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BEHAVIORAL RESPONSES TO HIGHER PREDATION RISK IN A SUBARCTIC POPULATION OF THE SEMIPALMATED PLOVER

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Abstract. We studied dispersal, mate retention, apparent survival, and renesting in a subarctic breeding population of the Semipalmated Plover (*Charadrius semipalmatus*) near the southern limits of its breeding range on Akimiski Island, Nunavut, Canada, from 2002 to 2007. The risk of predation at this site is higher than in more northern parts of this species' range. Dispersal of breeding birds was biased toward females, as found also at Churchill, Manitoba, a more northerly location. Mate retention was low both within (33.3%) and between (6.5%) seasons and much lower than previous estimates from Churchill. Return and encounter rates of adult males were higher than those of females, but apparent survival of adult males and females did not differ and was lower than that reported for Churchill. Within a season, renesting after a failed nest attempt was common (53%) with some pairs nesting three times in a season. Differences between the two study areas in rates of renesting may help to account for persistence of the southern population. Differences in weather at the two latitudes affect the duration of the breeding season and appear to have significant consequences for the strength of social monogamy but not for general patterns of dispersal.

Key words: dispersal, mate fidelity, Semipalmated Plover, shorebird, apparent survival, Akimiski Island, Nunavut, subarctic, Charadrius semipalmatus.

Respuestas Comportamentales a Riesgos de Depredación Mayor en una Población Subártica de *Charadrius semipalmatus*

Resumen. Estudiamos la dispersión, la retención de parejas, la supervivencia aparente y la anidación repetida en una población subártica reproductiva de *Charadrius semipalmatus*, cerca del limite sur de su distribución reproductiva en la isla Akimiski, Nunavut, Canadá, desde 2002 a 2007. El riesgo de depredación es más alto en esta localidad que en las porciones más al norte del rango de distribución de esta especie. La dispersión de aves reproductivas tuvo un sesgo hacia las hembras, como también se encontró en Churchill, Manitoba, una localidad que se encuentra más al norte. La retención de pareja fue baja tanto dentro de una estación (33.3%) como entre estaciones (6.5%) y fue mucho menor que las estimaciones previas para la localidad de Churchill. El retorno y las tasas de avistamiento repetido de machos adultos fueron más altas para los machos que para las hembras, pero la supervivencia aparente de los machos y de las hembras adultas no fue diferente y fue más baja que la reportada para los individuos de Churchill. Dentro de una estación, la anidación repetida después de un intento frustrado de anidación fue común (53%), siendo que algunas parejas anidaron hasta tres veces en una estación. Las diferencias de las tasas de anidación repetida entre los dos sitios de estudio pueden ayudar a dar cuenta de la persistencia de la población sureña. Las diferencias del clima a esas dos latitudes afectan la duración de la época reproductiva y parecen tener consecuencias significativas para la intensidad de la monogamia social, pero no para los patrones generales de dispersión.

INTRODUCTION

Species with geographically broad breeding ranges face a wide variety of physical and biological conditions. The persistence of local populations at the extremes of these gradients implies trade-offs that allow fitness in each region to be equivalent or nearly so. Recent evidence for lower predation risk at high latitudes (a 3.4% decrease with each degree of increasing latitude from James Bay to Ellesmere Island, Nunavut; McKinnon et al. 2010) offers a compelling explanation for why birds can breed so far north despite higher costs of migration, shorter breeding seasons, and years of little or no reproduction (Mayfield 1978, Boyd and Piersma 2001). Simultaneously, it raises the question of why individuals of arctic breeding species continue to breed at the southern extreme of the range in the face of such high predation risk. We examined a southern (subarctic) breeding

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population of the Semipalmated Plover (*Charadrius semipalmatus*) to test the hypothesis that equivalent fitness might be achieved through behavioral strategies (e.g., dispersal, mate retention, and renesting).

In birds, dispersal can have important implications for survival and breeding success. In shorebirds migrating long distances, dispersal of breeders is usually low (Jackson 1994, Handel and Gill 2000). The mating system affects patterns of dispersal (Greenwood 1980). In socially monogamous species, dispersal of breeders is strongly related to mate retention, as pairs that are tenacious to one another are often also tenacious to the same breeding territories (Flynn et al. 1999). In many species, males establish and defend the breeding territories so if divorce does occur it is the female that disperses farther, resulting in female-biased breeding dispersal (Greenwood 1980, Clarke et al. 1997). There is also variation within species in the degree to which this generalization holds (Clarke et al. 1997).

