associated with nest age that remains unexplored. Future study of the proximate causes of such variation would add considerably to our understanding temporal effects on individual behavior, fitness, and population dynamics.

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Table 2.1. Hypothesis driven a priori models of Western Sandpiper daily nest survival 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_{CONSTANT}
Effect of year only	S_{YEAR}
Effect of nest age only	S_{AGE}
Linear seasonal trend	S_{T}
Quadratic seasonal trend	S_{TT}
Linear seasonal trend plus year	$S_{\text{T} + \text{YEAR}}$
Linear seasonal trend plus nest age	$S_{\text{T} + \text{AGE}}$
Linear seasonal trend plus year and nest age	$S_{\text{T} + \text{AGE} + \text{YEAR}}$
Quadratic seasonal trend plus year	$S_{\text{TT} + \text{YEAR}}$
Quadratic seasonal trend plus nest age	$S_{\text{TT} + \text{AGE}}$
Quadratic seasonal trend plus year and nest age	$S_{\text{TT} + \text{AGE} + \text{YEAR}}$
Phase II: mate and site experience models	
Base model(s) from phase one of model construction	S_{BM}
BM + effect of mate experience	$S_{\text{BM} + \text{MATE}}$
BM + effect of female site experience	$S_{\text{BM} + \text{FEMALE}}$
BM + effect of male site experience	$S_{\text{BM} + \text{MALE}}$
BM + effect of female + male site experience	$S_{\text{BM} + \text{FEMALE} + \text{MALE}}$
BM + effect of mate experience + female site experience	$S_{\text{BM} + \text{MATE} + \text{FEMALE}}$
BM + effect of mate experience + male site experience	$S_{\text{BM} + \text{MATE} + \text{MALE}}$
BM + effect of mate experience + female + male site experience	$S_{\text{BM} + \text{MATE} + \text{FEMALE} + \text{MALE}}$

Table 2.2. Pairing of Western Sandpipers in relation to number of years breeding experience at Kanaryarmiut Field Station, Yukon-Kuskokwim Delta, Alaska (2000–2005, $N_{\text{pairs}} = 430$).

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

Table 2.3. Mate-fidelity rates of Western Sandpipers at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska.

Year	At least one mate returned					Both mates returned		
	Percentage that					Percentage that		
	changed mates ¹	divorced ²	reunited ³	uncertain status ⁴	Pairs	divorced ²	reunited ³	Pairs
1998–1999	54.2	20.8	4.2	20.8	24	83.3	16.7	6
1999–2000	42.4	12.1	15.2	30.3	33	44.4	55.6	9
2000–2001	20.7	25.9	25.9	27.5	58	50.0	50.0	30
2001–2002	40.5	9.5	11.9	38.1	42	44.4	55.6	9
2002–2003	36.4	20.0	18.1	25.5	55	52.4	47.6	21
2003–2004	43.6	29.1	12.7	14.6	55	69.6	30.4	23
2004–2005	50.9	11.3	18.9	18.9	53	37.5	62.5	16
Total	39.7	19.1	16.6	24.6	320	53.5	46.5	114

¹One bird returned and mated with a new individual.

²Both members of a pair returned and each mated with a new individual.

³Both members of a pair returned and reunited.

⁴Prior or current pairing status not confirmed.

Table 2.4. 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 ^b	Model statistics ^a			
	K	Deviance	ΔAIC_c	w_i
S_{TT}	3	1749	0.0	0.33
$S_{\text{TT} + \text{YEAR}}$	4	1747	0.4	0.27
$S_{\text{TT} + \text{AGE}}$	4	1748	1.1	0.19
$S_{\text{TT} + \text{AGE} + \text{YEAR}}$	5	1746	1.3	0.17
$S_{\text{T} + \text{AGE} + \text{YEAR}}$	4	1754	7.6	<0.01
$S_{\text{T} + \text{AGE}}$	3	1756	7.8	<0.01
S_{T}	2	1759	8.0	<0.01
$S_{\text{T} + \text{YEAR}}$	3	1757	8.01	<0.01
S_{AGE}	2	1770	19.3	<0.01
S_{YEAR}	2	1785	34.0	<0.01
S_{CONSTANT}	1	1788	34.9	<0.01

^a Model fit by the number of parameters (K), deviance, model weight (w_i), and the difference in Akaike's Information Criterion (ΔAIC_c) from the best-fit model.

^b 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 2.5. Summary of model selection results for Western Sandpiper daily nest survival that included the effects of year, seasonal variation, and nest age, as well as mate and site experience effects (Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005, $N_{\text{nests}} = 430$).

Model structure ^b	Model statistics ^a			
	K	Deviance	ΔAIC_c	w_i
S _{TT + AGE + YEAR + FEMALE + MALE}	7	1728	0.0	0.45
S _{TT + AGE + YEAR + FEMALE + MALE + MATE}	8	1728	1.9	0.17
S _{TT + AGE + YEAR + MALE}	6	1732	2.6	0.12
S _{TT + YEAR + FEMALE + MALE}	6	1733	3.9	0.07
S _{TT + AGE + FEMALE + MALE}	6	1734	4.9	0.04
S _{TT + YEAR + MALE}	5	1736	5.1	0.04
S _{TT + YEAR + FEMALE + MALE + MATE}	5	1733	5.7	0.03
S _{TT + AGE + MALE}	7	1737	6.2	0.02
S _{TT + FEMALE + MALE}	4	1738	6.9	0.01
S _{TT + AGE + FEMALE + MALE + MATE}	6	1734	6.9	0.01
S _{TT + MALE}	5	1740	7.3	0.01

^a Model fit by the number of parameters (K), deviance, model weight (w_i), and the difference in Akaike's Information Criterion (ΔAIC_c) from the best-fit model.

^b Model factors included: YEAR, daily nest age (AGE), a linear seasonal trend (T, not shown), a quadratic seasonal 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).

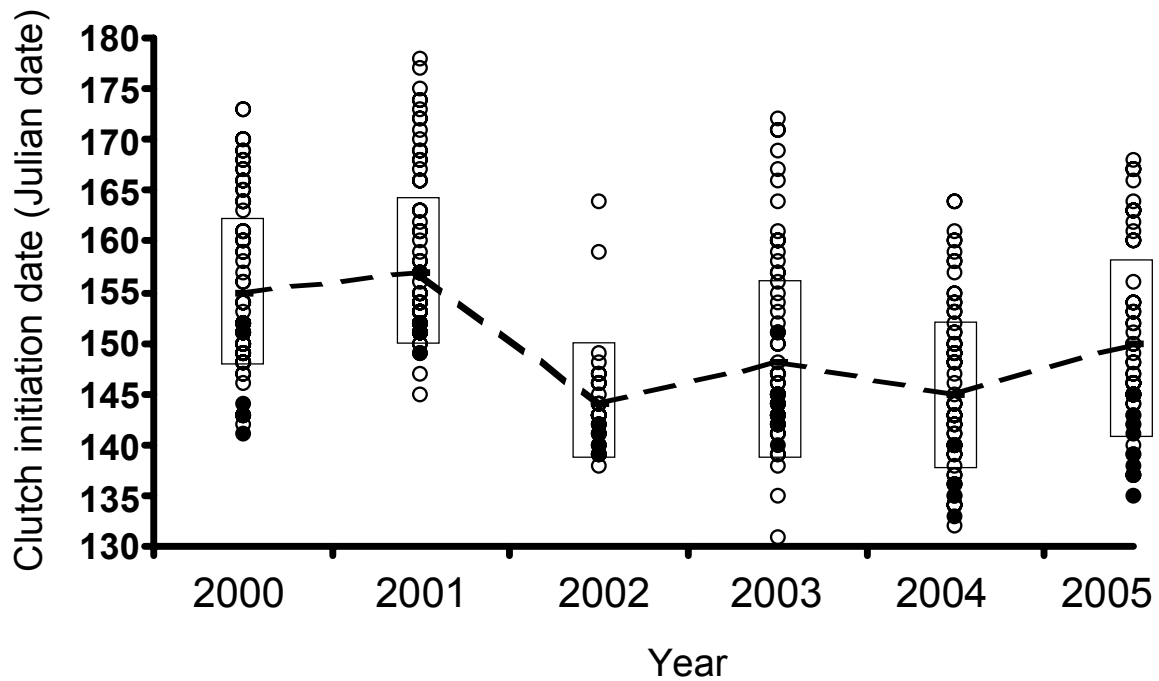


Figure 2.1. Western Sandpiper clutch initiation dates at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (2000–2005, N = 430). Open circles represent pairs attempting reproduction together for the first time and closed circles represent pairs that bred together during the previous season. The dashed line indicates mean annual clutch initiation date ($\pm 1SD$, open rectangles).

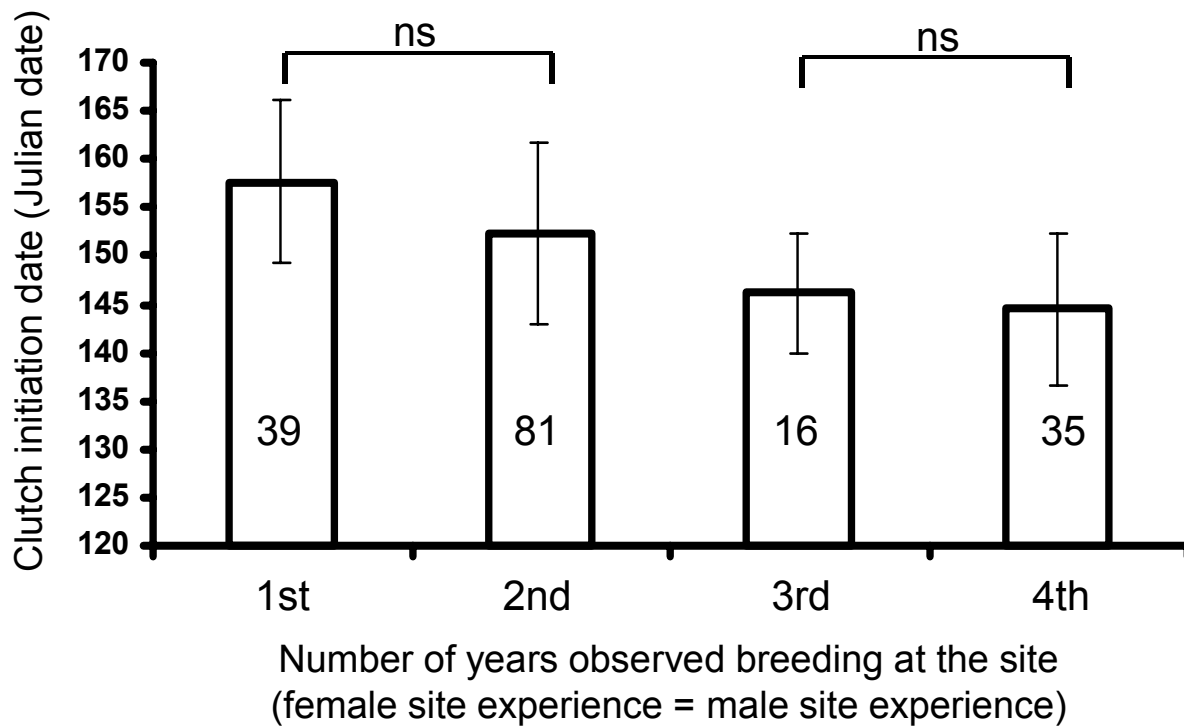


Figure 2.2. Mean \pm SD clutch initiation dates for Western Sandpiper pairs with no prior mate experience and zero to three years site experience at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (2000–2005, N = 171). All mean comparisons statistically different except as indicated, all $p < 0.001$.

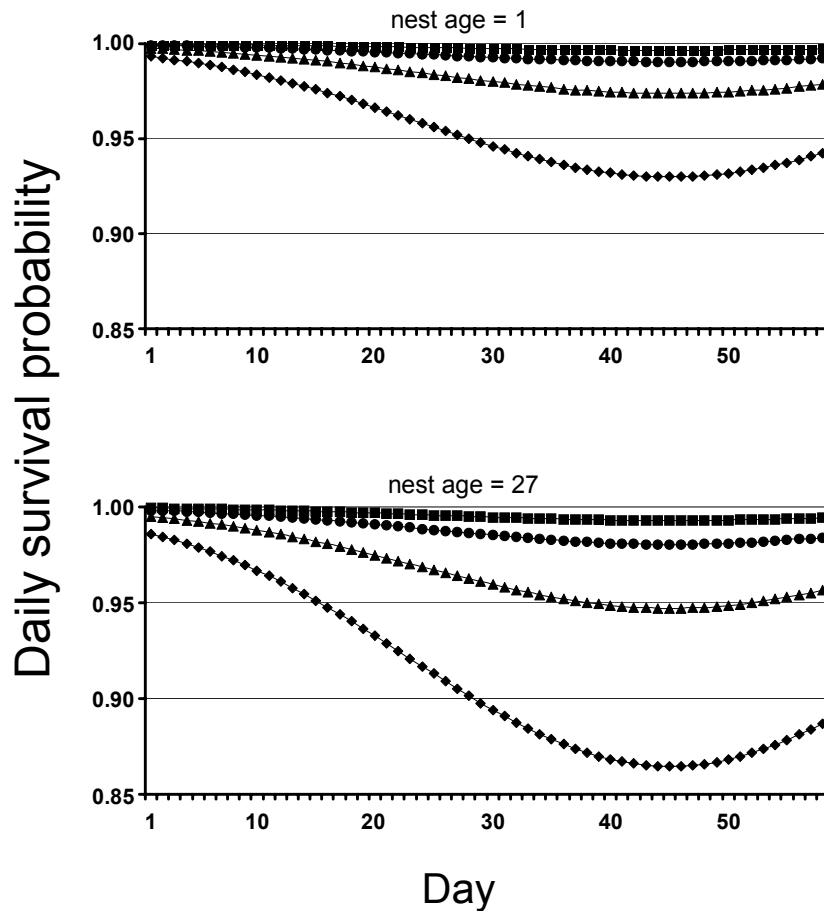


Figure 2.3. The effects of nest age (1- and 27d-old nests) and site fidelity (1st–4th year observed breeding at the site) on the daily survival rates of Western Sandpiper nests at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005, as a function of time of season (Day). Female site experience = male site experience; number of years observed breeding at the site: diamonds = 1st, triangles = 2nd, circles = 3rd, squares = 4th. Day 1 corresponds to 11 May and day 59 corresponds to 8 July.

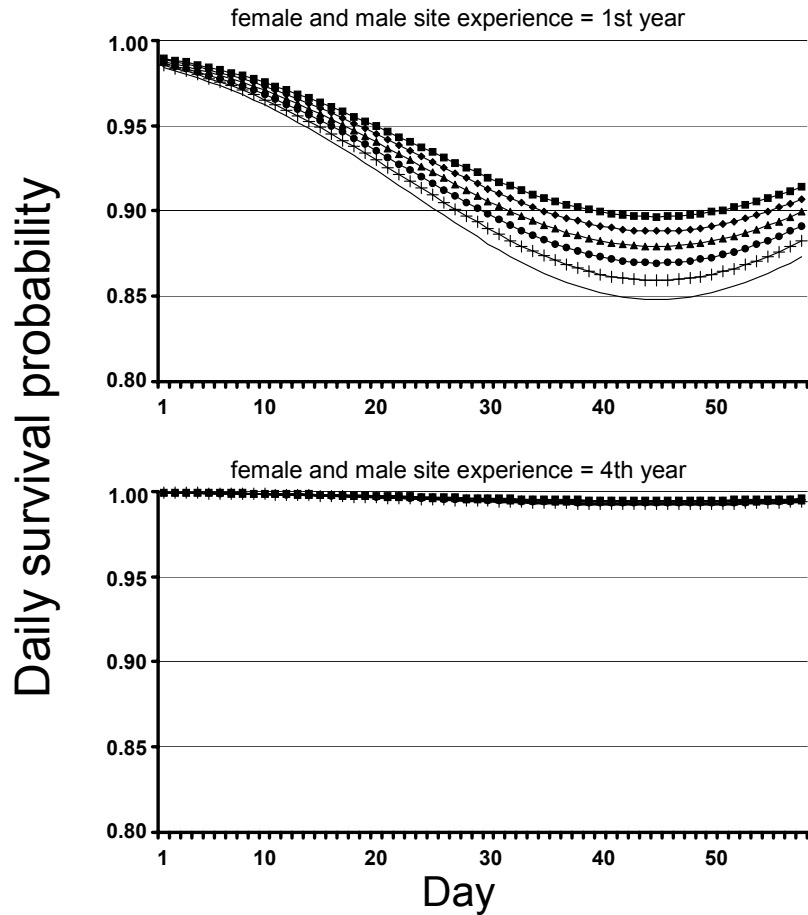


Figure 2.4. The effects of site fidelity (1st and 4th year observed breeding at the site) and year on the daily survival rates of Western Sandpiper nests at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005, as a function of time of season (Day). Female site experience = male site experience (first or fourth year observed breeding at the site), squares = 2000, diamonds = 2001, triangles = 2002, circles = 2003, crosses = 2004, plain line = 2005. Day 1 corresponds to 11 May and day 59 corresponds to 8 July.

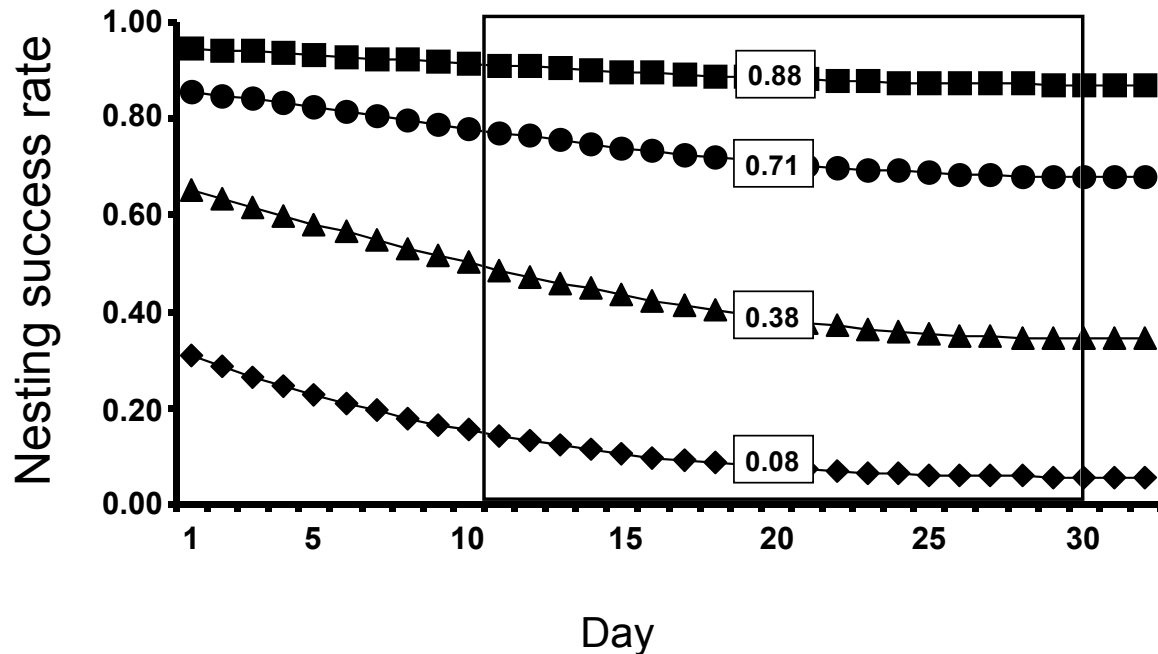


Figure 2.5. Predicted nest survival rates (the probability that a nest survives the 27d incubation period beginning on day x) for Western Sandpipers with varying breeding experience at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005. Nest survival was calculated using the logistic regression equation from the best model, where the nest began at age 1 on day x and continued to age throughout the 27d incubation period. This calculation was possible from 11 May to 11 June (days 1–32), where day refers to the starting date for each nest survival calculation. Nest survival estimates for pairs with 0–3 years site experience are given for nests initiated on 2 June (day 20, overall mean initiation date, $N_{\text{nests}} = 430$, open rectangular area = $\pm 1\text{SD}$). Female site experience = male site experience; number of years observed breeding at the site: diamonds = 1st, triangles = 2nd, circles = 3rd, squares = 4th.

