PHILOPATRY, NEST SITE TENACITY, AND MATE FIDELITY IN SEMIPALMATED PLOVERS (*CHARADRIUS SEMIPALMATUS*) BREEDING AT CHURCHILL, MANITOBA.

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ABSTRACT

Philopatry, nest site tenacity, and mate fidelity in
Semipalmated Plovers (*Charadrius semipalmatus*) breeding at
Churchill, Manitoba.

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Philopatry, nest site tenacity, and mate fidelity were
examined in a population of Semipalmated Plovers near
Churchill, Manitoba in 1994 and 1995. Natal philopatry in
the population was very low (0.4%), and adult return rates
(female 40%; male 51%) were similar to those found for other
shorebirds. Adult return rates to the general study area
were not different between the sexes. However, female
Semipalmated Plovers which divorced or re-paired between
breeding seasons were significantly less nest site tenacious
than females which reunited with their previous mates and
males of all pairing status.

Previous reproductive success generally did not affect
return rate, site tenacity, or mate fidelity in this
population. When both members of a pair returned to the
study area, they were more likely to reunite with each other
(67%) than to divorce (33%), and in 1995, pairs which
reunited nested significantly earlier and had greater
hatching success than novel pairs. The stability of the
plovers' breeding habitat likely contributes to the nest
site tenacity and mate fidelity of this population,
suggesting that although general theories regarding site and
mate fidelity can be postulated, local conditions may have a
large impact on the dispersal and reproductive life-history
of the populations under study.

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INTRODUCTION

Philopatry is broadly defined as a faithfulness to a natal or breeding area, and is recognized in many species of birds and mammals (Greenwood 1980, Thompson and Hale 1989, Dhindsa and Boag 1992). In most species that exhibit natal or breeding philopatry, there is a sex bias in dispersal; the direction of this bias is thought to be a consequence of the mating system (Greenwood 1980, Greenwood and Harvey 1982, Colwell and Oring 1989, Thompson and Hale 1989, Groen 1993, Johnson et al. 1993).

In a mating system in which one sex defends a resource or territory important for mate acquisition or rearing of offspring, that sex is expected to benefit from being more philopatric, as familiarity with an area is presumed to facilitate territory, mate, and food acquisition, and to improve defense and predator avoidance (Greenwood and Harvey 1982, Haig and Oring 1988). The opposite sex would then be freed from the constraint of resource defense, and should therefore exhibit greater flexibility in both natal and breeding dispersal. In addition to philopatry, site tenacity, which is represented by the number of territories

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or actual nest site distance moved between years by a breeding individual, is considered advantageous for the same reasons (Gratto *et al*. 1985, Jackson 1994).

Avian mating systems vary widely, but even in socially monogamous species with male resource-defense, a split in the pair bond between breeding seasons provides an opportunity for variation in individual return rate and site tenacity (Wilcox 1959, Soikkeli 1967, Holmes 1971, Lenington and Mace 1975, Gratto *et al*. 1985, Thompson and Hale 1989, Groen 1993, Jackson 1994, Thompson *et al*. 1994). Differential rates of philopatry by adults and juveniles are also common in many birds (Lenington and Mace 1975, Darley *et al*. 1977, Harvey *et al*. 1979, Gratto *et al*. 1985, Groen 1993). When the level of adult philopatry is high, the return of juveniles to their natal site is expected to be low, as they would be at a disadvantage in terms of experience and habitat familiarity when competing with established breeders (Greenwood and Harvey 1982). This movement of young birds away from their natal area would also reduce the likelihood of mating with a close relative. In a male resource-defense mating system, natal, as well as breeding, dispersal is more extensive among females

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(Greenwood and Harvey 1982), although in juveniles the return rate may be so low as to make any sex bias undetectable (Gratto et al. 1985, Thompson et al. 1994).

Factors other than sex have been found to influence philopatry and site tenacity. These include mate fidelity, previous reproductive success, age, and site stability (Redmond and Jenni 1982, Gratto et al. 1985, Haig and Oring 1988, Bradley et al. 1990, Reed and Oring 1993, Jackson 1994). Connections here can become complicated, as previous success, age, and site stability can all influence mate fidelity, and mate and site fidelity can affect any subsequent reproductive success. Separating out the relationships between any two of these factors can be difficult.