Breeding dispersal can be related to previous experience. When an individual breeds successfully with a mate or at a location in one season, it may be adaptive to return to that site in subsequent seasons, a logic that applies to males and females equally. In most shorebirds studied, individuals of at least one sex are less likely to disperse from a previous breeding site where they were successful than from a site where nests were depredated or destroyed (e.g., Spotted Sandpiper, *Actitis macularius*, Reed and Oring 1993; Black-necked Stilt, *Himantopus mexicanus*, James 1995; American Avocet, *Recurvirostra americana*, Robinson and Oring 1997; Piping Plover, *Charadrius melodus*, Weins and Cuthbert 1988; Western Snowy Plover, *C. alexandrinus nivosus*, Colwell et al. 2007; Kentish Plover, *C. a. alexandrinus*, Sandercock et al. 2005; Black Turnstone, *Arenaria melancephala*, Handel and Gill 2000).

Mate retention can also be an adaptive behavior, enhancing breeding success through the benefit of previous experience with a mate (Schieck and Hannon 1989). However, new pairings do not necessarily result in reproductive success lower than that of older pairings (Ens et al. 1996, Flynn et al. 1999, Handel and Gill 2000, Sandercock et al. 2000, Pyle et al. 2001, Johnson and Walters 2008), and nest failure does not necessarily promote divorce (Dhondt et al. 1996, Robinson and Oring 1997, Sandercock et al. 2000).

Patterns of dispersal and mate retention can be influenced by both intrinsic and extrinsic pressures (Weins and Cuthbert 1988, Reed and Oring 1993, Handel and Gill 2000, Johnson and Walters 2008). Long-lived birds are presumed to accrue greater reproductive advantage through mate retention because of the opportunity to gain familiarity and hence cooperation with a previous mate (Rees et al. 1996). For short-lived birds, by necessity, mate retention is lower simply because previous mates are not available. Within a species, apparent survival rates of populations may differ, also affecting local rates of mate retention (Newton and Wylie 1996).

Within the geographic distribution of a single species, extrinsic pressures such as predation risk (McKinnon et al. 2010) and weather severity (Summers and Nicholl 2004) can vary, and these factors may help to explain patterns of mate retention and breeding dispersal (Sanz 2001). Under high nest-predation pressure, birds may disperse farther after nest failure, seeking refuge from predation, a dispersal that can lead to a change of mates (Redmond and Jenni 1982). Alternatively, if weather limits the length of the breeding season, individuals may find it advantageous to retain the same mate and site to save time searching for a new mate (Rowley 1983, Johnston and Ryder 1987, Ens et al. 1996, Flynn et al. 1999, Handel and Gill 2000). The length of the breeding season might also determine the opportunity to renest, to move to another nest site, or to change mates after nest failure (Lank et al. 1985, Johnson et al. 2008, Naves et al. 2008).

The Semipalmated Plover is a small, short-lived, socially monogamous shorebird (Zharikov and Nol 2000) with biparental care (Sullivan Blanken and Nol 1998). This species has been well studied at Churchill, Manitoba, in a subarctic region with harsh winters and short summers. At that location breeding dispersal is female-biased and mate retention both within and between breeding seasons is the rule. A minority of birds divorce in following seasons, and there is no record of divorce within a breeding season for the relatively rare attempts at renesting (Flynn et al. 1999). We studied a second population of this species, breeding at the southern edge of its range over 500 km south of Churchill, on Akimiski Island, Nunavut, in James Bay (Nguyen et al. 2003). On Akimiski Island, nest loss due to predation is very high, ranging from 44% failure in 2002 to 63% failure in 2004 (Nguyen et al. 2006). By contrast, the rate of nest failure at Churchill is lower (30–40% annually; Nol et al. 1997, Nol and Blanken 1999) with little annual variability (E. Nol, unpubl. data). We predicted that dispersal should be greater at Akimiski than at Churchill because of this higher rate of nest predation and that mate retention should be lower as a consequence of greater dispersal, as birds attempted to move away from predation risk. Given higher rates of nest predation, we also compare adults' return rates and calculate apparent survival, predicting both lower return rates and apparent survival of adults at Akimiski, which might, in turn influence rates of mate retention. Finally, we predicted rates of renesting to be greater at the southern location because of increased and generally earlier nest losses relative to the length of the breeding season (Lank et al. 1985).