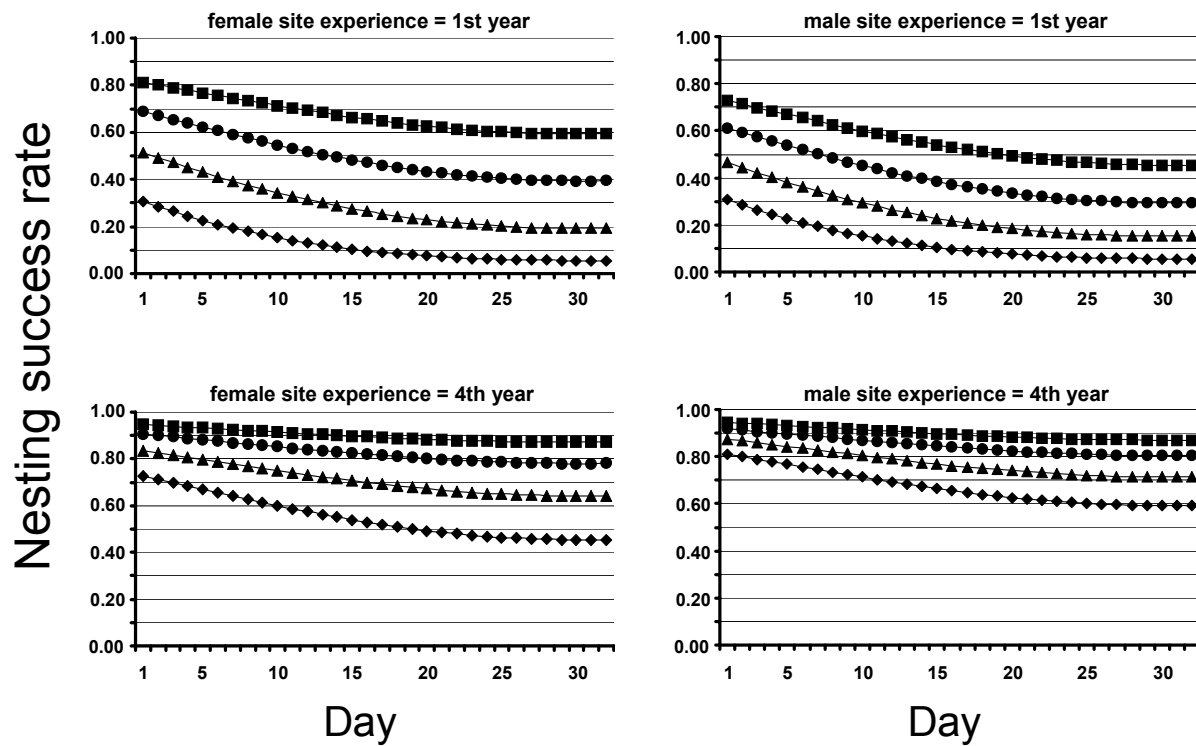


Figure 2.6. Predicted nest survival rates (the probability that a nest survives the 27d incubation period beginning on day x) for Western Sandpiper pairs with varying breeding experience at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 2000–2005. Nest survival was calculated using the logistic regression equation from the best model, where the nest began at age 1 on day x and continued to age throughout the 27d incubation period. This calculation was possible from 11 May to 11 June (days 1–32), where day refers to the starting date for each nest survival calculation. Female and male site experience (number of years observed breeding at the site) was held constant at one and four years while varying mate site experience between 1–4 years (number of years mate bred at site: diamonds = 1st, triangles = 2nd, circles = 3rd, squares = 4th).

Chapter 3: Proximate and ultimate factors that promote aggregated breeding in the Western Sandpiper

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Abstract

We report that Western Sandpipers (*Calidris mauri*) on Alaska's Yukon-Kuskokwim River Delta exhibited aggregated breeding behavior at a relatively small spatial scale (1999–2001, 2003–2005). Prior to clutch initiation, males performing song flight displays on a 36 ha plot were aggregated as were subsequent initial nesting attempts on the plot. We tested three hypotheses commonly invoked to explain aggregated breeding in territorial species (social mate choice, predation, and material resources hypotheses), and found support for the material resources hypothesis, as dispersed individuals were more often associated with tundra habitat patches, and aggregated individuals nested more often in undulating-tundra habitat patches compared to patch availability. The pattern of habitat occupancy conformed to an ideal despotic distribution with aggregated nesting birds in undulating-tundra patches experiencing lower reproductive success. On our study plot, older, more aggressive males solicited females more often, and defended larger, more dispersed sites in tundra habitat patches, compared to younger, less aggressive males that were aggregated in undulating-tundra habitat patches. Breeding aggregations are often concentrated on or near a critical resource. In contrast, Western Sandpiper breeding aggregations occur when dominant and/or older individuals exclude younger, subordinate individuals from preferred habitat.

KEYWORDS: *Calidris mauri*, space use, habitat, reproduction, despotic distribution

Introduction

Breeding aggregations have been observed in numerous aquatic and terrestrial animals including fish (Itzkowitz 1978), insects (Muller 1998, Sumpter and Broomhead 2000), reptiles (Stamps 1988), primates (Treves 2000), and birds (Stamps 1988; Muller et al. 1997). Presumably, animals aggregate when the benefits of doing so exceed the costs of social interaction. The benefits of joining a breeding aggregation may be either resource-based, where (in birds) individuals select habitats that offer foraging opportunities or safe nesting sites (natural selection), or driven by sexual interactions and mate choice (sexual selection hypotheses, Tarof and Ratcliffe 2004).

Mechanistic and evolutionary processes that result in avian breeding aggregations have most often been studied among colonial nesting species, where nesting (and not foraging) is the primary activity within the aggregation and lekking species, where only mate choice and reproduction occur (reviewed by Bradbury and Gibson 1983, Brown and Brown 2001). Among colonial nesting species, potential costs of nesting in close proximity to conspecifics (increased levels of: resource competition, intraspecific brood parasitism, nest predation, and parasite transmission) appears to be offset by direct benefits including increased food finding efficiency (material resources hypothesis, Kiester and Slatkin 1974; information center hypothesis, Wittenburger and Hunt 1985), reduced predation due to group defense or the dilution effect (predation hypothesis, Hamilton 1971), or increased opportunities for extra-pair copulations (hidden lek hypothesis, Wagner 1997). Among lekking species, theory on the evolution and maintenance of aggregative behavior suggests individuals aggregate in response to: the patchy distribution of ecological factors (e.g., display sites or predators, material resources and predation hypotheses), the patchy distribution of conspecifics (males cluster in areas where

females tend to be found, low-quality males cluster around high-quality males), or because females prefer aggregations of males (social mate choice hypothesis; Allee 1951, Darling 1952).

Aggregation of multi-purpose breeding territories is a common form of spatial structure in animals, and occurs when individuals establish territories in close proximity to conspecifics which results in clusters of territories in apparently homogeneous breeding habitat (Tarof and Ratcliffe 2004). Study of breeding aggregations among socially monogamous avian species (>90% of the world's birds, Lack 1968) has revealed that the spatial distribution of breeding activities is most often correlated with optimal displaying/nesting habitat, areas with high food availability, low predation risk, and species specific foraging and reproductive strategies (material resources, predation, and hidden lek hypotheses; reviewed by Hildén 1965, Cody 1985, Morse 1989; but see Tarof and Ratcliffe 2004).

Monogamous avian breeding aggregations offer a manageable natural system for testing alternative hypotheses explaining the relative influence of social and environmental factors on the spatial distribution and behavior of individuals. Avian breeding behavior is typically observable, aggregations can be measured accurately and habitat characteristics can be quantified with reasonable effort. Shorebirds (Charadriiformes) exhibit some of the most elaborate and overt breeding displays of any avian group (Miller 1985). The 24 species of sandpiper in the subfamily calidridine (Charadriiformes, Scolopacidae) exhibit every described mating system, with territoriality and mating strategy sometimes varying within a species (Oring 1982). Studies of intra- and inter-specific variation in calidridine sandpiper social systems have contributed greatly to understanding the evolution of social behavior (Pitelka et al. 1974, Miller 1979, Oring 1982, Oring and Lank 1985). The study of calidridine sandpiper spatial structure offers an

opportunity to extend our understanding of how ecological and social factors affect the distribution of breeding animals.

During eight years of study in Western Alaska (1998–2005), we observed apparent aggregation of initial nesting attempts by a territorial calidridine sandpiper, the Western Sandpiper (*Calidris mauri*, Fig. 3.1). Western Sandpipers are socially and genetically monogamous (i.e., extra-pair paternity is rare) 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 that are defended against conspecifics, from which territorial males advertise for mates using species-specific displays (Brown 1962, Holmes 1971). Territories range from 0.2–0.3 ha, and males often defend display territories in close proximity to one another. Territorial males regularly engage in chases and intense fighting; however, after some clutches are completed, it is not uncommon for unpaired males to display over nesting habitat in which females have previously initiated nests (Holmes 1971, Lanctot et al. 2000). Breeding displays are often performed with one or more other males simultaneously, but not in a duetting fashion (Lanctot et al. 2000). Adult Western Sandpipers obtain some food in the vicinity of their nests but more commonly forage in separate feeding areas along the shores of lakes, rivers, and sloughs, and in the low-lying marshes (Holmes 1971, Lanctot et al. 2000).

In our study, we provide statistical support that Western Sandpipers exhibit aggregated breeding behavior. We then evaluate three hypotheses commonly invoked to explain aggregated breeding in territorial animals: (1) The social mate choice hypothesis, which predicts that aggregated males have improved success at attracting social partners compared to solitary individuals; (2) The predation hypothesis, which predicts that aggregated breeding reduces predation via antipredator strategies; and (3) The material resources hypothesis, which predicts

that individuals aggregate in response to patchily distributed resources (vegetation and/or food). We tested the social mate choice hypothesis by comparing clutch initiation dates and female age between aggregated and dispersed nesting birds, the predation hypothesis by comparing nest success between aggregated and dispersed nesting birds, and the material resources hypothesis by comparing vegetation associated with aggregated and dispersed nesting birds.

Methods

Study site and general field methods

We studied Western Sandpiper breeding behavior at the Yukon Delta National Wildlife Refuge's Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (61°22' N, 165°07' W). Vegetation surrounding Kanaryarmiut Field Station is a complex of lakes, sloughs, wetlands, and upland tundra corresponding to the "lowland moist low scrub" community described by Jorgenson and Ely (2001). Upland tundra vegetation is dominated by lichens, *Sphagnum* spp., *Betula nana*, *Salix fuscescens*, *Ledum decumbens*, *Empetrum nigrum*, *Rubus chamaemorus*, *Eriophorum* spp., and *Poa eminens*, and wetland and lakeshore margin vegetation is predominately characterized by sedges (*Carex mackenziei*, *C. rariflora*), and grasses (*Poa eminens*, *Calamagrostis* spp., *Eriophorum* spp.; Ely and Raveling 1984). The upland tundra vegetation community is a mosaic of patches that can be classified into three basic types. First is upland tundra that contains graminoid species (hereafter tundra-grass, corresponding to dwarf shrub-graminoid tundra in Johnson and McCaffery 2004). The second type is upland tundra that lacks a graminoid component (hereafter tundra, corresponding to dwarf shrub tundra in Johnson and McCaffery 2004). The third is undulating-tundra, characterized by greater vertical relief that

results in retention of water for longer periods after spring thaw and a sedge and grass component.

The breeding population of Western Sandpipers at Kanaryarmiut Field Station was continuously monitored for eight years (1998–2005) as part of a long-term demographic study; however, effort varied across years. In 1998 and 2002, demographic data were primarily gathered 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 at this site (1999–2001 and 2003–2005), data were collected on an additional 20ha surrounding the original plot (36ha total; mean \pm SD number of nests monitored per yr = 113 ± 25 , mean \pm SD number of adults banded per yr = 89 ± 16). Further, individual behavioral data were recorded on the 36ha plot during the last three years of study (2003–2005). We only used data gathered during those years when the larger study plot was surveyed because of temporal variation in effort and to maintain consistency in analyses across years.

Two to four observers surveyed the 36 ha study plot daily from early May through late July for banded birds, nests, and broods. Adults and chicks were marked with a U.S. Fish and Wildlife Service identification band as well as with unique UV-stable color band combinations at the nest. The location and behavior of banded birds was recorded daily (2003–2005). The locations of nests and banded individuals were mapped using ArcMAP (ESRI GIS and mapping software) and nests were monitored through hatch, predation, or abandonment. After hatch, sandpiper parents and broods were resighted, mapped, and parent and chick behaviors were recorded once (1999–2001) or twice (2003–2005) daily until they fledged, were depredated, or abandoned. We produced vegetation maps in the field by manually delineating vegetation

patches (tundra, tundra-grass, undulating-tundra) on aerial photographs. Polygons were then digitized and georeferenced using ArcMAP (ESRI GIS and mapping software).

Measures of aggregation

Any classification of random, aggregated, and even distributions in nature comprises arbitrary distinction made along a continuum of these three spatial patterns. However, the homogeneous Poisson process is the only point process that is the equivalent of complete spatial randomness (Poole 1974, Pielou 1977). Testing for complete spatial randomness relies on comparing an observed spatial pattern with patterns expected for a homogeneous Poisson process. Measures of dispersion may be calculated from the distribution of individuals among sample plots or distances between individuals within a population (nearest neighbor distances, Diggle 1983). For example, we may calculate nearest neighbor distances for initial nesting attempts on a study plot, then simulate a random distribution with the same number of points within that area, and compare the observed nearest neighbor distances with those expected from a completely random process (i.e., homogeneous Poisson).

We plot observed nearest neighbor distances (solid line) against hypothetical nearest neighbor distances under complete spatial randomness (straight dashed line) to evaluate whether an observed spatial pattern may have been generated by a completely random process (Fig. 3.2, Diggle 1983). If a spatial distribution is random there is a straight-line relationship between observed nearest neighbor distances and a completely random distribution (Fig. 3.2). This straight-line relationship is the probability that empirical nearest neighbor distances take on a value equal to or less than the nearest neighbor distances expected under complete spatial randomness. If our plot of observed nearest neighbor distances falls to the left of the straight

line, this indicates there is a greater probability of having nearest neighbor distances less than that under complete spatial randomness (Fig. 3.2). An excess of short nearest neighbor distances compared to complete spatial randomness implies a spatially aggregated distribution. In contrast, if our plot of empirical data falls to the right of the straight line, this indicates fewer short distances than expected under complete spatial randomness, hence, a spatially even distribution (Fig. 3.2).

We used the SAS macro collection for nearest neighbor analysis of a spatial point pattern (Schabenberger and Pierce 2002) to determine whether Western Sandpiper initial nesting attempts were spatially aggregated on our study plot annually. This macro collection computed nearest neighbor distances for initial nesting attempts on the 36 ha plot each year, simulated 1000 datasets for each year with the same number of nests randomly distributed across the plot to provide an estimate of complete spatial randomness, calculated sample averages for estimates of complete spatial randomness (upper and lower simulation envelopes), and compared observed nearest neighbor distances with estimates of complete spatial randomness using Monte-Carlo significance tests.

We also used the SAS macro collection for nearest neighbor analysis of a spatial point pattern to determine if displaying males were spatially aggregated on our study plot on a daily basis during 2003–2005. These data were gathered by two observers simultaneously surveying from the middle of the plot towards its periphery. Care was given to avoid double counting of individuals while surveying the plot. We only recorded the initial location where displaying males were observed. For spatial analysis of displaying males, we selected all days between 10 May and 10 June for which we observed at least 20 displaying males on the plot (average

number of days per year \pm SD = 17 ± 2 , mean number of displaying males per day \pm SD = 27 ± 3). We did not observe ≥ 20 males displaying on the plot in a single day outside of this period.

Nearest neighbor distance and individual male behavior

We examined individual male behavior and their spatial distribution prior to being paired with a fertile female during 2003–2005. We identified males that were not yet paired with fertile females using nest initiation data (Lanctot et al. 2000). From those, we selected males with a minimum of 10 display flight observations for analyses (minimum of four hours between consecutive observations). This process resulted in the selection of 32 males over a three-year period with a mean of 18 observations/individual. Using these data, we estimated relative display area size for each male by drawing minimum convex polygons around the location of display flights. We also computed the proportion of observations in which males exhibited behavior in five behavioral classes (display flight, chase, fight, solicit, and self-maintenance). We considered a male to have performed a display flight if he vocalized at a height of at least 5 m for a minimum of 5 s, chasing behavior entailed a male flying after one or more conspecifics, physical contact with a conspecific denoted fighting behavior, the tail-up courtship stance described by Holmes (1973) was used to quantify solicitation, and self-maintenance behaviors included loafing, sleeping, and preening. As a measure of spatial dispersion, we calculated the distance from each initial nesting attempt on the plot to its two nearest neighbors using ArcMAP (ESRI GIS and mapping software). We then examined the relationship between male behaviors prior to being paired with a fertile female and the sum of the distances from each male's initial nesting attempt to the two nearest neighboring nests using Spearman rank correlation (Zar 1999).

Testing the material resources hypothesis

Habitat use in relation to availability

To examine the relationship between spatial dispersion and habitat patches (tundra, tundra-grass, undulating-tundra), we delineated aggregated and dispersed nesting birds by separating nearest neighbor distances (sum of the distances from each nest to its first two nearest neighbors, Appendix 3.1) into quartiles annually. This resulted in nearly a three-fold difference in nearest neighbor distances between the first and fourth quartiles of aggregated and dispersed nesting birds (Table 3.1). We then overlaid initial nesting attempts on our vegetation map (Fig. 3.1), and calculated the number of nests within each habitat class to determine whether aggregated (1st nearest neighbor distance quartile) and dispersed (4th nearest neighbor distance quartile) nesting birds differentially nested in specific habitat patches. We compared the number of aggregated and dispersed nesting birds in each habitat type annually to the number of nests expected in each habitat type if birds utilized habitat in relation to availability using chi-square goodness of fit tests (Zar 1999). Similarly, we evaluated the locations where the earliest arriving males (first five days males were observed displaying each year) were observed performing display flights. We compared the number of displaying males in each habitat patch type to the number of males expected in each habitat type if birds utilized habitat in relation to availability using chi-square goodness of fit tests. We also examined male and female age in relation to initial nest placement among the three habitat patch types (tundra, tundra-grass, undulating-tundra). We grouped birds into three age classes for this analysis (minimum age, number of years observed breeding at the site = 1, 2, ≥ 3). We randomly selected a single nesting observation for birds observed in multiple years for this analysis to avoid pseudoreplication, and used chi-square goodness of fit

tests to determine if habitat patch use among age classes varied from that expected based on availability.

Microhabitat associated with nests and birch availability among habitat patches

During 2004, we examined microhabitat associated with Western Sandpiper nests (N = 128) by comparing the proportion of five vegetation types (birch, grass, herb, moss, lichen) and the amount of vertical relief within a 1 m² frame centered on each nest and a random point within 40m of each nest. We used matched-pairs logistic regression to examine microhabitat variation between nest sites and associated random points (Johnson and Oring 2002). We compared potential models beginning with a model containing all six predictor variables using step-wise elimination to achieve the most parsimonious regression model that accurately represented the data. Akaike information criteria (AIC) were 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).

Holmes (1971) reported that Western Sandpipers breeding on the Yukon-Kuskokwim River Delta usually place nests under dwarf birch (*Betula nana*). To determine whether birch availability varied among habitat patches (tundra, tundra-grass, undulating-tundra), we sampled the proportion of birch within a 1m² frame centered on 543 points evenly distributed across the plot in 2004. We compared the proportion of birch among habitat classes using analysis of variance by ranks (Kruskal and Wallis 1952).

Testing the social mate choice hypothesis

Minimum age in relation to nest dispersion

We used contingency tables to examine the relationship between Western Sandpiper minimum age and nest dispersion (Zar 1999). We constructed a 2 x 3 contingency table for each sex with aggregated (1st nearest neighbor distance quartile) and dispersed (4th nearest neighbor distance quartile) nesting birds as rows and minimum age (number of years observed breeding at the site = 1, 2, \geq 3) as columns to test whether Western Sandpiper age was independent of nest dispersion.