Mate Fidelity - Although social monogamy is common in avian mating systems it has never, until recently, generated much interest largely due to the view that unusual mating systems could contribute more to the understanding of the evolution of avian social systems (Gowaty and Mock 1985). However, even in monogamous systems selection of a new mate can occur throughout an individual's lifetime (Gowaty and Mock 1985,

Gratto *et al.* 1985, Jones and Montgomerie 1991, Ens *et al.* 1993). This mate switching may be enhanced in a migratory species where the separation of the pair outside the breeding season is common due to differential migration times and different wintering areas.

Evidence for reproductive advantages of mate retention comes primarily from studies of long-lived seabirds. These individuals may change mates annually for a number of years early in their reproductive career, during which time increasing age and breeding experience may influence egg size, laying date, and reproductive success. When a compatible mate and breeding site are obtained, retention of these can lead to increased reproductive success (Rowley 1983, Bradley *et al.* 1990). In birds with a shorter lifespan, including many small shorebirds, it may not benefit their lifetime fitness to spend several years experimenting with different mates and breeding sites.

The benefits of mate retention accrue to both males and females, but if males acquire and defend the breeding territory, then the choice to remate or divorce may lie with the female. Evidence for this is inferential, but considerable. Divorced, but not re-paired, female Willow

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Tits advanced their laying date and bred successfully,
whereas divorced males either remained unpaired or had low
reproductive success (Orell *et al.* 1994). As well, female,
but not male, Blue Tits improved their reproductive success
following a divorce when compared to faithful pairs (Dhondt
and Adriaensen 1994). In addition, in species with male
territoriality, divorce has been connected with both site
and male mate quality. In some species divorce rates are
greatest in low quality sites (Desrochers and Magrath 1993),
and with low quality males, as measured by ornamentation
(Jones and Montgomerie 1991). Therefore, any improvement in
mate or site quality following divorce should be more likely
to manifest in females rather than males.

Reproductive Success - If mate fidelity is generally
advantageous, why would a female or a pair choose to
divorce? Interyear gains in mate and/or site quality should
be an ultimate means for increasing future reproductive
success. It is difficult to determine whether divorce is a
proximate result of avoidance of the previous mate or of the
previous territory, but in either situation, one would
expect low reproductive performance in one year to be

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correlated with an increased divorce rate and low site tenacity the next (Thompson and Hale 1989, Beletsky and Orians 1991, Dhondt and Adriaensen 1994), although this is not always the case (Forslund and Larsson 1991, Dhindsa and Boag 1992, Bridges 1994).

If interyear switching of site or mate in response to low reproductive success is a mechanism for increasing future reproductive success, this benefit should manifest itself in higher hatching or fledging success in the year subsequent to the switch. This may be related to the life span of the species, as success seems to be more closely linked to the breeding age of the female in long-lived birds (Ens et al. 1993). However in species with a relatively short life span, pairs may not be able to afford the time to spend a year or two in a poor relationship "cementing" the pair bond to ensure future breeding success. In addition, if the time for mate and or site assessment and selection is short, it may be more advantageous for an individual to return to a mate with at least some breeding experience, regardless of previous reproductive performance.

The Semipalmated Plover (*Charadrius semipalmatus*) is a small, seasonally monogamous shorebird that winters on both Atlantic and Pacific coasts from the southern United States to the tip of South America, but breeds across northern Canada from the Queen Charlotte Islands to New Brunswick (AOU checklist 1983). As noted in an earlier study, marked adults in the Churchill, Manitoba population of this species returned to the same area in successive years to breed (M. Sullivan Blanken pers. comm.). This species exhibits biparental care, but females leave the brood approximately 8 days before the male, and males appear on the breeding territories in the spring before the females (pers. obs.). Despite this yearly separation, some individuals reunite with their former partners in successive seasons.