METHODS

STUDY AREA

We studied Semipalmated Plovers on the northeast shore of Akimiski Island (53° 06′ N, 80° 57′ W), Nunavut, Canada, from 2002 to 2007. Located in western James Bay, Akimiski Island covers ~3800 km^2 (Leafloor et al. 2000). Our focal study area was a narrow strip along the contours of the coast, approximately 10 km^2 (10 km × 1 km) of depositional ridges of sand or gravel surrounded by intertidal and supratidal salt marshes and mudflats (Nguyen et al. 2003). The dominant vegetation on Akimiski Island's shoreline changes gradually from creeping alkali grass (*Puccinellia phryganodes*) in the intertidal zone to red fescue (*Festuca rubra*), Baltic rushes (*Juncus* spp.), and willows (*Salix* spp.) in the supratidal zone (Leafloor et al. 2000). Within the study area, Semipalmated Plovers nested in a variety of microhabitats including sand/gravel ridges, transitional gravel/mudflat, *Puccinellia*-dominated mudflat, and mudflats without vegetation (Nguyen et al. 2003).

NEST SEARCHING AND MONITORING

We searched for and located breeding pairs throughout each breeding season (May–July) by walking through suitable habitat and observing males' aerial displays over a territory. We located nest cups by searching occupied territories carefully or watching from a distance as one parent returned to the nest. Nests were checked every 3 to 5 days. We categorized nests as successful if one or more eggs hatched, confirmed by observing one or more nestlings in or near the nest or by finding eggshell fragments in the nest cup (Mabee 1997) and agitated adults in the area. We categorized a nest failure as due to predation if eggs disappeared before day 24 of the incubation period (Nol and Blanken 1999) and there were no agitated parents with chicks present, or if there was obvious evidence of predation near the nest (i.e., broken and stained eggshells, predator feces, or tracks; Mabee 1997). We considered a nest abandoned if it was unattended by parents and eggs were cold on two or more subsequent visits. The 151 nests included in our study were those of banded individuals that were recorded nesting twice or more during the study period, 2002–2007.

We used walk-in nest traps with a keyhole design to capture adult plovers at their nests. We determined the sex of adults by observing differences in plumage (Teather and Nol 1997). Occasionally, we confirmed an individual's sex by comparing its plumage with its mate's or by behavior (i.e., copulation). If we were uncertain of an individual's sex, we omitted the bird from any sex-grouped analyses. We gave each adult a unique combination of three Darvic color bands and a numbered Canadian Wildlife Service aluminum band.

We categorized mating patterns within or between years (W/B) as (1) *reunited* if the pair reunited for subsequent nest attempts, (2) *divorce* if both banded members of a pair were seen alive but mated with other individuals for subsequent nest attempts, or (3) *re-paired* if only one member of a pair was found on a subsequent nest attempt and it was paired with a new individual. As nest searching took place throughout the breeding season, we made a consistent effort to search for re-paired or divorced birds breeding outside their previous territory but within the study area.

We calculated between-year dispersal distances as the distance between a banded individual's last nest of one year and its first nest of the subsequent year (Flynn et al. 1999). We calculated within-year dispersal distances as the distance an individual moved from a failed nest to a replacement nest in the same season, on the basis of timing assumed to be the next attempt. Distance data were $\log_{10}$-transformed for analysis to attain both normality and homogeneity of variances.

STATISTICAL ANALYSES

We first determined whether there was a significant added variance component due to an individual's characteristic dispersal patterns, using a mixed-model ANOVA with individual as a random factor and sex as a fixed factor. This analysis was based on multiple measurements from 23 individuals (total 72 distance measurements). Differences among individuals did contribute substantially to the variance (41.1% of variation). Therefore, we included the individual's identity as a random factor in all analyses. We tested for the effect of year dispersed and year settled on dispersal distance between seasons. We compared within- and between-year (W/B) dispersal distances by sex and tested for effects of sex and success on dispersal distance. We could not combine these three explanatory variables of interest (sex, W/B, and success) because all within-year movements were due to nest failure. Finally, we tested for the effect of sex and mate retention (reunited, divorced, or repaired) on dispersal distance. All the above tests were general linear mixed models developed with the software program JMP.