Clutch initiation date in relation to nest dispersion and habitat

We used SAS PROC MIXED to compare mean clutch initiation date, for initial nesting attempts between aggregated and dispersed nesting birds (ANOVA, Littell et al. 2002). Initiation date was the dependent variable in the model, and nest dispersion was a two-level fixed factor independent variable (aggregated = 1st nearest neighbor distance quartile, dispersed = 4th nearest neighbor distance quartile). We also included year as a random factor in the model to control for annual variation. Residuals were normally distributed (Shapiro-Wilk tests $P > 0.10$) and had homogeneous variance after a square root transformation. We compared mean initiation date using Least Square Means ($\alpha = 0.05$). Based on habitat analyses, we also performed an a posteriori analysis comparing mean clutch initiation date between birds that nested in or out of undulating-tundra habitat while controlling for year effects. This analysis was similar to that described above except the independent variable was a two-level fixed factor (nests in undulating-tundra habitat, nests *not* in undulating-tundra habitat).

Testing the predation hypothesis

We compared nest success between aggregated and dispersed nesting birds using logistic regression. For this model, the dependent variable, nest success (at least one egg hatched in a clutch), was a binomial response (1 = successful, 0 = unsuccessful). Nest dispersion was a categorical variable with two levels (aggregated = 1st nearest neighbor distance quartile, dispersed = 4th nearest neighbor distance quartile), and we included year (categorical) and initiation date (continuous) as covariates in the model as these factors are known to influence nest success in many avian species (Lack 1954, Martin 1987). Based on habitat analyses, we also performed an *a posteriori* analysis examining nest success between habitat types. As described above, we used logistic regression to model the probability of nest success based on whether birds nested in or out of undulating-tundra habitat while controlling for initiation date and year effects. In this model, habitat type was a categorical variable with two levels (undulating-tundra, not undulating-tundra).

Results

During six years of study (1999–2001 and 2003–2005), we individually color banded 453 adult Western Sandpipers and located and monitored 680 nests. Four hundred and thirty-three of these nests were initial nesting attempts on the 36ha plot (mean number of initial nesting attempts per year \pm SD = 72 ± 10).

Aggregation patterns

Displaying males exhibited an aggregated spatial distribution, and subsequent initial nesting attempts attended by those males also were aggregated. Displaying males exhibited an

aggregated spatial distribution on the study plot during approximately 80% of observation days when we observed ≥ 20 displaying males (2003, 83% of observation days, N = 18 d; 2004, 82% of observation days, N = 17 d; 2005, 87% of observation days, N = 15 d). Western Sandpiper initial nesting attempts were spatially aggregated on the 36ha plot throughout the course of this study (1999, $\chi^2 = 31.0$, $P < 0.001$, N = 62; 2000, $\chi^2 = 36.2$, $P < 0.001$, N = 92; 2001, $\chi^2 = 35.2$, $P < 0.001$, N = 100; 2003, $\chi^2 = 41.8$, $P < 0.001$, N = 70; 2004, $\chi^2 = 38.0$, $P < 0.001$, N = 85; 2005, $\chi^2 = 39.0$, $P < 0.001$, N = 69; 1000 simulations/yr).

The observed distribution of nearest neighbor distances for initial nesting attempts in 2003 (Fig. 3.1) indicated a spatially aggregated distribution (Fig. 3.3). The plot of observed nearest neighbor distances (solid line, Fig. 3.3) falls to the left of the straight line relationship expected under complete spatial randomness (straight dashed line, Fig. 3.3) which indicates there is a greater probability of having nearest neighbor distances less than expected under complete spatial randomness. The plot of observed nearest neighbor distances also falls outside the simulation envelope for complete spatial randomness (irregular dashed lines, Fig. 3.3) indicating significant spatial aggregation. For brevity, we present the map of initial nesting attempts and plot of nearest neighbor distribution against complete spatial randomness for a single year (2003, Fig. 3.1 and 3, respectively), the comparable results for the remaining five years of study were similar.

Nearest neighbor distance and individual male behavior

Dispersed nesting males performed song-flight displays over a relatively larger area compared to aggregated nesting males prior to being paired with a fertile female (Fig. 3.4). Dispersed nesting males also were observed chasing conspecifics and soliciting females more often compared to

aggregated nesting males (Fig. 3.4). There was no correlation between nearest neighbor distance and the number of song-flight displays, amount of fighting, or self-maintenance behavior observed among males (all $r \leq 0.2$, all $P > 0.25$, $N = 32$).

Material resources hypothesis

Habitat use in relation to availability

During 2003–2005, the earliest arriving males displayed more often over tundra habitat and less often over undulating-tundra habitat than expected if birds utilized habitat patches in relation to availability (Fig. 3.5). Among initial nesting attempts, dispersed nests were more often in tundra habitat patches, less often in tundra-grass, and occurred in relative proportion to availability of undulating-tundra (Fig. 3.6). Whereas, aggregated initial nesting attempts were observed more often in undulating-tundra habitat patches, less often in tundra, and in relative proportion to availability in tundra-grass (Fig. 3.6). Younger males were more often associated with nests in undulating-tundra habitat patches, less often in tundra, and in relative proportion to availability in tundra-grass (Fig. 3.7). In contrast, older males were more often associated with nests in tundra habitat patches, less often in tundra-grass, and were never observed nesting in undulating-tundra (Fig. 3.7). Regardless of age, initial nesting attempts in the three habitat patches did not vary from that expected if females utilized habitat patches in relation to availability (1yr $\chi^2_{0.05, 2} = 2.1$, $P > 0.25$, $N = 89$, 2yrs $\chi^2_{0.05, 2} = 1.1$, $P > 0.50$, $N = 27$, ≥ 3 yrs $\chi^2_{0.05, 2} = 0.6$, $P > 0.50$, $N = 13$).

Microhabitat associated with nests and birch availability among habitat patches

Matched-pairs logistic regression revealed the proportion of birch (all models, $\chi^2_1 \geq 11.1$, $P < 0.001$) and graminoids (four top-performing models, $\chi^2_1 \geq 7.4$, $P < 0.01$) within 1 m² (all other predictor variables, $\chi^2_1 \leq 1.0$, $P > 0.5$, Table 3.2) were the dominant microhabitat predictors of nest presence. The top-performing model contained only birch and graminoids and this model had > 2 times the support of the next best performing candidate model. There was a consistent positive association of birch and a negative association of graminoids with nest sites compared to random points in the four top-performing models (Table 3.2; range of odds ratios, birch = 1.08–1.09, graminoids = 0.95–0.96). Birch availability varied among habitat patches ($\chi^2_2 = 9.7$, $P < 0.01$), with lower amounts of birch available per 1 m² in tundra-grass habitat compared to tundra and undulating-tundra patches (Fig. 3.8).

Social mate choice hypothesis

Minimum age in relation to nest dispersion

Results did not indicate a difference in male or female age between aggregated and dispersed nests (Fig. 3.9; males $\chi^2_{0.05, 2} = 3.10$, $P > 0.10$, $N = 238$, females $\chi^2_{0.05, 2} = 1.59$, $P > 0.25$, $N = 129$).

Clutch initiation date in relation to nest dispersion and habitat

Mean clutch initiation date was June 1st (mean Julian date \pm SE all years combined = 152 ± 2). There was no difference in mean clutch initiation dates between aggregated and dispersed nests ($t_{213} = -1.50$, $P = 0.14$), or between nests located in or out of undulating-tundra habitat ($t_{426} = -0.91$, $P = 0.36$).

Predation hypothesis

Logistic regression did not indicate that nest success significantly varied between aggregated and dispersed nesting birds (Fig. 3.10; $\chi^2_1 = 0.02$, $P = 0.90$, $N = 220$); however, there was significant annual variation in nest success during the course of study ($\chi^2_5 = 11.76$, $P = 0.04$, $N = 220$). The logistic regression model examining nest success between habitat types indicated that nest success varied between nests located in and out of undulating-tundra habitat (Fig. 3.11, $\chi^2_1 = 4.2$, $P = 0.04$, $N = 433$). Nests that were *not* in undulating-tundra patches were 63% more likely to hatch compared to nests within undulating-tundra patches (odds ratio = 1.63, 95% Wald confidence limits 1.02–2.61).

Discussion

Western Sandpipers exhibited aggregated breeding behavior at a relatively small spatial scale within suitable nesting habitat (36 ha). Prior to clutch initiation, male song flight displays were spatially aggregated, and subsequent initial nesting attempts on the plot also were aggregated. Several shorebird species are semicolonial nesters where a single breeding site may contain dense colonies, loose colonies, and solitary nesting pairs (e.g., American Avocet, *Recurvirostra americana*, Robinson et al. 1997). Some plover species nest as solitary pairs but also may nest semi-colonially (i.e., Piping Plover, *Charadrius melodus*, Haig 1990; Semipalmated Plover *C. semipalmatus*, Armstrong and Nol 1993), and loose nesting aggregations have been reported in Marbled Godwits (*Limosa fedoa*, Taverner 1942, Skeel 1983), Whimbrel (*Numenius phaeopus*, Nowicki 1973), and Upland Sandpipers (*Bartramia longicauda*, Buss and Hawkins 1939). Further, male Baird's Sandpipers (*Calidris bairdii*) appear to be aggregate while performing

display flights early in the season (Parmelee et al. 1967, Myers et al. 1982). Data support the material resources hypothesis as at least a partial explanation for aggregated breeding in Western Sandpiper. Dispersed individuals were more often associated with tundra habitat patches, and aggregated individuals nested more often in undulating-tundra patches. Data did not support the social mate choice or predation hypothesis although both are commonly invoked to explain aggregated breeding in territorial animals. There also was support for an ideal despotic distribution with lower reproductive success associated with aggregated nesting birds in undulating-tundra patches.

Social mate choice hypothesis

If sexual selection favors male aggregation because it facilitates social mate choice (Allee 1951, Darling 1952), then breeding aggregations of Western Sandpipers may represent an adaptive male strategy. Facilitation of mate choice would be especially important among birds in which female choice is constrained temporally because of a compressed breeding season (Veen et al. 2001) or when male parental care is important (Gowaty 1996), such as in the Western Sandpiper. If aggregated males are more attractive than solitary males, or if unpaired females more easily detect aggregated males (Real 1990), we would expect aggregated males to acquire a mate (and subsequent clutch) earlier than more dispersed individuals. We failed to find support for the social mate choice hypothesis in Western Sandpipers as mean clutch initiation date did not vary between aggregated and dispersed nesting birds. Because of the time constraints associated with arctic breeding, it is possible that there is little-to-no opportunity for substantial variation in clutch initiation date for Western Sandpipers. Regardless of temporal constraints on clutch initiation date, male aggregations could still facilitate social mate choice if aggregated males

were able to attract higher quality females compared to dispersed individuals. However, we found no evidence that more experienced females were associated with aggregated nests compared to dispersed nests.

Predation hypothesis

We failed to find support for the predation hypothesis as an explanation for aggregated breeding in Western Sandpipers. The predation hypothesis (Hamilton 1971, Pulliam 1973) predicts that bird's aggregate because clustering of individuals reduces predation via proximate antipredator mechanisms. However, results from six years of data revealed no consistent variation in nest success between aggregated and dispersed nesting birds.

Material resources hypothesis

The material resources hypothesis predicts that individuals aggregate in response to patchily distributed resources (vegetation and/or food, Kiestler and Slatkin 1974). We found support for the material resources hypothesis in that aggregated nests were more often associated with undulating-tundra habitat patches and dispersed nests were more often in tundra patches. The disproportionate use of undulating-tundra patches by aggregated birds resulted in a reduction in their use of tundra patches, but they did place nests in tundra-grass patches in relative proportion to habitat availability. In contrast, as a result of their disproportionate use of tundra patches, dispersed nesting birds used tundra-grass habitat patches less than expected, but used undulating-tundra habitat patches in relative proportion to availability.

Previous investigations have suggested that social organization, territorial behavioral, and nest dispersion have coevolved to increase a species' ability to exploit resources (food, habitat,

and mates) over both space and time (Holmes 1966, 1972, Oring and Knudson 1972, Graul 1973, Pitelka et al. 1974, Safriel 1975, Emlen and Oring 1977). Among monogamous Arctic breeding sandpipers, such as the Western Sandpiper, it has been assumed "...that most if not all species in this group are dispersed relatively evenly over the available habitat each year." (Pitelka et al. 1974). Although territory size, and subsequently breeding density, may vary as a result of whether food is primarily acquired on (Dunlin, *Calidris alpina*) or off (Western Sandpiper) the nesting territory (MacLean 1969, Soikkeli 1967, Holmes 1970, 1971), large fluctuations in densities within a species at particular sites have not been reported (Pitelka et al. 1974). Holmes (1971) suggested that high densities of Western Sandpipers in some areas of western Alaska are related to the patchy distribution of suitable nesting habitat (upland tundra; dwarf shrub-heath tundra in Holmes 1971). As a result, Holmes (1971) reported that the overall distribution of Western Sandpiper in western Alaska is clumped, but within suitable nesting habitat birds are regularly dispersed. Our results are contrary to this observation. Although Holmes' study site was merely 30 km northwest of ours, it is possible that upland tundra vegetation was more homogeneous at his site compared to ours, and this could result in the discrepancy in observed breeding distribution between studies. Holmes (1971) did not delineate vegetation patches within upland tundra habitat as we did, thus we are not able to compare upland tundra vegetation community composition between the two sites.

Ideal free and ideal despotic distributions

Our results can be interpreted in terms of the theory of ideal free and ideal despotic distributions (Fretwell and Lucas 1970, Fretwell 1972). In situations conforming to the ideal free distribution, animals move freely among habitats and assort themselves in proportion to resource availability.

However, once a critical density is attained in preferred habitats, individual fitness is reduced in preferred habitats and individuals begin to colonize less preferred habitat where competition is less. This results in individual fitness being equal over a range of habitats, resources, or other conditions. Alternately, the ideal despotic distribution model predicts that subordinate individuals are constrained in their choice of habitat by dominant individuals (Messier et al. 1990), resulting in differences in fitness among habitats.

Primary assumptions of this model are that different habitats provide varying opportunities for individual fitness, and that competition will ensue where resources are limited (Leibold 1995). Based on our observations that dispersed individuals more often nested in tundra habitat patches (Fig. 3.6), displayed over larger areas, chased conspecifics and solicited females more often (Fig. 3.4), that the earliest arriving males primarily displayed over tundra and tundra-grass habitat patches (Fig. 3.5), and that older males nested in tundra and tundra-grass but not in undulating-tundra patches (Fig. 3.7), we conclude that there is competition among males for tundra and tundra-grass habitat patches.

For the breeding distribution of Western Sandpipers to conform to an ideal despotic distribution, fitness must vary among habitat patches. On our study plot, nests in tundra and tundra-grass habitat patches that males appeared to prefer were more likely to hatch compared to nests in undulating-tundra patches (Fig. 3.11). We can only speculate as to why nest success was lower in undulating-tundra patches, but we did observe mink (*Mustela vison*) regularly using these patches to move across the landscape from one lakeshore to another, and both Arctic (*Alopex lagopus*) and red (*Vulpes vulpes*) fox commonly used vertical structure, such as frost heaves, to apparently surprise prey while foraging near the study site. Greater vertical relief associated with undulating-tundra patches also may provide such concealment for foraging fox

on our study plot. Regardless of the mechanism(s) underlying variation in reproduction, we conclude that Western Sandpipers exhibited a despotic breeding distribution on the study-plot, with subordinate males forced to aggregate their nests in undulating-tundra habitat patches where fitness is reduced.

Microhabitat associated with nests and birch availability among habitat patches

There is one intriguing inconsistency in our interpretation of our results. Dispersed males nested in tundra habitat patches more often than expected based on availability, less often in tundra-grass than expected, but in relative proportion to availability of undulating-tundra patches. If nesting in undulating-tundra resulted in reduced fitness via lower nest success, why were older, more aggressive, males utilizing undulating-tundra at all? Why were these individuals not utilizing tundra and tundra-grass patches to the exclusion of undulating-tundra?

At the risk of committing a logical error, habitat patches used by dispersed nesting birds may be partially explained via nest site microhabitat. Analysis of nest site microhabitat features revealed that Western Sandpiper nests were more often associated with areas containing a higher percentage of dwarf birch and a lower percentage of graminoid species. Coupling the preceding with the fact that dwarf birch availability was lowest in tundra-grass habitat patches (Fig. 3.9), it is reasonable to suppose that reduced use of tundra-grass patches by dispersed nesting birds, but continued use of undulating-tundra patches, is the result of birds avoiding graminoid species and preferentially placing nests near dwarf birch. However, such reasoning does not explain nest placement among aggregated nesting birds, as those birds used tundra-grass habitat patches in relative proportion to availability, but reduced their use of tundra patches. Continued use of tundra-grass and reduced use of tundra patches by aggregated individuals may be the result of aggregated individuals making the best of a bad situation. Aggregated males appeared to be

subordinate to dispersed individuals, so they may have been excluded from using habitat other than tundra-grass and undulating-tundra patches.

Differences in habitat preference also may reflect variation in display site characteristics and habitat preference based on display versus nest site characteristics may or may not be mutually exclusive. Further, the juxtaposition of habitat patches in relation to foraging sites (i.e., what is near tundra versus what is near undulating tundra) may relate to display and/or nest site quality and influence population spatial structure. To disentangle the relative influence of display versus nest site characteristics, future study first needs to determine what constitutes a high quality display site and then examine display site quality in relation to population spatial structure.

Conclusions

Western Sandpipers exhibited a spatially aggregated breeding distribution on a 36 ha plot in Western Alaska. Displaying males were aggregated on a daily basis as were initial nesting attempts on an annual basis. We found support for the material resources hypothesis, as dispersed individuals were more often associated with tundra habitat patches, and aggregated individuals nested more often in undulating-tundra patches. There also was support for an ideal despotic distribution with lower reproductive success associated with aggregated nesting birds in undulating-tundra patches. Although we may typically think of breeding aggregations as being concentrated on or near a critical resource, Western Sandpiper breeding aggregations appear to result from dominant and/or older individuals excluding younger, subordinate individuals from preferred habitat.

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Table 3.1. Sum of distances between initial Western Sandpiper nesting attempts and two nearest neighbor nests on a 36 ha plot at Kanaryarmiut Field Station, Yukon-Kuskokwim Delta, Alaska (1999–2001, 2003–2005).

Quartile (N)	Median (m)	Mean (m) \pm SD	Range (m)
1 (120)	52	50 \pm 15	13 – 74
2 (120)	75	75 \pm 9	53 – 97
3 (117)	99	98 \pm 12	75 – 124
4 (121)	137	147 \pm 36	102 – 278

Table 3.2. Multi-model inference based on results from matched-pair logistic regression of Western Sandpiper nest sites and matched random points. Model parameters denote the proportion of each vegetation type within 1m² of nest sites and matched random points. Δ_i is the rank of each model by rescaling AIC values such that the model with the minimum AIC value has a value of zero, and w_i is the likelihood of the model given the data. Odds ratios indicate percentage increase (birch) or decrease (graminoids) in the odds of a nest being present (i.e. 8–9% increase in the odds of a nest being present when birch was present, 4–5% decrease in the odds of a nest being present when graminoids were present).