Previous studies of monogamous shorebirds have reported a wide range in the rate of perennial (between seasons) monogamy and site tenacity (Soikkeli 1967, Oring and Lank 1982, Gratto *et al.* 1985, Haig and Oring 1988, Thompson *et al.* 1994). If site tenacity is important in promoting mate fidelity, I would expect the stability of the breeding habitat to influence both of these variables; species breeding in ephemeral sites might return to previous sites,

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and therefore previous mates, at lower frequencies. This study was undertaken to investigate the degree of mate and site fidelity in Semipalmated Plovers nesting in the Churchill, Manitoba area, and to measure the effects of sex, reproductive success, and mate and site quality on these two indicators of dispersal patterns.

Semipalmated Plovers at Churchill nest primarily on gravel ridges which are rarely affected by storms, fluctuating water levels, or human disturbance, although occasionally affected by late snow cover. Due to the stable nature of their nesting habitat, I expect individuals in this population to exhibit a high incidence of mate and site fidelity. The temporal constraints of their northern breeding range may augment this tendency, in that there is little opportunity for evaluation of new sites and mates, and this lack of opportunity may also reduce the likelihood of change in a year following poor reproductive success.

Study area - This study was conducted in the breeding

seasons (June to August) of 1994 and 1995 in and around the

town of Churchill, Manitoba (58°45'N 95°04'W) to the

Churchill Northern Studies Centre (CNSC), 30 km to the east.

The study area encompassed approximately 384 km^2 of roads,

tundra, lakes, and gravel ridges, although not all of this

area was considered suitable nesting habitat for

Semipalmated Plovers. Preliminary banding was carried out

during a previous study undertaken in 1992 and 1993

(Sullivan Blanken 1996).

Semipalmated Plovers breed on coastal mudflats, outcrop

ridges, and gravel ridges up to 6 km inland in Churchill

(Jehl 1973). Nesting habitat is characterized by gravel

ridges mixed with *Dryas integrifolia*, with surrounding

vegetation sparse and rarely exceeding 10 cm in height.

Dominant vegetation on the coastal mudflats is *Honckenya*

peploides and *Senecio congestus;* on outcrop ridges is *D.*

integrifolia, Rhododendron lapponicum, Arctostaphylos

alpina, Empetrum nigrum and *Salix reticulata;* on gravel

ridges is *D. integrifolia, Saxifraga oppositifolia, E.*

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nigrum and *S. reticulata* (Johnson 1987). Within each
territory there were several scrapes (depressions in the
substrate), but only the nestcup used was lined with small
twigs and *D. integrifolia*.

Field Methods - All suitable areas between the town of
Churchill and the Churchill Northern Studies Centre that
were accessible by road were included in the study area
(Fig. 1). Nests were located by walking transects through
suitable nesting habitat and sighting adult Semipalmated
Plovers conducting distraction displays. All suitable
nesting habitat within the study area was searched at least
twice during June (main incubation period) and areas around
a nest with a marked individual in one year were intensively
searched at least twice to a radius of 1 km in successive
years.