Return rates were calculated as the percentage of individuals that returned any year subsequent to the year they were banded. Banded individuals may not return to the study site because of mortality or emigration. Additionally, returning individuals may go undetected within the study site. As encounter probabilities might vary by study area (Sanz 2001), to determine whether differences in survival might explain differences in patterns of mate retention, we calculated estimates of apparent survival and encounter probability (White and Burnham 1999) to be compared with similar estimates from the Churchill study area. We used program MARK to construct Cormack–Jolly–Seber models that estimate apparent survival, φ, and encounter probability, p (White and Burnham 1999, Sandercock et al. 2005). We used recapture and resighting data for all birds banded from 2002 to 2006 and tested for sex and time (year) effects on apparent survival and encounter probability. We considered sex and time (year) effects because these are often found to affect apparent survival of plovers (Larson et al. 2000, Colwell et al. 2007). As the sample period was relatively short (five intervals) and our sample of adults small, we chose to not evaluate additional covariates (e.g., annual weather). Candidate models were ranked according to Akaike's information criterion corrected for small sample size (Hurvich and Tsai 1989) and overdispersion (QAIC$_c$; Burnham and Anderson 2002). We considered the most parsimonious

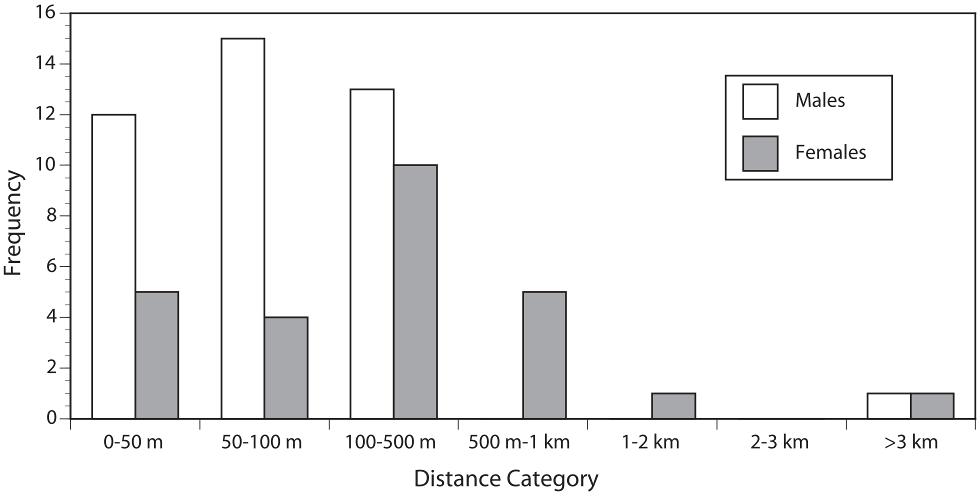

FIGURE 1. Frequency of breeding dispersal distances by male and female Semipalmated Plovers at Akimiski Island, Nunavut. Distances are those between consecutive nests (both within and between seasons) of marked individuals.

subset of models to be those for which $\Delta QAIC_c < 4$. We used the global model $\{\varphi_{sex \times time}\, p_{sex \times time}\}$ of sex and time effects for apparent survival, φ, and encounter probability, *p*, to determine an overdispersion-correction factor of $c = 1.1887$ by the median *c* approach. We report apparent survival, φ, and encounter probability, *p*, from the top-ranking model.

To determine differences between Churchill and Akimiski Island in weather during the periods of arrival and incubation, we compared weather data from the latitude of each. For Akimiski Island, we used data for the months of May and June (2002–2007), from Kuujuarapik, Quebec, the weather station nearest Akimiski Island at a similar latitude; correlations (*r*) between these temperatures and those for a subset of years on Akimiski were >0.90 (R. Brook, unpubl. data). For Churchill, we used data from Environment Canada for the years of study at that site from which we draw the comparative data (1992–1998). We calculated the number of degree days over zero on the basis of average daily temperatures with a threshold of 0 °C (Billings 1973), as invertebrates breeding in the Arctic (the Semipalmated Plover's main prey) become active at temperatures above freezing (Libera 2007). We used $\alpha = 0.05$ to assess the significance of all test results.

RESULTS

From 2002 to 2007, we banded 126 adult Semipalmated Plovers on Akimiski Island: 51 males, 72 females, and three of unknown sex. Fifty-one individuals (25 females, 25 males, and one bird of unknown sex) nested twice or more in the study period (both within and between years).