Model	Δ_i	w_i	Odds ratio	
			Birch	Graminoids
birch, graminoids	0.0	0.58	1.08	0.95
birch, graminoids, herbs	1.6	0.26	1.08	0.95
birch, graminoids, herbs, relief	3.5	0.10	1.08	0.95
birch, graminoids, herbs, relief, moss, lichen	5.4	0.04	1.09	0.96
birch	7.2	0.02	1.08	-

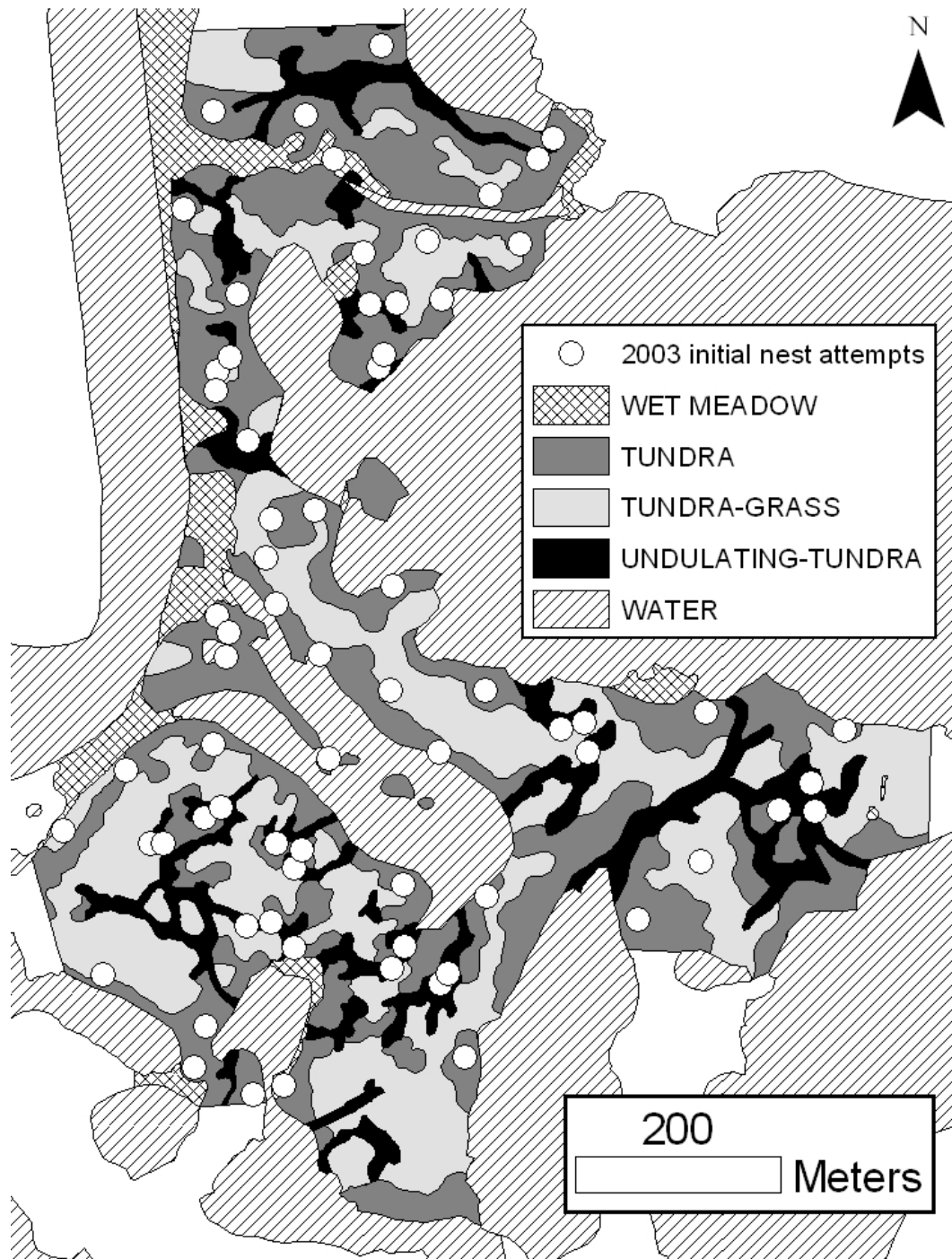


Figure 3.1. Habitat map and initial nesting attempts of Western Sandpipers at the Yukon Delta National Wildlife Refuge's Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (2003). Habitat in white areas was not quantified.

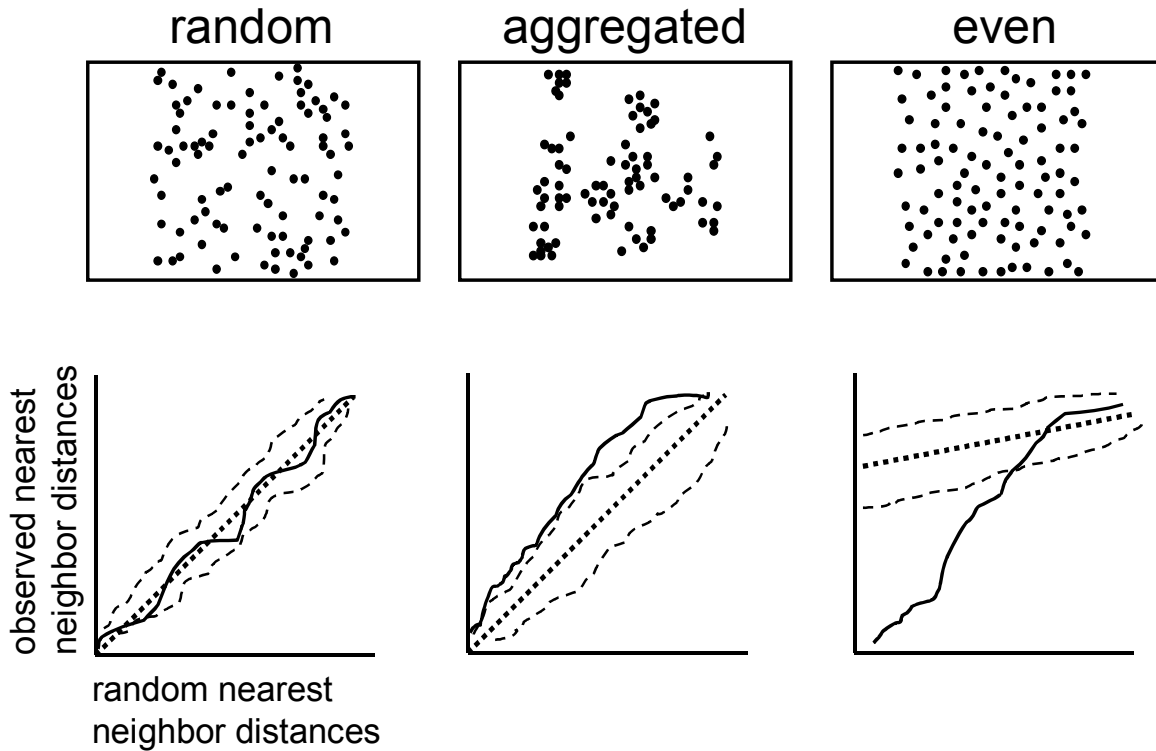


Figure 3.2. Three hypothetical spatial distributions (random, aggregated, and even) with corresponding plots of observed nearest neighbor distances along the y-axes (empirical distribution functions, solid line) and nearest neighbor distances expected under complete spatial randomness along the x-axes (cumulative distribution function, straight dashed line). Irregular dashed lines in each plot provide upper and lower simulation envelopes for nearest neighbor distances under complete spatial randomness and represent sample averages.

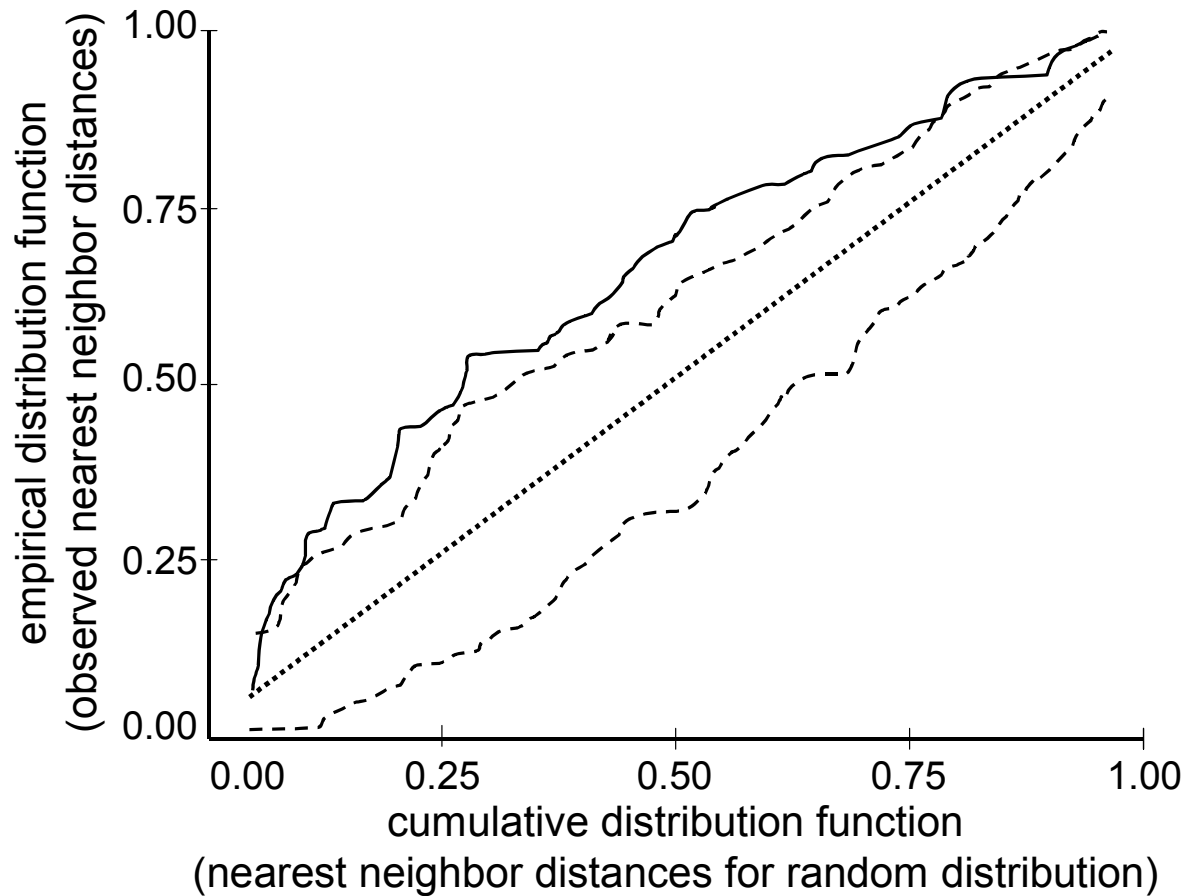


Figure 3.3. Plot of the empirical distribution function of observed nearest neighbor distances for Western Sandpiper initial nesting attempts on the study plot in 2003 (solid line) versus the cumulative distribution function of a hypothetical distribution of nearest neighbor distances under complete spatial randomness (straight dashed line). Irregular dashed lines provide upper and lower simulation envelopes for the cumulative distribution function based on 1000 Monte Carlo simulations.

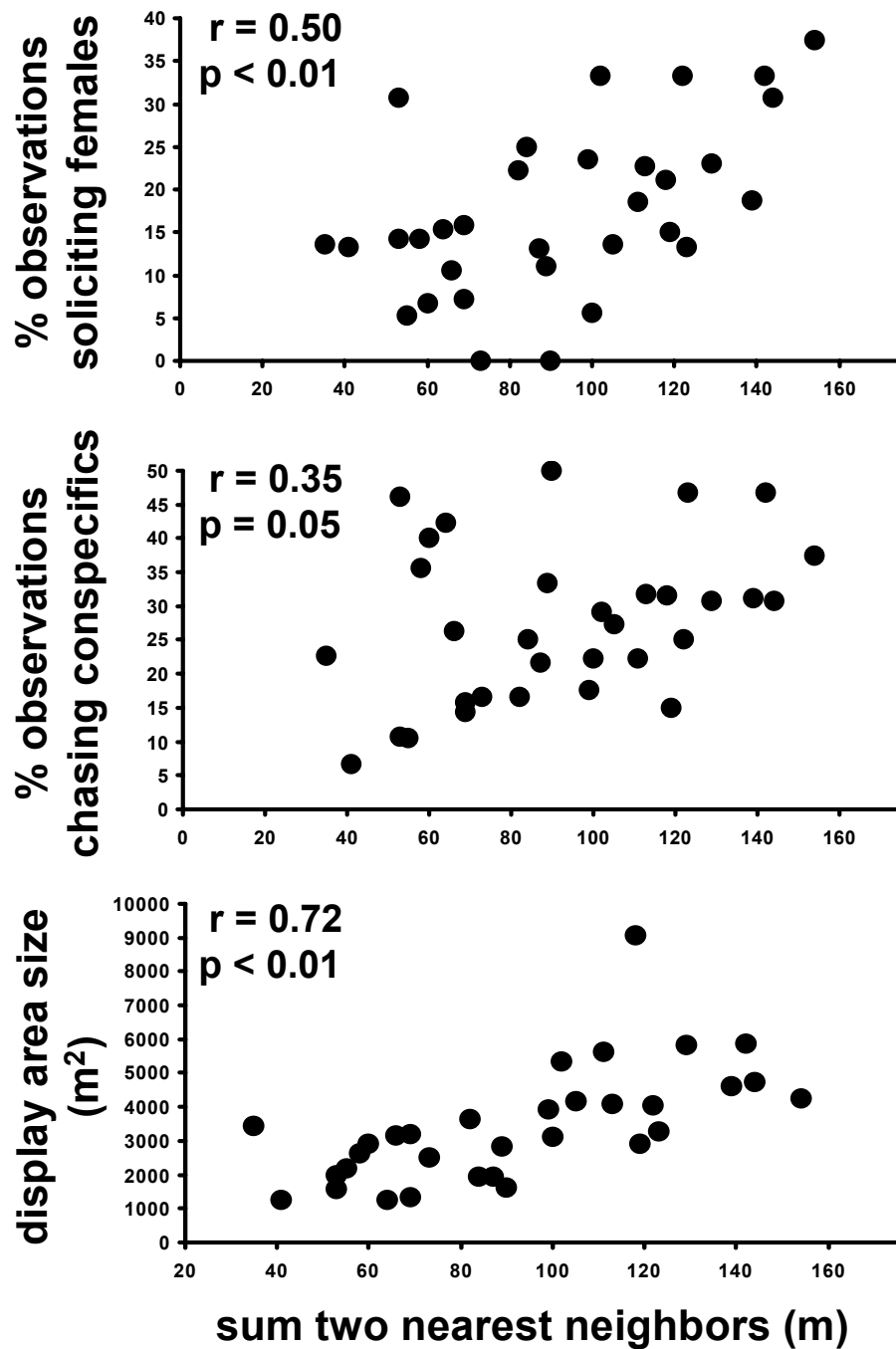


Figure 3.4. Spearman rank correlations between individual male ($N = 32$) behaviors (proportion of observations soliciting females and chasing conspecifics, and display area size) prior to being paired with a fertile female and the sum of the distances from subsequent initial nesting attempts to the two nearest neighbor nests (2003–2005).

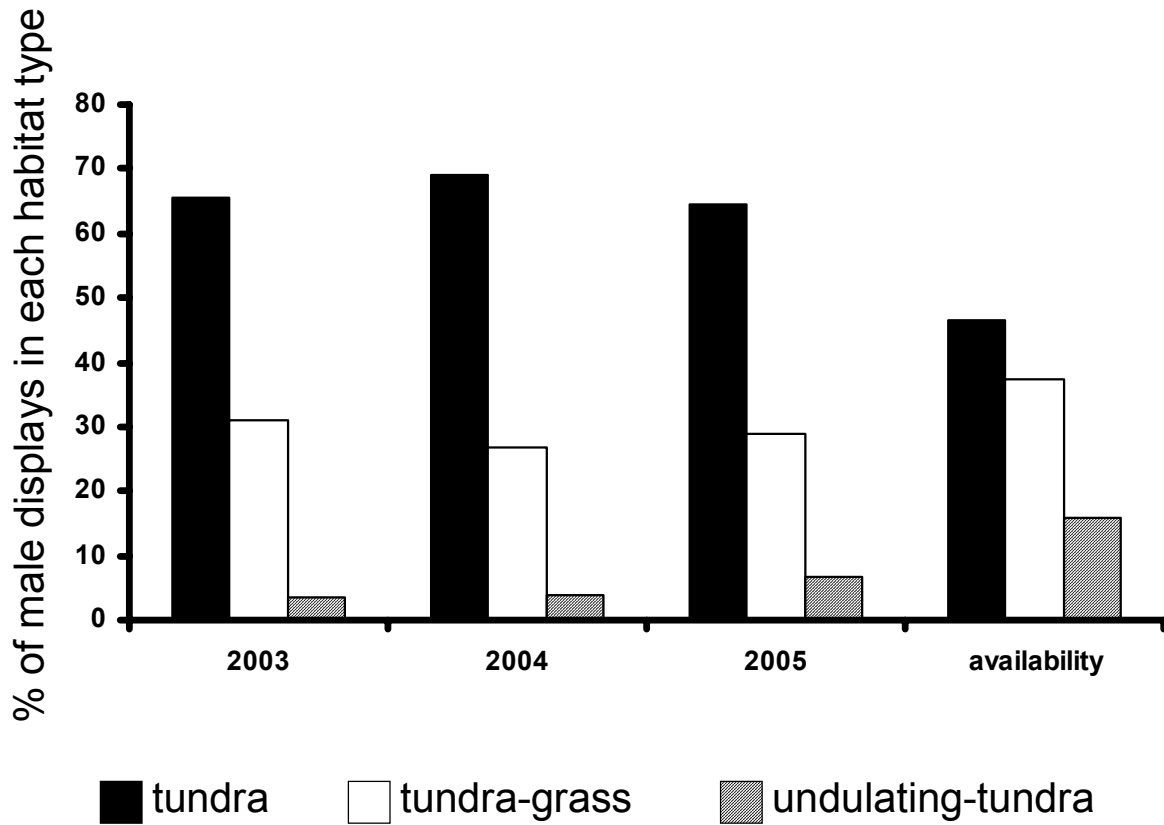


Figure 3.5. Proportion of male Western Sandpiper display-flights observed over three habitat patch types during the first five days males were observed displaying on the study plot annually (2003–2005). Habitat use by displaying males differed significantly from that expected if birds utilized habitat patches in relation to availability (2003 $\chi^2_{0.05,2} = 5.4$, $P < 0.10$, $N = 29$; 2004 $\chi^2_{0.05,2} = 6.0$, $P < 0.05$, $N = 26$; 2005 $\chi^2_{0.05,2} = 6.4$, $P < 0.05$, $N = 45$).