Fewer than 10% of the nests were found during the
laying period; the rest were found during incubation. For
those nests found during incubation, the length, width, and
weight of the eggs were taken, and the date of hatch was
estimated from a regression equation (Appendix 1). This was
considered accurate to within four days, and nests were
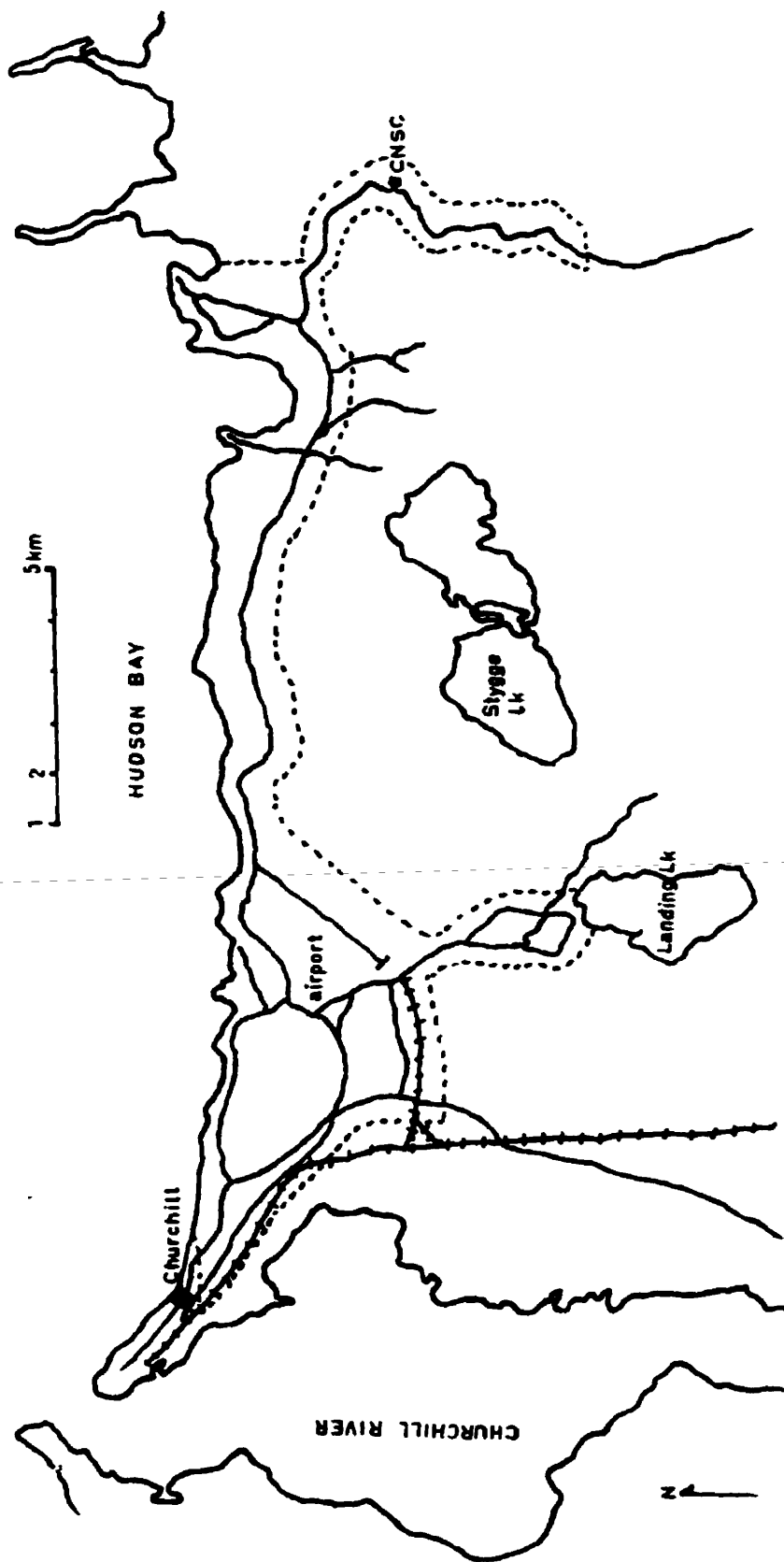
Figure 1. Map of Churchill, Manitoba; study area indicated by dotted line.

checked for pipping eggs every two days close to the hatch date. To reduce chance of discovery by predators, nests were not marked, but were mapped for facilitation of location in current and subsequent years.

Plumage dimorphism is sufficient to accurately distinguish the sex of breeding adults (E. Nol unpubl. data). Typically, males have more extensive and blacker crown and breast bands, and lack much of the white supercilium. All adults were consistently identified to the same sex both within and between years.

Adults were trapped on the nest with either a walk-in keyhole trap or a Potter trap. The circular walk-in trap was constructed of hardware cloth (40 cm in diameter and 30 cm high; 10 cm by 10 cm keyhole) with a cotton net top; the square Potter trap (25 cm by 25 cm by 25 cm) was made of 2 mm wire, and had a treadle (10 cm by 10 cm) placed over the nestcup triggering a drop door (15 cm wide by 10 cm high). To reduce stress (a possible stimulus for dispersal) traps were removed if the adult did not return within 30 minutes, and were monitored continuously so the adult was removed soon after entering (after Jackson 1994).