BREEDING DISPERSAL

The individual dispersing farthest was a male banded in 2003 in a Snow Goose (*Chen caerulescens*) colony (53° 11′ N, 81° 25′ W) to the west of the camp on Akimiski Island. In 2004, this bird moved to the focal study area from 30.8 km to the east. Most dispersal distances were shorter by an order of magnitude (Fig. 1; median distance moved by females: 323.1 m; by males, 61.7 m). We found no significant effect of year on distances moved (year dispersed, $F_{4,24} = 1.51$, $P = 0.23$; year settled, $F_{4,24} = 1.14$, $P = 0.36$). In models including sex and previous nest success or sex and W/B, there were no significant effects of either previous nest success or W/B on dispersal distances (nest success, $F_{1,39} = 0.25$, $P = 0.62$; W/B, $F_{1,47} = 0.74$, $P = 0.39$). Nor were there any interaction effects (sex × success, $F_{1,39} = 0.08$, $P = 0.77$; sex × W/B, $F_{1,47} = 0.19$, $P = 0.67$; Table 1). In both previous analyses we found a strong sex effect ($F_{1,39} = 9.65$, $P = 0.004$ and $F_{1,47} = 5.91$, $P = 0.02$, respectively; Fig. 1, Table 1). Divorced and repaired males dispersed much shorter distances than divorced and repaired females with no significant interaction (sex, $F_{1,6} = 7.64$, $P = 0.03$; mate retention, $F_{1,6} = 0.03$, $P = 0.88$; sex × mate retention, $F_{1,6} = 3.78$, $P = 0.10$; Fig. 2). Three pairs reunited after nest failure in the same year and dispersed 109 m, 906 m, and 1028 m, respectively (mean = 681 m), whereas one pair reunited in a successive year and dispersed 33 m.

TABLE 1. Dispersal distances (m) of Semipalmated Plovers on Akimiski Island, Nunavut, by nest success before dispersal (successful vs. unsuccessful) and by whether the movement to a new breeding territory took place between breeding seasons (between-year) or within a breeding season (within-year).

	Males		Females	
	n	Mean (95% CI)	*n*	Mean (95% CI)
Successful	16	71 (29–177)	17	191 (113–324)
Unsuccessful	30	76 (53–110)	25	287 (159–520)
Between-year	37	75 (48–117)	32	221 (141–347)
Within-year	17	105 (60–185)	13	246 (105–577)

FIGURE 2. The mean and 95% confidence intervals of distance moved to subsequent nest of divorced and re-paired males ($n = 4$ and 14, respectively), divorced and repaired females ($n = 4$ and 11), and reunited pairs ($n = 4$) on Akimiski Island, Nunavut.

MATING PATTERN

Of 15 pairs of which both birds were uniquely banded and one or both returned in some subsequent year, only 1 pair (7%) reunited, 4 pairs (27%) divorced (both members of the pair returned but joined a different partner), and 1 individual from each of 10 other pairs (67%; 7 males and 3 females) re-paired with an unbanded bird and its original mate was never re-encountered. Of 7 banded pairs whose nests failed and which attempted nesting once or twice more in the same year, 3 pairs (43%) reunited, 1 pair (14%) divorced, and one bird of the other 3 pairs (43%) re-paired with a new mate. Thus, for subsequent nesting attempts, pairs reunited only four times (4/22, 18%).

RETURN RATES AND APPARENT SURVIVAL

Of 113 adult birds sexed and banded 2002–2006, 57 were resighted in a subsequent year (50%). Sixty-five percent of males (30 of 46) returned, and 40% of females returned (27 of 67; Table 2). The best-supported model explaining apparent survival, φ, and encounter rate, p, included a sex effect on encounter rate (Table 3). Three of four of the top-ranking candidate models included a sex effect on either survival or encounter rate, but none included a year effect (Table 3). The estimated apparent survival rate, φ, from the top model was 0.649 ± 0.046 SE (both sexes combined), whereas the encounter rates for males and females were 0.781 ± 0.080 SE and 0.517 ± 0.085 SE, respectively.

RENESTING

Twenty-seven of 51 banded adults (53%) attempted renesting within a season after a failed attempt. The proportion of all nesting attempts that were replacement nests varied from 0% (0/14) in 2004 to 33.3% (7/21) in 2007.