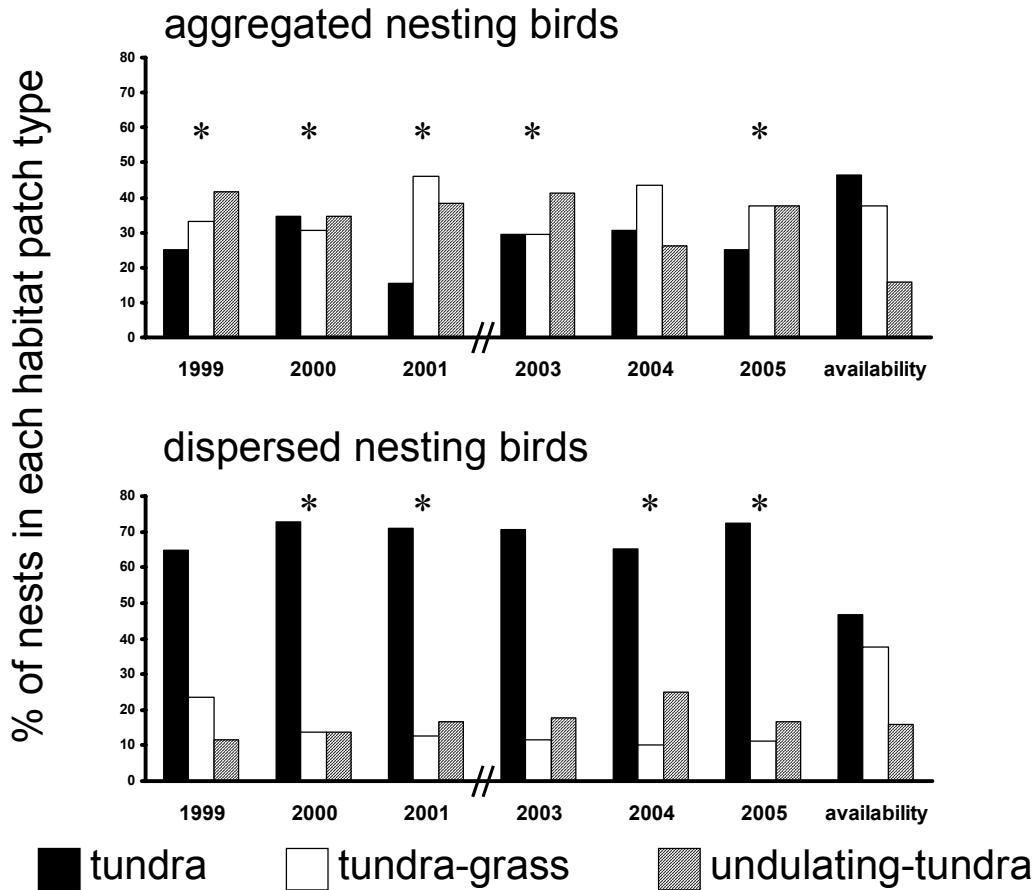


Figure 3.6. Proportion of initial nesting attempts by aggregated and dispersed nesting birds in three habitat patch types on a 36ha plot annually (1999–2001, 2003–2005). Habitat use for both aggregated and dispersed nesting birds differed significantly from that expected if birds utilized habitat patches in relation to availability (* = $P < 0.05$). Aggregated nesting birds: 1999 $\chi^2_{0.05, 2} = 6.3$, $P < 0.05$, $N = 12$, 2000 $\chi^2_{0.05, 2} = 6.2$, $P < 0.05$, $N = 23$, 2001 $\chi^2_{0.05, 2} = 14.3$, $P < 0.001$, $N = 26$, 2003 $\chi^2_{0.05, 2} = 8.2$, $P < 0.025$, $N = 17$, 2004 $\chi^2_{0.05, 2} = 3.0$, $P > 0.10$, $N = 23$, 2005 $\chi^2_{0.05, 2} = 6.3$, $P < 0.05$, $N = 16$; Dispersed nesting birds: 1999 $\chi^2_{0.05, 2} = 2.3$, $P > 0.25$, $N = 17$, 2000 $\chi^2_{0.05, 2} = 6.6$, $P < 0.05$, $N = 22$, 2001 $\chi^2_{0.05, 2} = 7.0$, $P < 0.05$, $N = 24$, 2003 $\chi^2_{0.05, 2} = 5.1$, $P < 0.10$, $N = 17$, 2004 $\chi^2_{0.05, 2} = 6.5$, $P < 0.05$, $N = 20$, 2005 $\chi^2_{0.05, 2} = 5.9$, $P < 0.05$, $N = 18$.

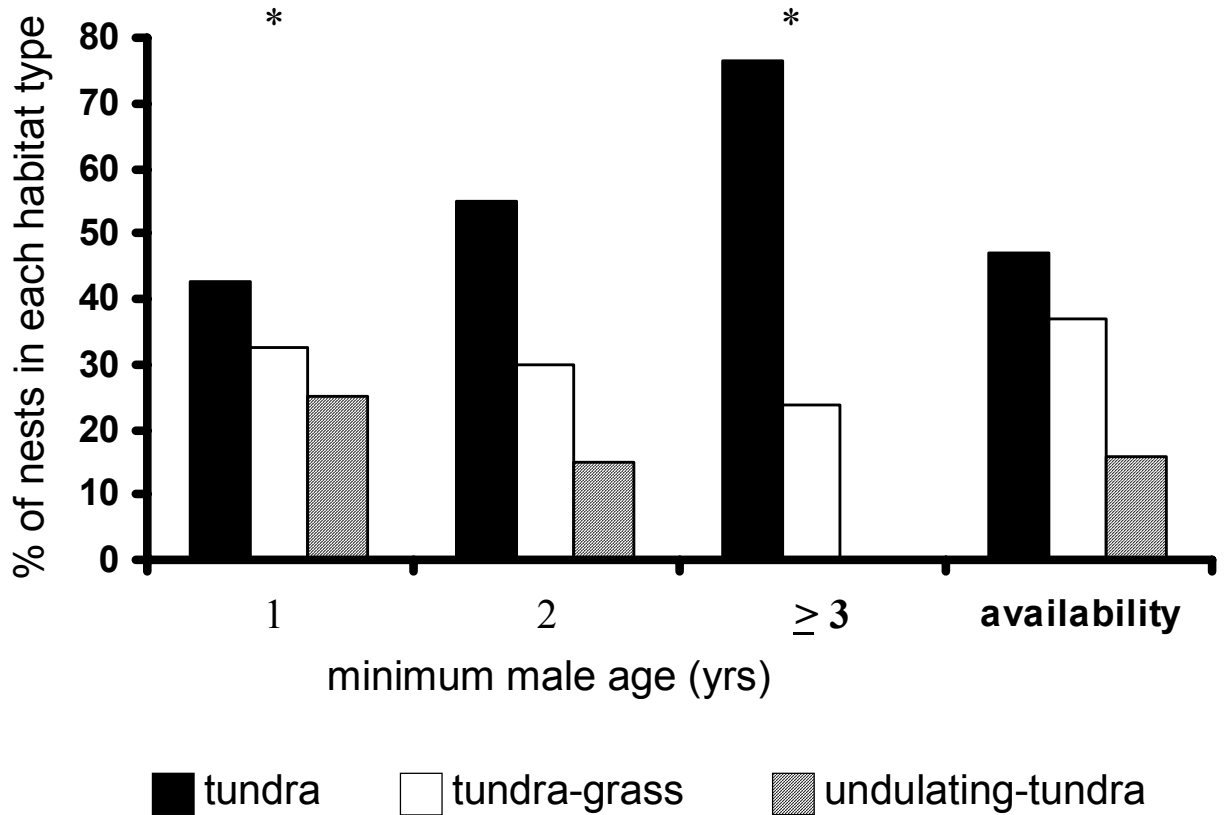


Figure 3.7. Proportion of initial nesting attempts in three habitat patch types in relation to minimum male age (# yrs observed breeding at the site). Habitat use for the youngest and oldest age classes (1st year and ≥ 3 years, respectively) differed significantly from that expected if birds utilized habitat patches in relation to availability (* = $P < 0.05$, 1yr $\chi^2_{0.05, 2} = 12.2$, $P < 0.01$, $N = 201$, 2yr $\chi^2_{0.05, 2} = 0.6$, $P > 0.95$, $N = 20$, ≥ 3 yrs $\chi^2_{0.05, 2} = 6.8$, $P < 0.05$, $N = 17$).

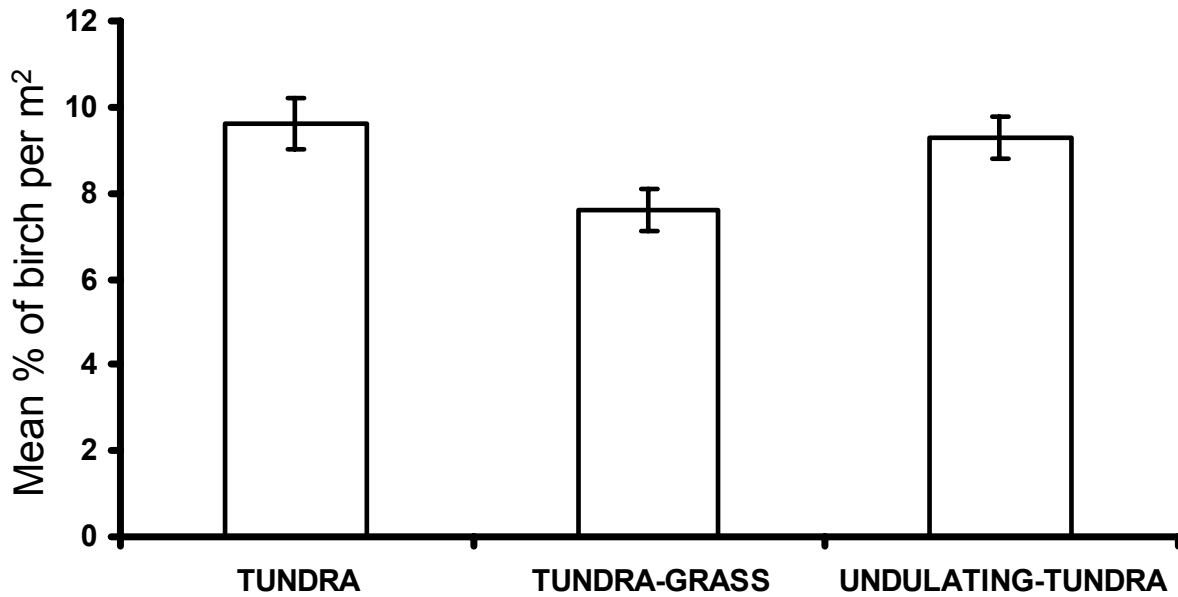


Figure 3.8. Percentage of dwarf birch (*Betula nana*) per square meter among three habitat patch types on a 36ha study plot at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska. Percentage of birch varied significantly among habitat patch types (Kruskal-Wallis test, $\chi^2_2 = 9.7$, $P = 0.008$, $N = 543$).

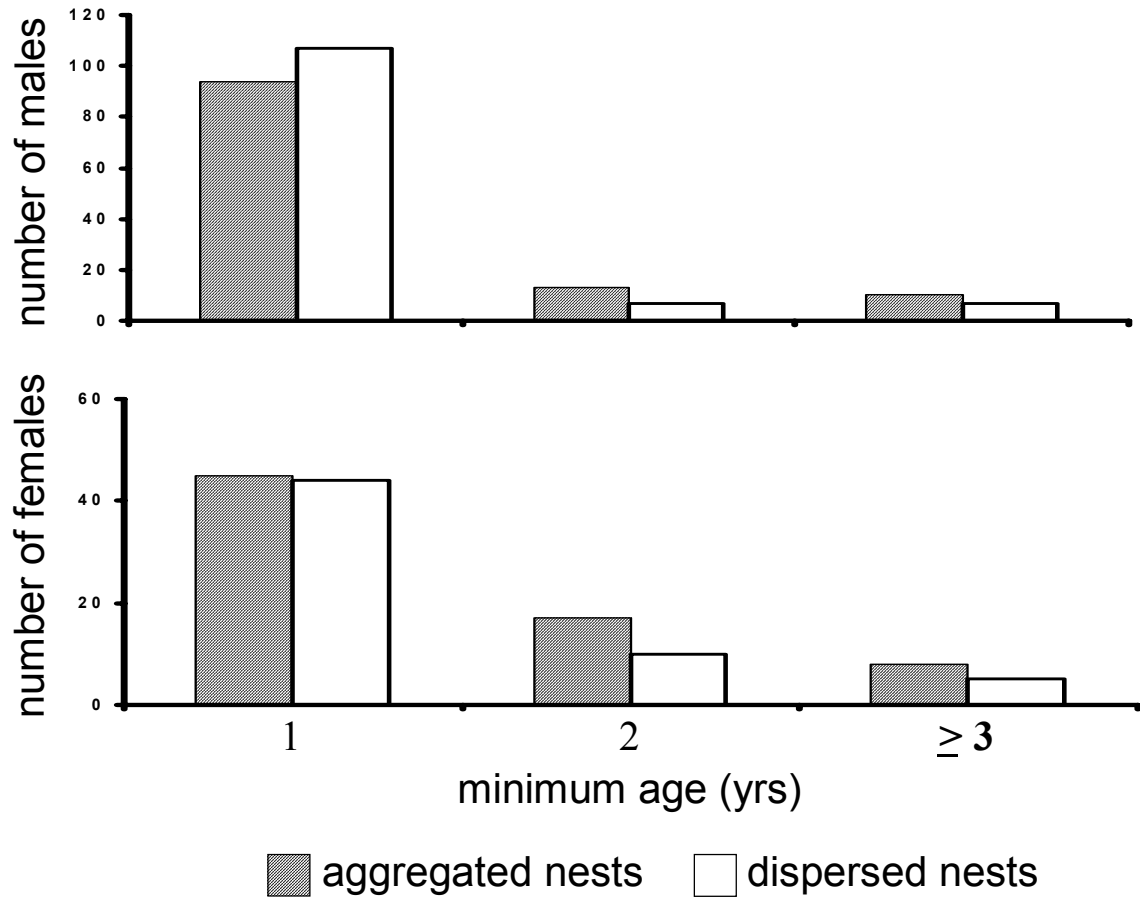


Figure 3.9. Number of male and female Western Sandpipers in three minimum age classes (# of years observed breeding at the site) associated with aggregated and dispersed nests.

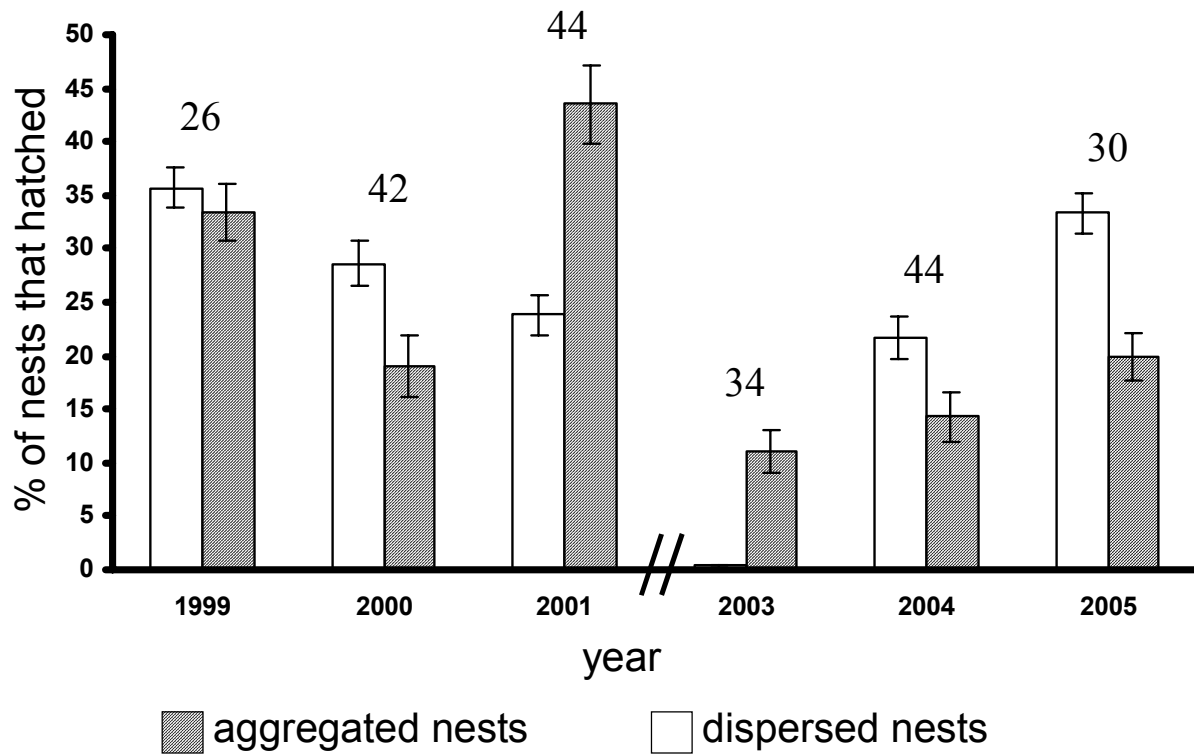


Figure 3.10. Percentage of aggregated and dispersed initial nesting attempts by Western Sandpipers to hatch (\pm SD) annually on a 36ha study plot at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska. Numbers above bars indicate sample sizes.

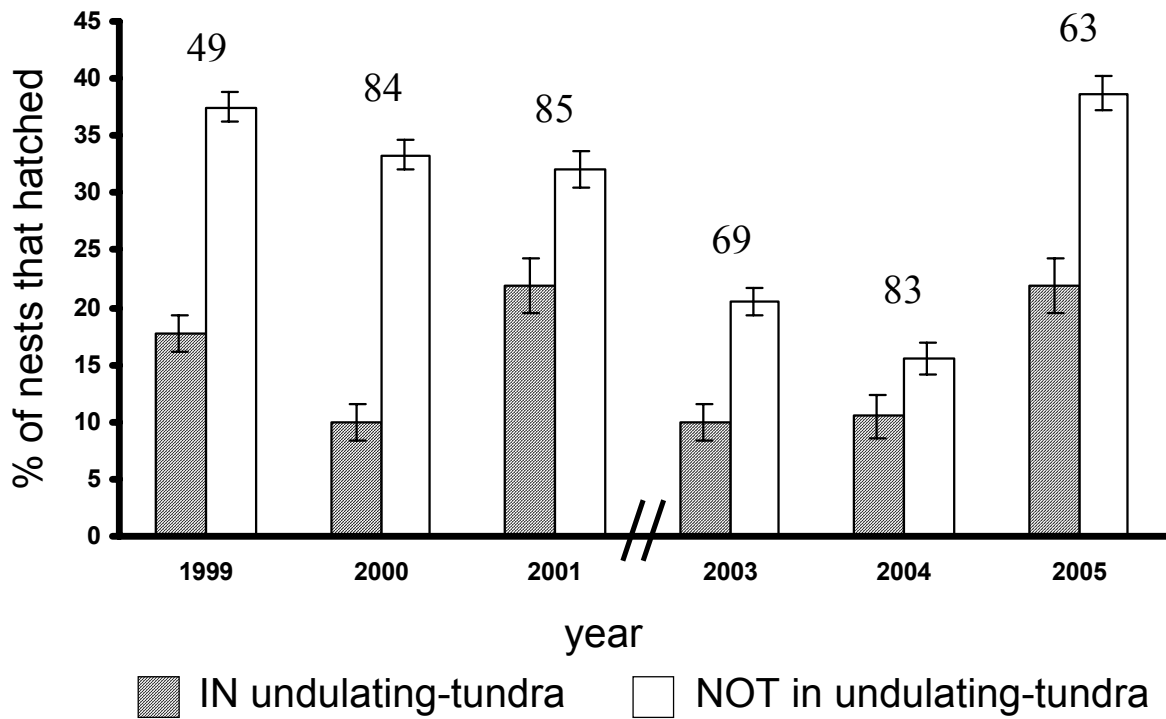
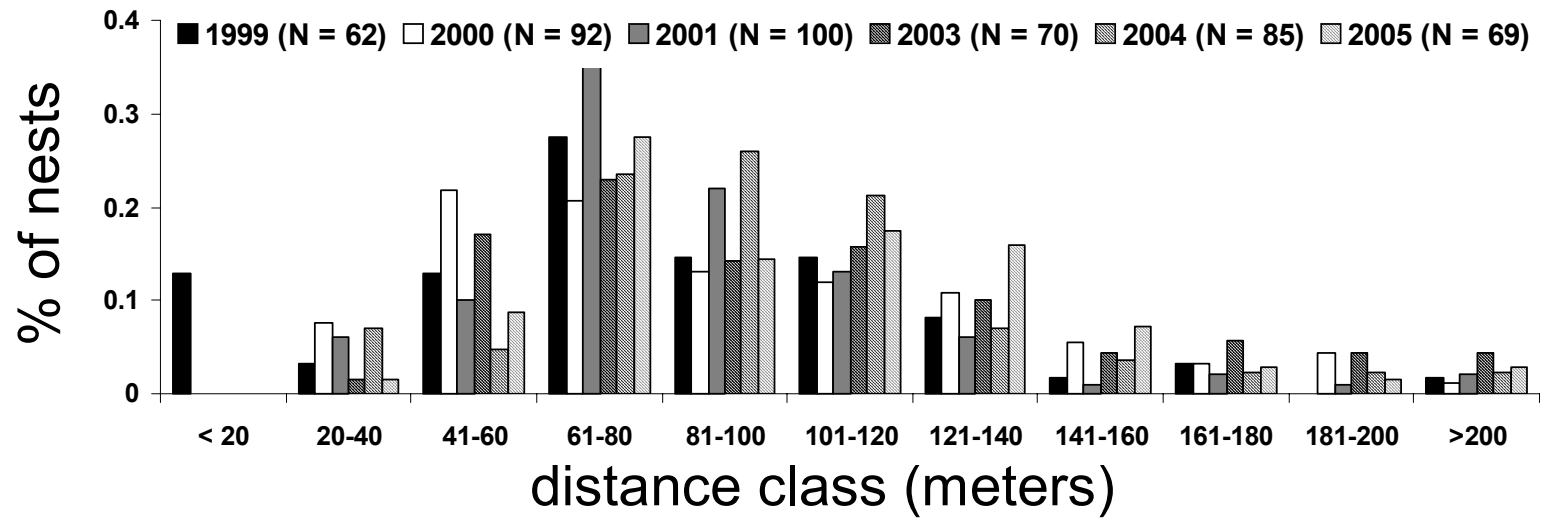


Figure 3.11. Percentage of Western Sandpiper initial nesting attempts to hatch (\pm SD) in two habitat categories annually on a 36ha study plot at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska. Numbers above bars indicate sample sizes.