Once captured, adults were banded on the metatarsus

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with a unique combination of a Canadian Wildlife Service (CWS) numbered aluminum band and three colour bands (A.C. Hughes). While in the hand, adults were weighed with a Pesola balance to the nearest 0.1 g, and the following measurements were taken with a pair of calipers to the nearest 0.1 mm: metatarsus length, culmen length (length of orange portion, length of black portion, total length), toe length, outer web length, black crown depth, and the length of the white supercilium. Flattened wing chord and the number of brown feathers in the black crown and black breast band were also measured. Measurements of bilateral structures were taken on the right side.

Nests were viewed from a distance every 3 to 7 days to check for attendance by an adult. Disappearance of clutches was attributed to predation unless another specific cause was obvious (e.g. tides). Around estimated hatch date nests were visited daily, and upon hatch chicks were caught by hand and banded with a brood-specific colour combination and a CWS numbered aluminum band. A small number of clutches hatched between visits, but hatch success was verified through resighting of chicks with the appropriate banded adults. A nest was considered successful if at least one

egg hatched.

After hatch, distance between nestcups in successive years was calculated for each marked individual. Distances of less than 700 m were measured with a meter tape (distances <30 m were measured to the nearest 0.05 m, distances of 30 m to 100 m to the nearest 0.10 m, and distances of 100 m to 700 m to the nearest meter). Distances greater than 700 m were calculated with a Global Positioning System (GPS) unit (accurate to within 10 m) or from air photos (scale 1:10 000 or 1:12 000). Daily air temperatures were measured at the Churchill Weather Office in Churchill, Manitoba, and were obtained from the Atmospheric Environment Service of Environment Canada.

The quality of an individual was assessed from morphological indicators. Mass, tarsus length and wing chord, as well as the ratio of mass to tarsus length are often used as estimators of body condition and individual quality (Lemel 1989, Fox et al. 1992, Richner et al. 1993). Plumage colouration (especially in males) is considered in many species to be an important indicator of fitness or quality (measured by nest attentiveness, overwinter survival, production of fledglings and fledgling weight),

and plumage brightness can be an important criterion in mate choice (Norris 1990, Hill 1991, Slagsvold and Dale 1994). As Semipalmated Plovers are sexually dimorphic with plumage variable within a sex, colouration was considered a potentially important factor in mate choice. Plumage characteristics measured were: length of white supercilium, depth of black crown stripe, amount of black relative to total culmen length, and number of brown feathers in the black crown and breast band.

The relative quality of a nest site was evaluated as the horizontal visibility around the nest-cup and the distance to the nearest foraging area. These were considered appropriate indicators of quality, as for some shorebirds, nest success is greater on territories with little vegetative cover (Metcalfe 1984, Gaines and Ryan 1988), and nests situated farther away from suitable foraging areas might result in greater initial chick mortality. Visibility was measured on the day after hatch as follows: a block of wood (12 cm x 5 cm x 4 cm) painted brown on the upper half and white on the lower half was placed in the nestcup. Viewed from a height of 50 cm at each of the four compass points, the percent area of the

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model visible was recorded at distances of 5, 10, 15, and 25 m.

Terminology - Throughout this study, "adult philopatry" (or "adult return rate") is defined as the number of adults banded in one year which were sighted in the study area in a subsequent year. "Natal philopatry" refers to the number of birds banded in the study area as juveniles which were sighted in the study area in subsequent years as adults (Gratto et al. 1985). These annual resighting rates represent minimum return rates, as individuals that return but disperse outside of the study area would not be observed.

"Site tenacity" is defined as the distance between nestcups of an individual in successive years (Gratto *et al.* 1985, Wiens and Cuthbert 1988). Some studies measure territory fidelity, or the number of breeding territories moved by an individual between years (Darley *et al.* 1977, Greenwood and Harvey 1982). While this may be more biologically meaningful it is often difficult to determine, especially for species with varying territory sizes. Breeding densities of Semipalmated Plovers vary widely

(Rippen Armstrong and Nol 1993); an accurate estimate of each territory would have required extensive behavioural observations (Haig and Oring 1988) and was considered logistically difficult for this study.