WEATHER

At the latitude of Akimiski Island, weather in May during the study period was characterized by over three times the average number of degree days than at Churchill (Kuujuarapik, 102.8 ± 33.9 SE; Churchill, 33.9 ± 27.0, $t_{11} = 2.47$, $P < 0.03$). During June, the number of degree days at the two locations

TABLE 2. Number of adult Semipalmated Plovers banded and subsequently resighted on Akimiski Island, Nunavut, from 2002 to 2007, by sex.

			Number observed				
	Year banded	Number banded	2003	2004	2005	2006	2007
Males	2002	4	3	3	3	3	2
	2003	24		11	7	2	3
	2004	3			3	1	0
	2005	11				6	1
	2006	4					2
Females	2002	20	9	4	4	3	1
	2003	20		7	5	1	1
	2004	2			0	0	0
	2005	15				4	4
	2006	10					2

TABLE 3. The four highest-ranking models and global model determined from program MARK describing apparent survival, φ, and encounter rate, p, of Semipalmated Plovers on Akimiski Island, Nunavut (Burnham and Anderson 2002).

Model	K[a]	–2 ln(likelihood)	ΔQAIC$_c$[b]	w_i
φp_{sex}	3	60.365	0.000[c]	0.629
$\varphi_{\text{sex}} p_{\text{sex}}$	4	60.332	2.043	0.227
φp	2	65.114	4.277	0.074
$\varphi_{\text{sex}} p$	3	63.658	4.396	0.070
$\varphi_{\text{sex} \times \text{time}}$ $p_{\text{sex} \times \text{time}}$ (global)	18	51.175	21.558	0.000

[a] Number of parameters.

[b] Quasi-likelihood Akaike information criterion corrected for small sample size and overdispersion, $c = 1.1887$.

[c] Lowest value of QAIC$_c$ = 357.715.

was similar (Kuujuarapik, 201.4 ± 25.5; Churchill, 235.5 ± 27.5, $t_{11} = 0.90$, $P = 0.39$).

DISCUSSION

We predicted differences between the two populations we studied in dispersal, mate retention, apparent survival and probability of renesting. In all variables but dispersal distance the more northern (Churchill) and more southern (Akimiski Island) populations differed, suggesting substantial plasticity in social systems even within a relatively conservative strategy of monogamous mating (Szekely et al. 2008).

DISPERSAL

At both latitudes, most dispersal of breeding Semipalmated Plovers appears to be by females. At both sites median dispersal distances are similar (median at Churchill 156 m for successful females, 1275 m for unsuccessful females; Flynn et al. 1999), despite the higher rate of predation on Akimiski Island. Exceptionally, within-year dispersal by two reunited males on Akimiski Island was over an order of magnitude greater than the median dispersal distances of males at this site. These extreme examples (both of about 1 km), coupled with the observation of a single male that dispersed over 30 km to the main Akimiski Island study area where densities of breeding plovers were generally higher, suggests that breeding males occasionally disperse long distances. The two reunited males may have, exceptionally, accompanied their normally dispersing females, whereas the male that moved over 30 km may have been moving from unsuitable habitat, or alternatively, toward a larger aggregation of nests. Similar long-distance dispersal by males has not been documented at Churchill (maximum dispersal of 131 m), although males that fail are less likely to return (Flynn et al. 1999). The lower return rate at the more northerly location could be due to death or because nest failure, at least for a small number of males, stimulates dispersal out of the focal study area. With the smaller number of nest failures at Churchill, we may not have been able to detect these events.

Previous nesting success on Akimiski Island also does not appear to influence dispersal, a result that contrasts with findings from Churchill (see above; Flynn et al. 1999) and from many other studies, mostly from temperate locations (see Introduction for references). The difference between the two studies of the Semipalmated Plover could be attributable to sampling bias (Biro and Dingemanse 2009), as the mean distance of dispersal of unsuccessful females on Akimiski Island was nearly 100 m greater than that of successful females, though the difference did not meet our criterion for significance.