Appendix 1.

Percentage of Western Sandpiper initial nesting attempts in 11 distance classes (sum of distances between nest and two nearest neighbor nests) on a 36 ha plot at Kanaryarmiut Field Station, Yukon-Kuskokwim Delta, Alaska (1999–2001, 2003–2005).

Chapter 4: Parent-offspring communication in the Western Sandpiper

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Abstract

Western Sandpiper (*Calidris mauri*) chicks are precocial and leave the nest shortly after hatch to forage independently. Chicks require thermoregulatory assistance from parents (brooding) for 5–7 days post hatch, and parents facilitate chick survival for 2–3 weeks post hatch by leading and defending chicks. Parental vocal signals are likely involved in protecting chicks from predators, preventing them from wandering away and becoming lost, and leading them to good foraging locations. Using observational and experimental methods in the field, we describe and demonstrate the form and function of parent-chick communication in the Western Sandpiper. We document four distinct calls produced by parents that are apparently directed toward their chicks (brood, gather, alarm, and freeze calls). Through experimental playback of parental and non-parental vocalizations to chicks in a small arena, we demonstrated: (1) chicks respond to the alarm call by vocalizing relatively less often and moving away from the signal source, (2) chicks respond to the gather call by vocalizing relatively more often and moving toward the signal source, (3) and chicks respond to the freeze call by vocalizing relatively less often and crouching motionless on the substrate for extended periods of time. We also discovered two distinct chick vocalizations (chick-contact and chick-alarm calls) during arena playback experiments. Results indicate that sandpiper parents are able to elicit anti-predatory chick behaviors, and direct chick movement and vocalizations through vocal signals. Future study of parent-offspring communication should determine whether shorebird chicks exhibit parental recognition through vocalizations and the role of chick vocalizations in parental behavior.

KEY WORDS: *Calidris mauri*, shorebird, parental care, precocial offspring, vocal signals, call function

Introduction

The ecology of precocial birds is considerably more dynamic during the first weeks of life compared to altricial species. Precocial chicks generally depart the nest shortly after hatch (within a few hours to a couple of days) and forage independently (Clutton-Brock 1991). Mound builders (Megapodiidae) are the most precocial of all birds with young that receive no post-hatch parental interaction or care (Elliot 1994). Parental care among most other precocial birds (Anatidae, Charadriiformes, Galliformes other than Megapodiidae) typically involves brooding offspring until they reach thermal-independence (5–10d), detecting and distracting predators, leading offspring to food, and in some species presenting or provisioning food to offspring (del Hoyo 1994, Porter, 1994, de Juana 1994, Carroll 1994, McGowan 1994, Martinez 1994). In contrast, altricial chicks remain in the nest for longer periods of time (1–2 weeks typically) and are regularly provisioned by one or both parents (Gill 1995). Nests buffer altricial chicks from considerable environmental stochasticity compared with the diverse ecological settings experienced by precocial chicks.

Through behavior, organisms can effectively abate environmental heterogeneity (Brandon 1988), and reliable communication between parents and precocial offspring may increase the probability of offspring survival if parents are able to direct young to resources such as food and shelter and alert them to the presence of predators. Specific calls are given by parents in many precocial or semi-precocial avian species to indicate the presence of food or to attract offspring to a provisioning parent (Collias and Joos 1953; Tinbergen 1960; Lind 1965; Norton-Griffiths 1969; Evans 1970a,b; Beer 1973; Buitron and Nuechterlein 1993). Laughing Gull (*Larus atricilla*) and Eurasian Oystercatcher (*Haematopus ostralegus*) parents use varying calls to indicate their distance from chicks (Norton-Griffiths 1969, Beer 1970a, Impekoven

1970), and parents of many bird species give alarm calls that elicit chicks to hide or freeze (Collias and Joos 1953; Tinbergen 1960; Lind 1965; Beer 1973; Impekoven 1970, 1976; Impekoven and Gold 1973). Parentally naïve chicks of some species respond differently to different calls (Collias and Joos 1953, Snapp 1969), and young of many avian species can distinguish parental calls from those of other individuals (Tschanz 1968; Beer 1969, 1970a,b; Evans 1970a,b; Impekoven and Gold 1973). Chicks may even begin responding to parental calls before hatch thereby facilitating rapid development of appropriate behaviors post-hatch (Grier et al. 1967; Tschanz 1968; Gottlieb 1971, 1988; Impekoven 1970, 1976; Impekoven and Gold 1973; Heaton and Galleher 1981; Buitron and Nuechterlein 1993).

Beyond the production of alarm calls by tending parents (Miller 1984, 1985 1996, Walters 1990), there is little known of parent-offspring communication among shorebirds (Charadriiformes; but see Norton-Griffiths 1969, Baker 1982). Predation rates on shorebird chicks is thought to be high (Norton 1973; Maher 1974; Safriel 1975; Walters 1982, 1990; Miller 1984; Lanctot and Laredo 1994; Johnson and Connors 1996; Nol et al. 1997; Handel and Gill 2000), and chick loss also may occur when individuals wander away and become lost (Evans & Pienkowski 1984, Gratto-Trevor 1991, Johnson 2002). Shorebird chicks have been observed traveling over a kilometer in a single day and regularly travel several hundred meters within a 4h period (Johnson & McCaffery 2004, Ruthrauff and McCaffery 2005). Parental knowledge of surrounding habitat (food and cover availability, predator densities and activity levels) may influence brood movement and habitat use if parents are able to efficiently direct offspring movements and behavior. We expect selection to have favored a reliable communication system between shorebird parents and chicks to increase the probability that chicks avoid predators, locate areas rich resources, and maintain brood cohesion during movement.

We describe parent-offspring communication in a Nearctic breeding shorebird, the Western Sandpiper (*Calidris mauri*). Western Sandpipers are small (25–30g), highly migratory shorebirds that predominately breed in western Alaska, and winter along the Pacific coast from California to Peru, and the Atlantic coast from New Jersey to Surinam (Connors et al. 1979, Wilson 1994). Western Sandpipers are socially and genetically (i.e., extra-pair paternity is rare) monogamous and exhibit biparental care of eggs and young; however, either sex, usually the female, may desert its mate and brood shortly after hatch (Holmes 1971, 1973; Blomqvist et al. 2002). Females initiate four-egg clutches from mid-May through late June that are incubated for approximately 21 days (Holmes 1971, 1973; Sandercock 1997). Precocial young leave the nest shortly after hatch, and fledge at 13–16d post-hatch (Holmes 1971, 1973). Post-hatch parental behaviors include brooding offspring until they reach thermo-independence (5–7 days) and leading and defending the brood. A single parent typically tends the brood (i.e., maintains parent chick distances of 0–10m), and the other parent generally remains alert while foraging > 20m away (Holmes 1971, 1973; Johnson and McCaffery 2004).

We have noted at least four distinct calls, produced by parents, that are apparently directed toward their chicks. Parents gave the ‘brooding call’ (Figure 4.1C) just prior to or while brooding offspring; chicks responded to the brooding call by moving directly to the vocalizing parent. When parents gave the ‘gather call’ (Figure 4.1A), chicks also responded by moving toward the vocalizing parent. The ‘alarm call’ (Figure 4.1B) was given when predators were in the immediate vicinity of or approaching the brood (10–50m). Parents often alarm called within 5–10m of predators. Parents gave the ‘freeze call’ (Figure 4.1D) when predators were directly beside or above chicks. Chicks responded to the freeze call by crouching on the substrate and remaining motionless. In this paper, we provide quantitative descriptions of these adult

vocalizations and two chick vocalizations (chick-contact and chick-alarm calls, Figure 4.1E–F), and test hypotheses about the function of adult vocalizations (based on the anecdotal observations just described) using arena experiments.

Methods

Study site and general field methodology

We studied parent-offspring communication in the Western Sandpiper 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 comprised of sedge and grass (lowland moist low scrub community, Jorgenson & Ely 2001, Johnson & McCaffery 2004). Two to four observers surveyed a 36ha study plot daily from early May through late July for banded birds, nests, and broods (2004–2005). Adults and chicks were individually marked at the nest with a U.S. Fish and Wildlife Service identification band as well as with unique UV-stable color band combinations. The location and behavior of banded birds was recorded daily. Nest locations were mapped and nests were monitored through hatch, predation, or abandonment. After hatch, sandpiper parents and broods were resighted (brood location mapped, parent and chick behaviors recorded) twice daily until they fledged, were depredated, or abandoned.

Acquisition and description of parental vocalizations

During 2004–2005, we recorded parent-offspring vocalizations from 15 sandpiper families using a HHB minidisc recorder (MDP-500) and a Senheiser microphone (ME 62) mounted in a 58.4cm

parabolic dish. We digitized recordings via RAVEN software (Cornell Lab of Ornithology) by sampling at 44.1kHz with 16-bit accuracy. We also used RAVEN software to produce spectrograms that were used to describe parental and chick vocalizations and to create playback signals for experimentation (frame length 512 points, Hann window, time grid resolution 5.8mS with 50% overlap, Fourier transformation size 512 points, 3db filter bandwidth 124Hz).

To describe parental vocalizations, we visually inspected and compared all spectrograms. We then randomly selected 20 sandpiper parents (selection process occurred separately within each sex; 10 male, 10 female) from the 15 family units that were vocally sampled and extracted 10 examples (sub-samples) of both the gather and alarm call for each parent. We used RAVEN software to measure the following call features and calculated means for each parent based on the 10 sub-samples: delta time (difference between begin and end time, s), low frequency (lower frequency bound, Hz), high frequency (upper frequency bound, Hz), delta frequency (difference between low and high frequency, Hz), maximum frequency (frequency at which maximum power occurred, Hz), and maximum power (dB).

The brooding call was difficult to record because of its low amplitude; further, parents appeared to hide themselves and their chicks from observers when brooding. Thus, attempting to record the brooding call caused disturbance of sandpiper families. Similarly, because parents only gave the freeze call when a threat to offspring was eminent, recording the freeze call either required prohibitive amounts of time or required us to approach the brood closely enough to be perceived as an eminent threat. We therefore only recorded the brooding call serendipitously ($n = 2$) and limited acquisition of the freeze call to one of the two parents from 12 broods (number of freeze calls per parent ranged from 1–6).

Arena experiment

To demonstrate parental vocalization function, we exposed 27 sandpiper chicks from 15 broods (1–4 chicks per brood) to parental vocalizations (gather, alarm, and freeze calls) in two field experiments between 19 June–9 July 2004–2005. In 2004, we presented chicks ($n = 13$) with parental call signals produced from their assumed parents. In 2005, we replicated the experiment and presented chicks ($n = 14$) with parental call signals that were produced from apparently non-related adults. We used previously recorded parental vocalizations to produce 141 parental call signals (60 gather call, 60 alarm call, 21 freeze call). Eight to twelve signals were produced for each sandpiper family (two alarm and two gather call signals for each parent, and 0–4 freeze call signals per brood). We created individual signals for each parent by splicing together 2–3 of their previously recorded calls (0.1–0.6s each) and repeating these calls for 30s with 2s of silence between successive calls. Parental call signals were used only once during experiments to avoid pseudoreplication.

Chicks were removed from banded broods one at a time and individually tested in an open-bottom arena constructed of plastic tubing and tarpaulin (1.5m x 1.5m x 0.5m), with a viewing window (60cm²) cut into each of the arenas' walls. Each experimental subject (individual chick) was exposed to four consecutive parental call signals within one of two treatment groups (gather call–alarm call–gather call–freeze call or alarm call–gather call–alarm call–freeze call, example of former treatment group provided in Figure 4.2) then returned to its family unit. Six chicks were only exposed to three parental call signals during experimental trials in 2004 because we were unable to procure a freeze call from their respective parents. Experiments were conducted on calm days, chick age ranged between 7–10d, and total handling time per chick was approximately five minutes.

During playback experiments, the arena was positioned on level upland tundra habitat approximately 200m away from the brood about to be tested. Two speakers were centered just outside the arena facing inward along two opposing walls, and we controlled both speakers from a position near a viewing window in one of the remaining two arena walls (Figure 4.2). Signal amplitude was standardized at $60 \pm 3\text{dB}$ at 4m from the speaker during signal presentation simulating the typical volume of vocalizing parents. When chicks were first placed in the experimental arena, they were kept under a cloth cylinder (12 x 20cm) on top of a square piece of cardboard (361cm^2) at the center of the arena. The cloth cylinder did not keep chicks in total darkness but did prevent any visual bias during signal presentation. Two pieces of metal tubing were lashed perpendicular to each other to form a “+”, and rested atop the area. Metal tubing served as a pulley system to release chicks, via rope, from under the cloth cylinder.

After 15s of silence, while chicks were still under the cloth cylinder, we presented them with a randomly selected signal of either the parental alarm or gather call for 30s from a randomly selected speaker (gather call for example in Figure 4.2, trial 1). After 30s of signal presentation, chicks were kept under the cloth cylinder for an additional 15s of silence before releasing them. After release, we recorded the initial direction of chick movement away from the arena center, and the location where chicks first made contact with an arena wall. During the first 30s after chick release, we also recorded the number of chick vocalizations and time spent on the signal presentation half of the arena (Figure 4.2, hatched area trial 1). We then randomly selected and presented a signal of the call that was not used during trial 1 for 30s from the opposite speaker (alarm call for example in Figure 4.2, trial 2). Throughout trial 2, chicks roamed about the arena and we recorded the number of chick vocalizations and time spent on the signal presentation half of the arena (Figure 4.2, hatched area trial 2). We then initiated a third

signal presentation (trial 3) broadcasting from the same speaker used in trial 2, but presenting a different signal of the call broadcast during trial 1 for 30s (gather call for example in Figure 4.2, trial 3). We recorded the number of chick vocalizations and time spent on the signal presentation half of the arena (Figure 4.2, hatched area trial 3). After trial 3, we presented chicks with a 30s signal of the freeze call from a randomly selected speaker (Figure 4.2, trial 4). We recorded the number of chick vocalizations, number of times chicks crouched motionless on the substrate, and total amount of time chicks spend crouching on the substrate. Chicks were returned to their family units immediately after trial 4. No birds were harmed during this study, and experimentation did not appear to impact chick survival to independence (26/27 experimental subjects successfully fledged).

Acquisition and description of chick vocalizations

We captured some chick vocalizations while recording parental vocalizations; however, chicks predominately foraged during these recording sessions and when chicks were vocalizing, parental calls or other ambient sounds regularly overlapped their vocalizations. Therefore, we made additional recordings of Western Sandpiper chicks during arena experiments by positioning a microphone just outside an arena wall ($n_{2004} = 4$, $n_{2005} = 13$). We digitized recordings of arena trials and produced spectrograms in the same manner previously described. We visually inspected and compared all spectrograms from arena trials to describe chick vocalizations. Through this process, we discovered two apparently distinct chick calls (chick-contact and chick-alarm calls, Figure 4.1E–F). Data from all recorded chicks ($n = 17$) were used to examine the relationship between chick call type (chick-contact, chick-alarm) and parental call signal (gather and alarm calls). Fourteen sandpiper chicks produced at least 10 calls of one type

(chick-contact or chick-alarm) and were included in spectrogram analyses. We extracted 10 examples (sub-samples) of either the chick-contact call or chick-alarm call from these 14 sandpiper chicks to describe chick vocalizations. We used RAVEN software to calculate the same call features that we examined during parental call analyses and calculated means for each chick based on the 10 sub-samples.

Statistical methods

Describing parental and chick vocalizations

We compared means of six call features (delta time, low frequency, high frequency, delta frequency, maximum frequency, and maximum power) of the parental gather and alarm calls using analysis of variance (ANOVA, Zar 1999). After a square root transformation of delta time, high frequency and delta frequency, residuals from all analyses were normally distributed (Shapiro-Wilk tests $p > 0.10$) and had homogeneous variances. We also compared means of call features of the chick-contact and chick-alarm calls using ANOVA. After a square root transformation of delta time and high frequency, residuals from all chick call analyses were normally distributed (Shapiro-Wilk tests, $p > 0.10$) and had homogeneous variances. Pairwise comparisons were obtained using Tukey's adjustment test ($\alpha = 0.05$), and we report means \pm SE of non-transformed data for parental and chick vocalizations.

Initial direction of chick movement and initial contact with an arena wall

We used the Hodges-Ajne test to examine whether initial direction of movement away from the arena center was uniformly distributed for each treatment group because this test does not assume any specific underlying distribution (Hodges et al. 1955, Ajne 1968, Bhattacharyya and

Johnson 1969). We tested whether initial direction of movement away from the arena center varied between the treatment groups (those presented with the alarm call signal first and those presented with the gather call signal first) and within each treatment group between the two experiments (2004–parental signals, 2005–non-parental signals) using Watson’s two-sample U^2 test for nonparametric data with ties (Watson 1962). We performed the Batschelet test for circular uniformity (Batschelet 1981) using a two-tailed binomial test (Zar 1999) to determine whether the initial direction of movement away from the arena center was concentrated near the signal source (for subjects presented with the gather call signal first) or concentrated along a trajectory opposite the signal source (those presented with the alarm call signal first). We used a two-tailed binomial test to determine whether the probability that subjects initially made contact with the arena wall nearest the signal source (for subjects presented with the gather call signal first) or the arena wall opposite the signal source (for subjects presented with the alarm call signal first) was random or not.

Chick responses to the gather and alarm calls throughout each trial

For both experiments (2004–parental signals, 2005–non-parental signals), we presented each subject (chick) with four consecutive trials within one of two treatment groups (gather–alarm–gather–freeze call signals or alarm–gather–alarm–freeze call signals). We compared chick responses (time spent on signal-presentation half of the arena and number of chick vocalizations) to the gather and alarm calls using a split-plot ANOVA with an augmented Latin rectangle design at the split-plot level (Cochran and Cox 1992, Littell et al. 2002). This was a completely randomized design at the individual chick level, with year (parental signals, non-parental signals) as a fixed effect. Each chick was one block of the Latin rectangle with the consecutive

experimental trial being the other block. The design is an augmented Latin rectangle because there were three experimental trials with two treatment groups appearing in an alternating fashion.

Time spent of signal-presentation half of the arena

We performed an analysis using SAS PROC MIXED to determine whether chicks presented with the gather call signal spent significantly more time on the signal presentation half of the arena compared to chicks presented with the alarm call signal. This analysis: compared chicks that initially heard the gather call with chicks that heard the gather call following an alarm call; and compared chicks initially hearing the alarm call and chicks hearing the alarm call after a gather call. We also contrasted time spent on the signal presentation half of the arena between the gather call and alarm call during each trial separately. The overall comparison between the gather and alarm calls was made using Least Square Means.

To determine whether chicks hearing the gather call spent significantly more time on the signal-presentation half of the arena than chance (time on signal-presentation half $> 15s$), and whether chicks hearing the alarm call spent significantly less time on the signal-presentation half of the arena than chance (time spent on signal-presentation half $< 15s$), 15s was subtracted from the observed time chicks spent on the signal-presentation half of the arena. Using this measure (time spent - 15s), we repeated the analysis above. The tests of whether the least square means were zero are then tests that determine whether time spent on the signal-presentation half of the arena varied significantly from chance. The step-down Bonferroni adjustment was used to account for the multiple testing of the means.

Number of chick vocalizations

To determine whether the number of chick vocalizations varied between chicks hearing the gather and alarm call signal, we performed an analysis similar to the analysis of time spent on the presentation half of the arena. The only differences were that responses (number of chick vocalizations) were square root transformed to satisfy assumptions for the analysis. We report the back-transformed means and 95% confidence intervals for the gather and alarm call signal groups.

Variation in chick call type

We asked whether chick call type (chick-contact and chick-alarm calls, Figure 4.1E–F) varied with parental call signal presentation using a twice-nested ANOVA (split-split-plot design). This analysis was similar to those used for the amount of time chicks spent on the signal-presentation half of the arena and the number of chick vocalizations (see above section, Chick responses to the gather and alarm calls throughout each trial) with an additional split level (chick call type) added to the analysis. Differences between means were adjusted using Tukey's adjustment.

Chick responses to the freeze call

We predicted that chicks would crouch on the substrate and remain relatively silent during presentation of the freeze call. After a square root transformation, we contrasted the number of chick vocalizations between the third experimental trial (either gather or alarm call signal presented) and the fourth experimental trial (freeze call signal) for both experiments (2004—parental signals, 2005—non-parental signals) using a paired-sample *t* test (Zar 1999). We report the mean (\pm SD) number of times chicks crouched motionless on the substrate during

presentation of the freeze call and the mean (\pm SD) amount of time chicks spent crouching (out of 30s).

Results

Parental and chick vocalizations

Spectrogram analyses indicated that call features differed among the four parental vocalizations and between the two chick vocalizations (Table 4.1). The parental gather call (Figure 4.1A) is a trill that lacks harmonic content and modulates between 2.1–4.0kHz, whereas the parental alarm call (Figure 4.1B) is a series of notes with several harmonics ranging in frequency from 1.6–18.5kHz (Table 4.1). The alarm call is longer in duration than the gather call, with greater power and a higher frequency at which maximum power occurs (Table 4.1). From limited sampling (8 and 10 calls recorded from two broods, 1 male, 1 female), the brooding call (Figure 4.1C) appears similar in structure to the gather call. The brooding call is a trill of short duration compared to either the gather or alarm calls (0.1 ± 0.01 s) with lower power (92 ± 0.9 dB) and a lower frequency at which maximum power occurs (2.1 ± 0.05 kHz). The freeze call (Figure 4.1D) is a single note containing three harmonics with a frequency range and maximum power similar to the alarm call (delta time = 0.14 ± 0.01 s, low frequency = 1580 ± 62 Hz, high frequency = 18891 ± 144 Hz, delta frequency = 17311 ± 179 Hz, maximum frequency = 3962 ± 39 Hz, maximum power = 122 ± 0.09 dB, $n = 12$ individuals). The chick-contact call (Figure 4.1E) is a trill modulating between 4.3–5.7kHz, whereas the chick-alarm call (Figure 4.1F) is a single note that may completely lack harmonic components or contain one or three harmonics ranging in frequency from 2.3–11.6kHz (Table 4.1). For consistency, we only included chick-alarm calls containing three harmonics in spectrogram analyses (Table 4.1).

Initial direction of chick movement and initial contact with an arena wall

Our data met the minimum sample necessary ($n = 8$) to test for circular uniformity at the 10% significance level for only one call type in either year (2004: $n_{\text{gather call}} = 7$, $n_{\text{alarm call}} = 6$; 2005: $n_{\text{gather call}} = 6$, $n_{\text{alarm call}} = 8$). We therefore used Watson's two-sample U^2 tests to compare chick responses to the gather and alarm call between years. We were unable to reject the null hypotheses that initial chick movement did not vary between years (gather call, $U^2_{7,6} = 0.033$, $p > 0.5$; alarm call, $U^2_{6,8} = 0.066$, $p > 0.5$). We then tested for circular uniformity for both years combined and found, for each parental call, that initial direction of movement away from the arena center was not uniformly distributed (Figure 4.3; gather call, $m_{0.05,13} = 1$, $0.10 > p \geq 0.05$; alarm call, $m_{0.05,14} = 1$, $0.10 > p \geq 0.05$).

We rejected the null hypothesis that initial chick movement between the two treatment groups (gather vs. alarm call) was from the same population or two populations having the same direction (2004, $U^2_{7,6} = 0.318$, $p < 0.01$; 2005, $U^2_{6,8} = 0.345$, $p < 0.005$; Figure 4.3). Chicks presented with the gather call signal concentrated initial movement toward the signal source (2004–2005, $C_{0.05(2),13} = 1$, $0.05 > p \geq 0.02$), whereas initial movement was concentrated along a trajectory opposite the signal source among chicks presented with the alarm call signal (2004–2005, $C_{0.05(2),14} = 1$, $0.02 > p \geq 0.01$). Chicks presented with the gather call signal made initial contact with the arena wall nearest the signal source more often than chance (2004, $C_{0.05(2),7} = 0$, $0.05 > p \geq 0.02$; 2005, $C_{0.05(2),6} = 0$, $0.10 > p \geq 0.05$; Figure 4.4), and chicks presented with the alarm call signal made initial contact with the arena wall opposite the signal source more often than chance (2004, $C_{0.05(2),6} = 0$, $0.10 > p \geq 0.05$; 2005, $C_{0.05(2),8} = 0$, $0.05 > p \geq 0.02$; Figure 4.4).

Time spent on signal-presentation half of the arena

There was a significant effect of parental call signal type (gather call vs. alarm call) on the amount of time chicks spent on the signal presentation half of the arena during the first three experimental trials (Figure 4.5). Chicks hearing the gather call signal spent twice as much time on the presentation half of the arena compared to chicks hearing the alarm call signal ($t_{1,50} = 9.03$, $p < 0.001$; time spent on signal presentation half of arena averaged across all three trials, gather call signal = 20.6 ± 0.4 s, alarm call signal = 10.3 ± 0.5 s). This pattern was the same in both experiments ($t_{24} = -0.27$, $p > 0.79$, 2004–parental signals and 2005–non-parental signals; Figure 4.5) and consistent across all three trials (trial 1, $t_{50} = -6.3$, $p < 0.001$; trial 2, $t_{50} = 5.1$, $p < 0.001$; trial 3, $t_{50} = -4.2$, $p = 0.001$). We found no evidence for presentation sequence effect, as the amount of time chicks spent on the signal presentation half of the arena was similar across all three trials for both treatment groups [all $p > 0.8$; i.e., gather call (trial 1)=gather call (trial 2)=gather call (trial 3), and alarm call (trial 1)=alarm call (trial 2)=alarm call (trial 3)]. Chicks hearing the gather call spent significantly more time on the signal-presentation half of the arena than chance ($t_{76} = 6.9$, $p < 0.001$, time on signal-presentation half > 15 s), and chicks hearing the alarm call spent significantly less time on the signal-presentation half of the arena than chance ($t_{76} = -5.8$, $p < 0.001$, time spent on signal-presentation half < 15 s).

Number of chick vocalizations

There was a significant effect of parental call signal type (gather call vs. alarm call) on the number of chick vocalizations during the first three trials (Figure 4.5). The number of chick vocalizations varied as a function of year (2004–parental signals, 2005–non-parental signals), treatment group (gather–alarm–gather–freeze call signals or alarm–gather–alarm–freeze call

signals) and trial number, and there were significant interactions between year and treatment group and treatment group and trial number (Table 4.2). Chicks hearing the gather call signal vocalized more often than chicks hearing the alarm call signal ($t_{1,49} = -6.37, p < 0.0001$; number of chick vocalizations averaged across all three trials, gather call signal = 22.1 ± 3.0 , alarm call signal = 12.5 ± 2.7). This pattern was significant during the first two trials (trial 1, $t_{49} = -3.8, p = 0.006$; trial 2, $t_{49} = -3.6, p = 0.01$; Figure 4.5); however, by the third trial chicks produced 17–21 vocalizations regardless of signal presentation ($t_{49} = -1.1, p = 0.88$).

We found no evidence for presentation sequence effect for the gather call signal, as the number of chick vocalizations given was similar across all three trials [all $p > 0.2$; i.e., gather call (trial 1) = gather call (trial 2) = gather call (trial 3)]. However, chicks presented with the alarm call signal in trial-3 produced more vocalizations compared to chicks hearing the alarm call in trial-1 ($t_{49} = -5.8, p < 0.001$). The number of vocalizations given in response to the alarm call signal was not significantly different between trials two and three ($t_{49} = -1.0, p = 0.9$), and there also was no difference in the number of vocalizations given in response to the alarm call signal between trials one and two ($t_{49} = -2.5, p = 0.16$; Figure 4.5). The number of vocalizations given varied between years with chicks vocalizing less during 2005 when non-parental signals were presented compared to 2004 when parental signals were presented ($t_{24} = -4.0, p < 0.001$; total number of chick vocalizations averaged across all three trials, 2004 = 24.2 ± 14.7 , 2005 = 10.5 ± 7.1).

Variation in chick call type

There was a significant effect of parental call signal (gather call vs. alarm call) on the number of each type of chick vocalization (chick-contact, chick-alarm) given during the first three

experimental trials ($t_{31} = -3.03, p = 0.005$; Figure 4.6). The number of each type of chick vocalization varied as a function of year (2004–parental signals, 2005–non-parental signals) and treatment group (gather–alarm–gather–freeze call signals or alarm–gather–alarm–freeze call signals), and there were significant interactions between call type and year and call type and trial number (Table 4.2). The chick-alarm call was given more often during 2004 when parental signals were presented compared to 2005 when non-parental signals were presented ($t_{47} = 4.93, p < 0.001$; mean number of calls per chick, 2004 = 39.8 ± 7.6 , 2005 = 14.5 ± 3.5); however, there was no difference in the number of chick-contact calls given between years ($t_{1,47} = -0.45, p = 0.97$). The chick-alarm call was given more often during the second and third trials compared the chick-contact call (trial-2, $t_{1,47} = 5.9, p < 0.001$, chick-alarm = 13.3 ± 3.0 , chick-contact = 1.8 ± 0.8 ; trial-3, $t_{1,47} = 6.6, p < 0.001$, chick-alarm = 14.2 ± 3.1 , chick-contact = 1.5 ± 0.7). There was no significant difference in the number of each call type given during the first trial ($t_{1,47} = -0.82, p = 0.97$), but the chick-contact call was given more often during the first trial compared to the second or third trials (trial-1 vs. trial-2, $t_{1,47} = 3.1, p = 0.046$; trial-1 vs. trial-3, $t_{1,47} = 3.28, p = 0.022$; mean number of chick-contact calls per chick, trial-1 = 7.4 ± 1.9). During the first trial, the chick-contact call was predominately given after presentation of the gather call signal (number calls post gather call signal = 11.5 ± 2.6 , number of calls post alarm call signal = 3.5 ± 2.4 , Figure 4.6).

Chick responses to the freeze call

Chicks always responded to the freeze call by squatting motionless on the substrate (mean \pm SD number of time chicks squatted in the substrate = $2.1 \pm 1.1, n = 21$). The amount of time chicks spent motionless on the substrate during presentation of the freeze call varied (mean \pm SD

amount of time spent motionless out of 30s = 14.0 ± 8.1 , range 2–30s), yet 71% of chicks were motionless for more than a third of the time when presented with the freeze call. In contrast, chicks never squatted motionless on the substrate when presented with a gather or alarm call signal. Compared to the preceding trial, chicks vocalized less often when presented with the freeze call (2004, $p < 0.001$; 2005, $p < 0.001$; mean \pm SD number of vocalizations during freeze call trial and preceding trial respectively, 4.8 ± 4.2 , 18.2 ± 12.9).

Discussion

We quantitatively described parental and chick vocalizations given by Western Sandpipers during brood rearing. We experimentally tested hypothesized parental call functions and found chick behavioral responses consistent with proposed call functions. Results indicate that Western Sandpiper parents are able to elicit anti-predatory chick behaviors, direct chick movement and vocalizations through vocal signals. Parental care, in the form of brooding, during the first days post-hatch is vital to chick survival. Continued care through the attainment of flight likely increases the probability of offspring survival, and parental vocalizations appear to play a key role during extended brood attendance. Previous study on parent-offspring communication among shorebirds is limited. Shorebird parents commonly give alarm calls when predators approach their brood (Miller 1984, 1985 1996; Walters 1982, 1990), and lapwing (*Vanellus* spp.) vocal responses to predators vary with predator class (mammal, bird, reptile) and location (terrestrial or aerial, Walters 1990). Eurasian Oystercatcher parents appear to use varying calls to indicate their distance from offspring (Norton-Griffiths 1969), and Dunlin (*C. alpina*) parental calls may exhibit sufficient variation for individual recognition (Baker 1982).

Western Sandpiper broods regularly travel several hundred meters a day and are more often associated with upland-tundra habitat containing a graminoid component than chance (dwarf shrub-graminoid tundra; Johnson and McCaffery 2004, Ruthrauff and McCaffery 2005). Although several environmental factors likely influence brood movement and habitat use (prey availability, thermoregulatory environment, predator distribution, vegetative cover), the relative importance of each factor is unclear, and factors explaining brood behavior are not mutually exclusive (Johnson and McCaffery 2004). Regardless of the proximate causes underlying brood movement and habitat use, our study has revealed that Western Sandpiper parents are able to direct chick movement and habitat use through vocal signals.

Gather and alarm calls

Our results indicate that the function of the gather call is to elicit chicks to move toward the vocalizing parent, and the alarm call functions to direct chick movement away from the vocalizing parent. The gather and alarm calls elicited consistent directional chick movement during arena experiments. Initial movement and initial contact with an arena wall were along the same trajectory for both the gather and alarm calls (Figures 3-4). Chicks hearing the gather call initially moved toward the signal source and initially made contact with the arena wall nearest the signal source. Concomitantly, chicks hearing the alarm call initially moved away from the signal source and initially made contact with the arena wall opposite the signal source.

Directional movement may function to move chicks toward an area rich in resources (e.g., high food availability or vegetative cover) or away from exposed sites or predators. For example, if a parent positioned itself in a specific location, such as a patch of dwarf shrub-graminoid tundra, and gave the gather call, chick movement would be directed toward that habitat patch. Similarly,

if a parent positioned itself near a predator and gave the alarm call, chick movement would be directed away from the predator.

Similar to their opposing effects on chick movement, the gather and alarm calls elicited contrary effects on chick vocal behavior. Chicks hearing the gather call were consistently more vocal compared to chicks hearing the alarm call (Figure 4.5). A dual response by chicks to the gather call, directional movement and increased vocalizations, is advantageous if chick vocalizations assist parents in locating individual offspring and facilitate gathering the brood. The alarm call appears to function not only to elicit directional movement of chicks away from the signal source but also to reduce the number of chick vocalizations, potentially offering auditory concealment from predators while retreating from the area. Chicks are probably not the only intended receiver of the alarm call. Parents increase their ability to attract a predator's attention by calling while moving toward it, and parents typically attempt to lead predators away from the brood while giving the alarm call in conjunction with a variety of injury-feigning and distraction displays (Brown 1962, Holmes 1973).

Freeze call

One function of the freeze call is to elicit hiding or concealment behavior in chicks. Chicks always squatted motionless on the substrate when presented with the freeze call in arena experiments, and chicks also vocalized relatively less often during presentation of the freeze call signal compared to the gather or alarm call signals.

Parental use of the alarm and freeze calls

Behavioral studies indicate that Western Sandpiper parents exercise context specific vocal responses to predators (personal observation), and chick responses to parental calls in both natural settings and arena experiments support this observation. Parents typically gave the freeze call when predators were on the ground within 10m of a chick or when aerial predators flew within 200m of the brood. When predators were observed on the ground greater than 10m from a brood, parents typically flew toward the predator and gave the alarm call. Parents appeared to give the alarm call when chicks could avoid predator detection by remaining relatively quiet and moving away from the predator. As previously mentioned, parental distraction displays and predator leading behaviors given in conjunction with the alarm call may increase the probability that offspring are able to move away from a predator's location and avoid detection. In contrast, when the best method of avoiding predators was to hide and remain silent, parents typically gave the freeze call before squatting motionless on the tundra themselves.

Selective use of the most efficient call to reduce predatory threats to offspring may be triggered by visual and/or auditory stimuli and governed by a few simple rules. Such as: when an aerial predator is detected within 200m of the brood give the freeze call, when any predator is detected within 10m of the brood give the freeze call, when any predator is detected on the ground 10–50m from the brood give the alarm call near the predator. Relatively simple stimulus-response behavioral patterns such as these would enable Western Sandpiper parents to reduce context specific predation threats to offspring by directing their chicks to take immediate evasive action (freeze call) or a more gradual escape (alarm call) when either is most advantageous.

Parental vs. non-parental signals

Total number of calls given by chicks varied between the two arena experiments with chicks vocalizing less during 2005 when non-parental signals were used. The reduction in chick vocal responses to non-parental call signals may indicate a weaker response to unfamiliar individuals. However, chicks did exhibit consistent directional movement and space use during both experiments, and although fewer vocalizations were given in response to non-parental signals, the relative number of chick calls given to each type of parental call signal was consistent across years. Young of many avian species can distinguish parental calls from calls of other individuals (Tschanz 1968, Beer 1969, 1970a,b, Evans 1970a,b, Impekoven and Gold 1973), and our results suggest this possibility for Western Sandpipers. Variation in subject handling time between years also may have influenced the number of chick vocalizations. Great effort was taken to standardize our protocols, but we undoubtedly became more efficient at handling subjects over the course of the study, which could have resulted in reduced stress and fewer vocalizations in the second year of the study. The number of individuals per brood used in arena experiments varied from one to four, and thus total disturbance to the brood and each subject varied. As a result of variability in total disturbance and our small sample size, we were unable to quantitatively examine the effects of handling time on total number of chick vocalizations.

Chick vocalizations

The type of call given by chicks (chick-contact or chick-alarm, Figure 4.1E–F) during arena experiments was contingent upon whether a parental call signal was being broadcast at the time and which parental call signal (gather or alarm call) was previously broadcast. The chick-contact call was predominately given during the first experimental trial after subjects were presented

with a gather call signal (Figure 4.6). No parental call signals were being broadcast during this time period. In contrast, chicks rarely gave the chick-contact call during the initial trial after being presented with an alarm call signal. During the second and third experimental trials when parental call signals were being broadcast, the chick-alarm call was commonly given and the chick-contact call was rarely given regardless of parental signal type. Although we named parental calls based on hypothesized functions that were subsequently demonstrated, we named chick calls based on the context when each call was given and do not imply function.

We noted the chick-contact call only during arena experiments. The chick-alarm call also was observed in the field, specifically when non-parental adults chased chicks from their nest site or brood location or when observers inadvertently separated a brood while walking the study-plot. Parents responded to the chick-alarm call by approaching the vocalizing chick. The chick-alarm call may represent a graded signal than takes the form of a single note lacking a harmonic component or a note with one or more harmonics (Figure 4.1F). We hypothesize the addition of harmonics to the chick-alarm call indicates increased disturbance to the chick. This hypothesis is based on anecdotal observation: chicks commonly gave a single note version of the chick-alarm call when a brood was mildly disturbed, such as when an observer stood relatively close to a brood. However, when an observer chased an individual chick to capture it, chick-alarm calls were produced with one or more harmonics.

Physical structure of vocalizations

The physical structure of a vocal signal affects a receivers' ability to locate its source whether the receiver is intended or not. Typically calls used to attract or locate other individuals are

composed of short notes with a broad frequency range, as broader frequency range within notes provides greater information concerning both direction and distance (Marler 1955).

Mobbing calls are typically of short duration with a broad frequency band that is easy to locate and attracts other birds to the site. The structure of the chick-alarm call (Figure 4.1F), when containing harmonics, is similar to mobbing calls of other species and likely functions to draw the attention of a tending parent, and field observations support this hypothesis. We broadcast chick-alarm calls to parents actively tending broods during preliminary experimentation, and found that nearly every adult in the area responded by mobbing the speaker. In fact, when broods were difficult to locate, we sometimes used this method to draw a tending parent toward the speaker thereby revealing its location.