MATE FIDELITY

Although in both populations most males are site-faithful, at Akimiski Island females are much less likely than at Churchill to return to a mate and his territory in subsequent seasons (Flynn et al. 1999). Differences between the two populations in the amount of time for assessing mates after arrival on the breeding grounds will provide different opportunities for females to assess potential partners. At both Akimiski Island and Churchill the breeding season is short, but Akimiski Island is both farther south and experiences fewer days with subzero temperatures in May than does Churchill, although June temperatures at the two sites are similar. Male Semipalmated Plovers make display flights when air temperatures are above 0 °C (E. Nol, unpubl. data). Below this temperature, birds sit quietly in sheltered areas, presumably because invertebrates are unavailable to them (Libera 2007). Therefore, the period when Semipalmated Plovers are able to actively seek mates begins earlier at the southern location, providing more time for potential partners to be assessed (Choudhury 1995, Lanctot et al. 2000, Sandercock et al. 2000).

As a consequence of the lower mate fidelity on Akimiski Island, breeding pairs consisting of reunited males and females are exceptional both in attempts at renesting and in subsequent years. This low fidelity contrasts with the nearly 60% of 48 pairs that stayed together in subsequent years at Churchill and the 100% of 11 pairs that reunited for attempts at renesting (Flynn et al. 1999). It is lower than rates of mate retention for many other species of socially monogamous shorebirds breeding in the Arctic (Sandercock et al. 2000, Jehl 2006, Johnson et al. 2008). Mate fidelity in successive seasons is promoted when pairs arrive on the breeding grounds at the same time (Gunnarsson et al. 2004, Battley 2006) and should be selected for when there is a cost to delaying mate choice (Amat et al. 1999, Handel and Gill 2000). Our study and those of Jones and Montgomerie (1991) and Lanctot et al. (2000) suggest a greater role for females than for males in mate choice. Our results indicate no difference in survival probabilities of the two sexes, suggesting that mate limitation (Sandercock et al. 2000) is not a factor in the high rates of re-pairing on Akimiski Island. However, average apparent survival of adults is lower on Akimiski Island than at Churchill (0.71 ± 0.036; Badzinski 2000). As apparent survival cannot distinguish death from emigration out of the study area (Sandercock 2003), the lower apparent survival could offer a partial explanation for the lower rate of mate retention on Akimiski Island, because in every year, on average, 8% fewer adults will return.

Accompanying these differences in rates of mate retention between the two populations is a large difference in the rate of attempted renesting. Renesting is rare at Churchill (2–8% annually; Flynn et al. 1999), yet over half of all nesting pairs on Akimiski Island renest after a failure. The higher rate of nest loss on Akimiski Island provides a mechanism for higher rates of re-pairing and divorce, as many other birds on Akimiski Island will have simultaneously also lost their nests, providing an abundance of potential new partners.

In two studies of the Western Sandpiper (*Calidris mauri*) in Alaska (Sandercock et al. 2000, Johnson and Walters 2008) conducted at different latitudes, similar differences emerge, with lower rates of reunification in the more southerly population (Johnson and Walters 2008). This pattern, coupled with the rates of mate fidelity in the Great (*Parus major*) and Blue (*Cyanistes caeruleus*) Tits lower among birds that flock in winter than in resident populations (Dhondt et al. 1996), suggests that the presence of, and opportunity to assess, different partners promotes pair dissolution and may be a general principle in socially monogamous species (at least in the absence of a cost to mate change; Ens et al. 1996).

On Akimiski Island, we were not able to assess whether a change in mates provided a reproductive advantage over mate fidelity because so few pairs reunited. At Churchill, reuniting pairs nested earlier and experienced higher hatching success in only one of four years of study (Flynn et al. 1999). Reuniting pairs of Black Turnstones (*Arenaria melanocephala*) did not benefit over individuals who mated with new partners (Handel and Gill 2000), nor does mate fidelity explain variation in nest survival of the Western or Semipalmated (*Calidris pusilla*) Sandpipers Sandercock et al. 2000, Johnson and Walters 2008) or the American Avocet (Robinson and Oring 1997). Therefore, at best, there appears to be only a slight advantage to mate fidelity for the Semipalmated Plover and possibly many other shorebirds (but see Heg et al. 2003 for the Eurasian Oystercatcher, *Haematopus ostralegus*).

We have identified some behavioral differences between two populations at different latitudes. The next step should be to identify lifetime fitness consequences of these behavioral responses to evaluate whether fitness is indeed equivalent across broad geographic distances. This will require long-term studies of marked individuals at multiple sites across a latitudinal gradient. Coupling these studies with those identifying connectivity between breeding and wintering populations (Marra et al. 2006) will aid in population-specific modeling and conservation planning.

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