Physical structure also determines the distance a sound will travel and how much distortion it will sustain before reaching the receiver. Interference, absorption, and scattering of sound waves by vegetation, the ground, and air progressively distort a sound, with low frequency sounds traveling further than high frequency sounds (Chappuis 1971, Morton 1975, Wiley and Richards 1982). The lower frequency bound of the chick-alarm call is nearly half that of the chick-contact call which would facilitate its use to attract parents from considerable distances. Sounds that are rich in temporal structure with complex frequency modulations are advantageous in open habitats because simple sustained notes tend to be distorted by temperature gradients and air turbulence (Chappuis 1971, Morton 1975). The chick-contact call (Figure 4.1E) does have considerable temporal structure and complex frequency modulation compared to the chick-alarm call, but does not have the frequency range nor as extreme a lower frequency bound as the chick-alarm call. We hypothesize the chick-contact serves in short-distance communication between parent and offspring. The chick-contact call may represent a compromise between providing too

much information about an individuals' location that may be intercepted by unintended receivers (predators) but enough information for a parent to effectively locate its source over relatively short distances.

The physical structures of adult vocalizations also support their hypothesized functions. The parental alarm call (Figure 4.1B) is a series of short notes with a broad frequency range that is typical of calls used to attract or locate individuals (Marler 1955). Such qualities are in accord with call function if parents give the alarm call to attract/distract predators from the brood and elicit directional movement of chicks away from the parents' location. The parental gather call (Figure 4.1A) may represent a structural compromise similar to that described for the chick-contact call. If parents give the gather call to draw chicks toward their location, temporal structure and complex frequency modulation within the gather call would serve this purpose over relatively short distances without broadcasting the parent and brood location to unintended receivers at greater distances.

Conclusions

Using observational and experimental methods in the field, we described and demonstrated the form and function of parent-chick communication in the Western Sandpiper. We documented four distinct calls produced by parents that are directed toward their chicks and potentially other receivers (brooding call, gather call, alarm call, freeze call). We discussed how these calls may be used by parents to elicit anti-predatory chick behaviors, and direct chick movement and vocalizations, and described two distinct chick vocalizations (chick-contact and chick-alarm calls). Future study of Western Sandpiper parent-offspring communication should determine whether chicks exhibit parental recognition through vocalizations and the role of chick

vocalizations in parental behavior. The inexpensive field assay technique we developed will likely serve equally well for study of parent-offspring communication in other precocial and semi-precocial species, being less intrusive and potentially more realistic than typical laboratory study.

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Table 4.1. Adult and chick call features (\pm SE) calculated from 20 adult Western Sandpipers (10 males and 10 females) and 14 chicks (10 sub-samples per adult/chick).

	Δ time	Low frequency	High frequency	Δ frequency	Max frequency	Max power
Adult calls						
Gather	0.446 \pm 0.03 A	2151 \pm 55 A	3922 \pm 111 A	1771 \pm 78 A	3166 \pm 89 A	99 \pm 1.0 A
Alarm	0.624 \pm 0.05 B	1643 \pm 70 B	18542 \pm 396 B	16899 \pm 427 B	3479 \pm 133 B	120 \pm 1.2 B
Chick calls						
Chick-contact	0.444 \pm 0.04 a	4289 \pm 77 a	5700 \pm 128 a	1411 \pm 70 a	5237 \pm 134 a	99 \pm 2.1 a
Chick-alarm	0.141 \pm 0.01 b	2314 \pm 78 b	11579 \pm 255 b	9266 \pm 236 b	5270 \pm 82 b	105 \pm 1.6 a

Δ time (difference between begin and end time, s), low frequency (lower frequency bound, Hz), high frequency (upper frequency bound, Hz), delta frequency (difference between low and high frequency, Hz), maximum frequency (frequency at which maximum power occurred, Hz), and maximum power (dB). Chick-alarm call means were computed only from calls with a harmonic component. Adult (upper-case) and chick (lower-case) means in columns with the same letter are not significantly different (Tukey's test, $\alpha=0.05$).

Table 4.2. Mixed-model repeated measures ANOVA results for chick responses to parental vocalizations during arena experiments.

Model	Effect	Num. DF	Den. DF	F	P
Number of chick calls					
	Year	1	24	16.2	<0.001
	Treatment	1	49	40.6	<0.001
	Trial	2	49	18.2	<0.001
	Year*Treatment	1	49	5.4	0.024
	Treatment*Trial	2	49	5.0	0.011
Time on signal side of arena					
	Year	1	24	0.1	0.792
	Treatment	1	50	81.5	<0.001
	Trial	2	50	0.1	0.945
	Treatment*Trial	2	50	1.1	0.356
Chick call type					
	Year	1	15	10.0	0.006
	Treatment	1	31	9.2	0.005
	Trial	2	31	0.5	0.605
	Call type	1	47	37.1	<0.001
	Year*Call type	1	47	14.5	<0.001
	Trial*Call type	2	47	19.0	<0.001

Model for time on signal side of arena is the same as model for time on signal side of arena differing significantly from chance. The responses were merely coded as time-15s in the latter. Effects: Year = parental signals (2004) or non-parental signals (2005), Treatment = alarm-gather-alarm-freeze call treatment group or gather-alarm-gather-freeze call treatment group, Trial = experimental trial number (1-3).

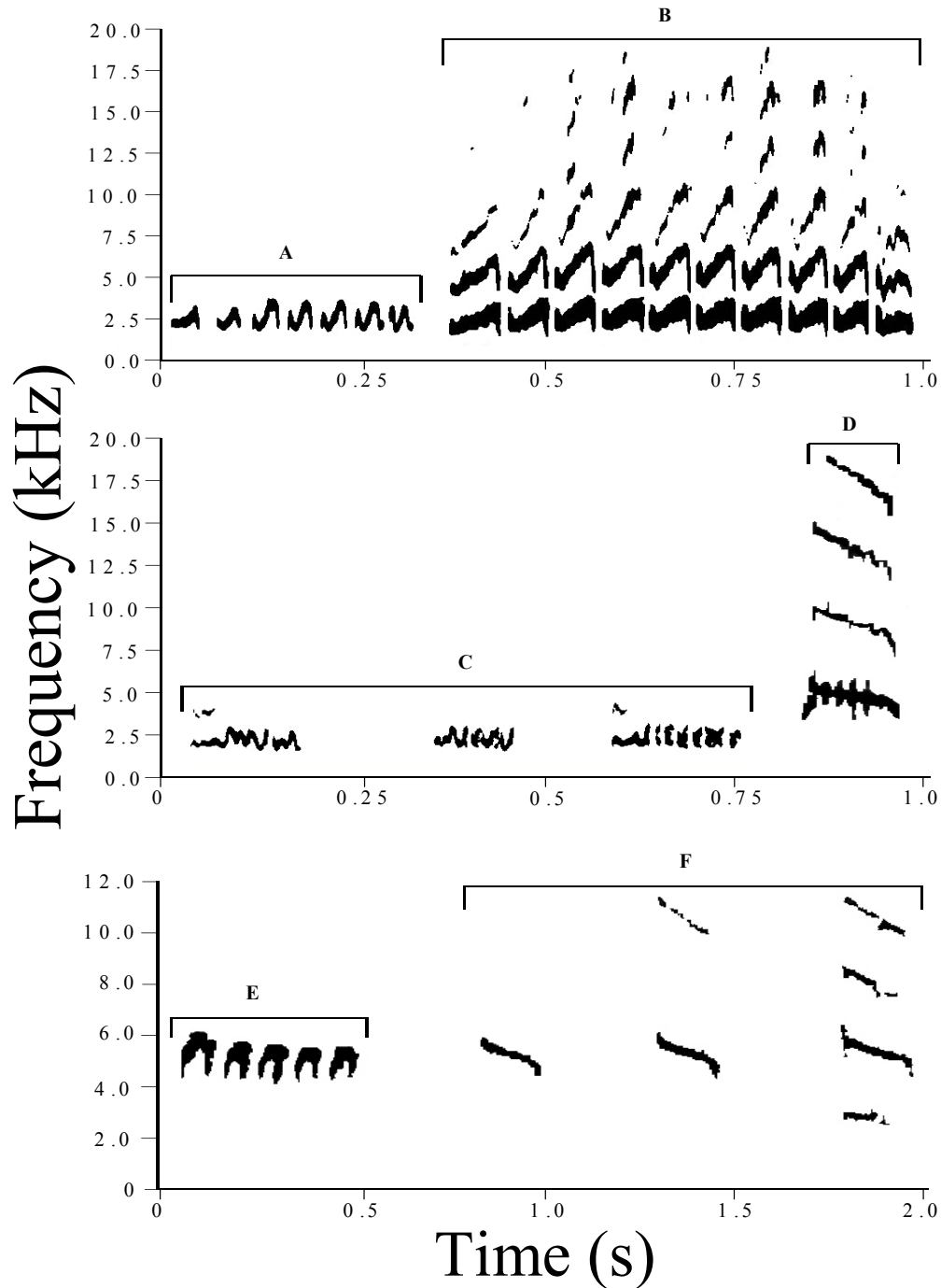


Figure 4.1. Spectrograms of Western Sandpiper parental and chick vocalizations from the Yukon Delta National Wildlife Refuge’s Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (61°22’ N, 165°07’ W). Parental calls: A-gather, B-alarm, C-brooding (three examples), D-freeze; Chick calls: E-chick-contact, F-chick-alarm (three examples).

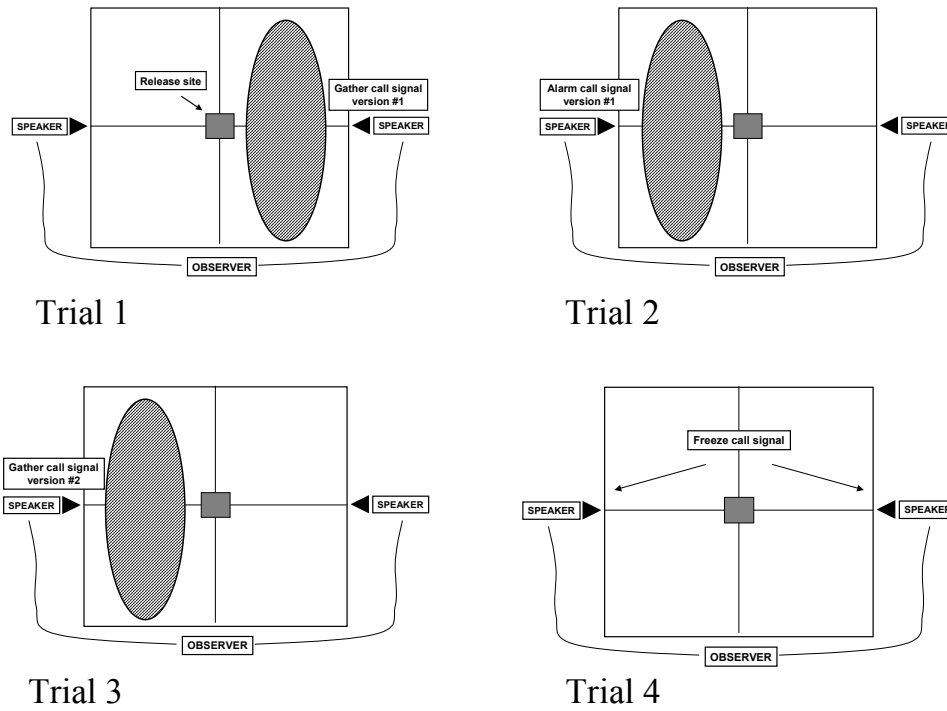


Figure 4.2. Example of arena (1.5m x 1.5m x 0.5m) experiment setup used to test parental vocalization function on Western Sandpiper chicks. Gray ovals represent signal presentation half of the arena for this example.

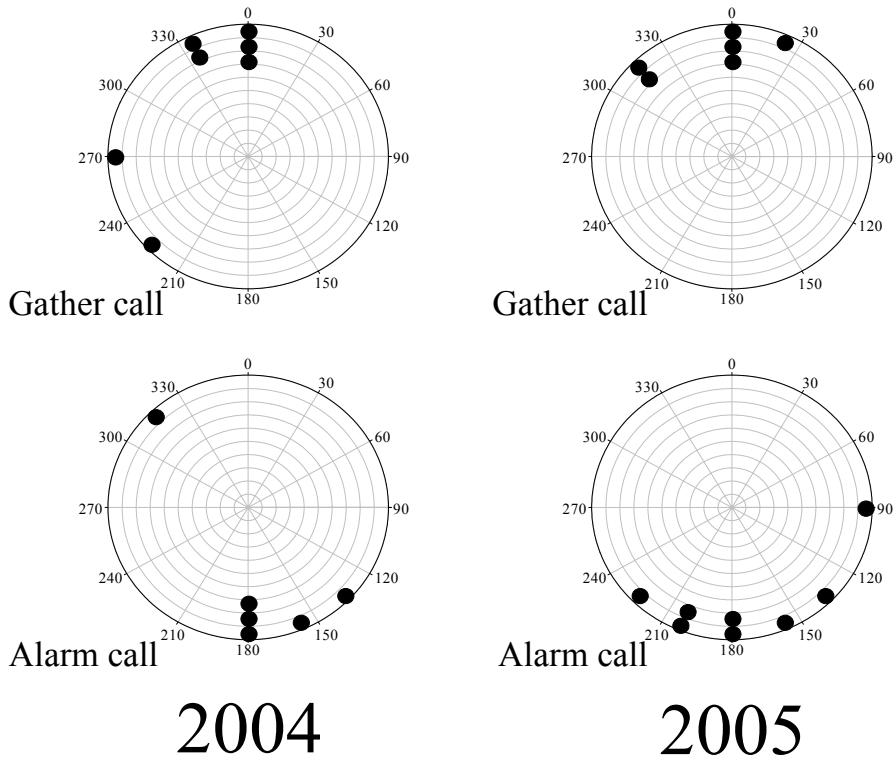


Figure 4.3. Initial direction of Western Sandpiper chick movement, away from the arena center, after hearing a signal of either the parental gather or alarm call (2004–parental signals, 2005–non-parental signals). For simplicity, figure depicts all signals being presented from the same direction (0°), when signal source was randomly varied while individually testing subjects.

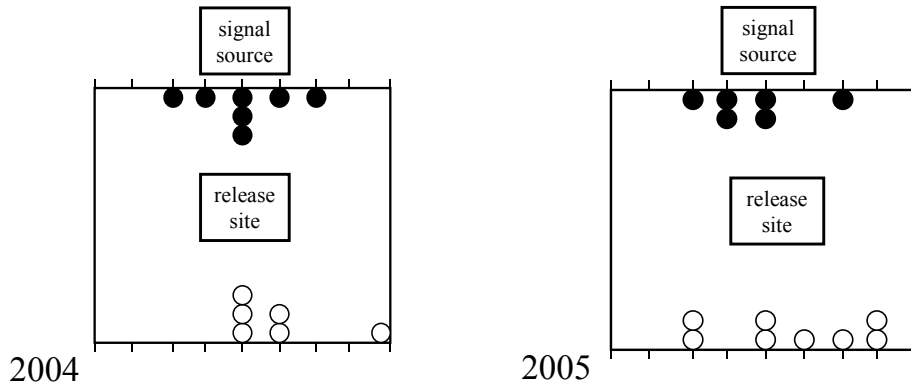


Figure 4.4. Location where Western Sandpiper chicks first made contact with an arena wall after hearing a signal of either the parental gather or alarm call (2004–parental signals, 2005–non-parental signals, filled circles = chicks initially presented with the gather call signal, open circles = chicks initially presented with the alarm call signal). For simplicity, figure depicts all signals being presented from the same direction. However, signal source was randomly varied while individually testing subjects.

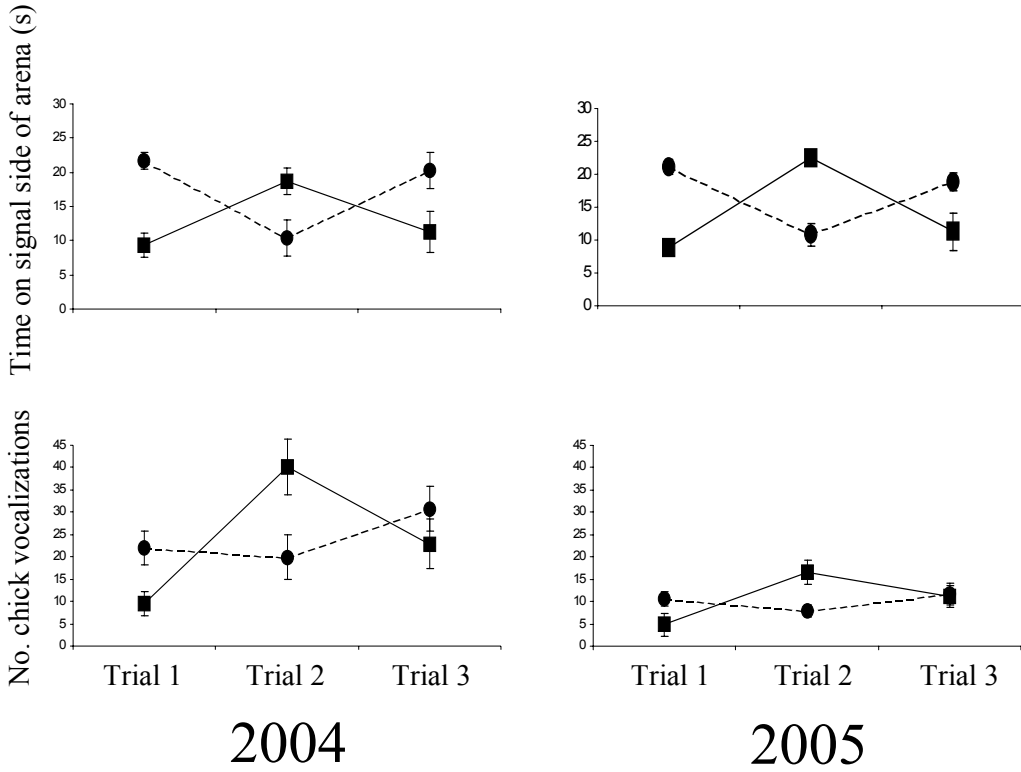


Figure 4.5. Mean responses (time spent on signal side of arena and number of Western Sandpiper chick vocalizations during each 30s trial) of chicks to parental call signals broadcast during three consecutive arena trials in two treatment groups (trials 1–3 signal sequence: circles connected by dashed line = gather–alarm–gather call signals, squares connected by solid line = alarm–gather–alarm call signals; 2004–parental signals, $n = 13$; 2005–non-parental signals $n = 14$).

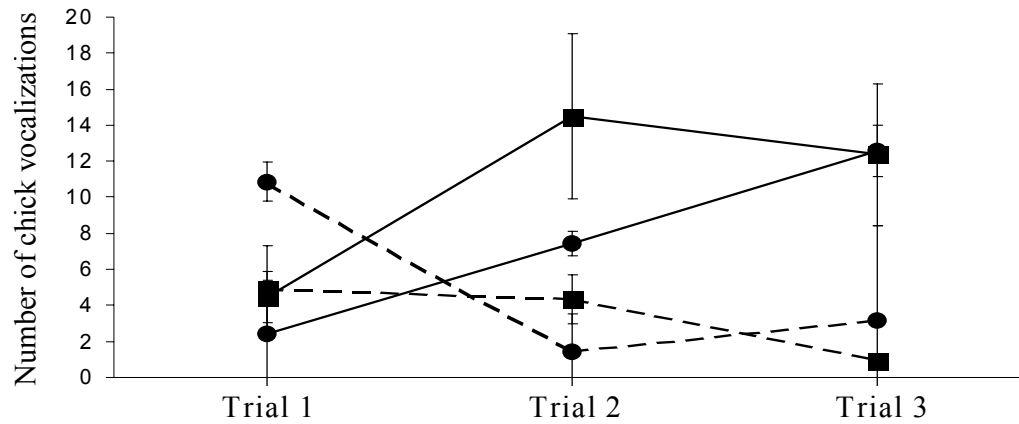


Figure 4.6. Mean (\pm SE) number of Western Sandpiper chick calls (solid lines = chick-alarm call, dashed lines = chick-contact call) given by chicks exposed to two treatment groups (trials 1–3 signal sequence: circles = gather–alarm–gather call signals, $n = 13$; squares = alarm–gather–alarm call signals, $n = 14$). Chick responses for trial 1 were recorded during 30s of silence following 30s of signal presentation. Chick responses for trials 2–3 were recorded during 30s of signal presentation.