Hatch success is used as the criterion for breeding or reproductive success, and a nest from which at least one egg hatched was defined as successful. A breeding pair is said to "reunite" if both individuals return and pair with each other in the following year; "re-pair" if only one of the pair returns in the following year; or "divorce" if both members return the following year but form pair bonds with different individuals.

Statistical analyses - All data were tested for normality, and nonparametric tests were used where appropriate. For calculations where data from more than one year were combined, individuals were represented more than once only if the variable was considered independent of the individual (factorial model ANOVA). Fisher's exact tests were used for all 2x2 contingency tables, and Log-linear models for frequency data with three or more variables (Gratto *et al.* 1985, SAS 1985). In any case where the direction of the

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outcome had been predicted on the basis of the literature, a one-tailed statistical test was used. For all tests, results were judged to be significant if $P<0.05$, but considered marginally significant when $P<0.10$. Paired t-tests were employed for comparisons of mate and site quality, and all measurements were taken in the year of pairing.

RESULTS

Sexual differences in natal and adult philopatry - In the Churchill study area, 57 nestlings were banded in 1988, 31 in 1992, 88 in 1993, and 83 in 1994. Of these 259 nestlings, only one (0.4%) was observed to return to the study area in a subsequent year to breed, therefore sexual bias in natal philopatry could not be assessed. One female banded as a nestling in 1988 returned in both 1994 and 1995 to breed, but was not seen in the intervening years. The distance between its natal and breeding sites is unknown, as the precise location of the natal site was not recorded. The number of years that elapsed between natality and year of first breeding is also unknown because there were no observers in Churchill during the period from 1989-1991.

Adult philopatry was measured as the number of returns in the year following banding (Table 1). Using all data (including birds nesting in the year following banding and those individuals which were known to return but for which no nest was found) I determined that there was no significant interaction between the factors of sex and year on rate of return (log-linear model, $\chi^2=1.96$, $P=0.38$) I

Table 1. Rate of return of adult Semipalmated Plovers to the study area in the year following banding at Churchill, Manitoba. Returns include all individuals sighted in the study area.

Year of banding	Year of sighting	Sex	Number of birds banded	Number of birds returned	% Returned
1992	1993	Female	9	3	33.3
		Male	14	5	35.7
1993	1994	Female	30	13	43.3
		Male	24	17	70.8
1994	1995	Female	26	10	38.5
		Male	29	12	41.4
Total		Female	65	26	40.0
		Male	67	34	50.7
1992+1993	1994	Female	39	19	48.7
		Male	38	20	52.6
1992+1993	1995	Female	65	30	46.2
+1994		Male	67	29	43.3

then tested for two-factor effects; neither year of observation ($\chi^2=4.56$, $P=0.10$) nor sex ($\chi^2=2.24$, $P=0.13$) alone had a significant effect on adult return rate, even though adult return rate was highest in 1994 and males returned at a higher rate than females in every year. There was also no significant difference in return rate between females (26 of 65 returned) and males (34 of 67) for all years combined (Log-liklihood ratio test, $G=1.94$, $P=0.16$).

High rates of nest success in 1994 (Table 2) probably contributed to the high observed return rate in that year, as in other years birds may have been missed if their nests were destroyed early and they did not attempt to renest. This should not have affected the relative return rates of the sexes, as in each year, males and females were banded in approximately the same proportions (Table 3). Return rate of individuals trapped in the current season was significantly lower than those individuals currently nesting but trapped one or more years previous (52 of 110 returned in current season, 28 of 43 in previous season; Log-likelihood ratio test, $\chi^2=4.00$, $P=0.047$).

Table 2. Nest success of Semipalmated Plovers in the Churchill, Manitoba study area. Samples sizes (in parentheses) are the number of nests monitored and do not include renesting attempts. (If a nest failed but the renest was successful, it was counted as one successful nest).

Year	Percent successful
1992	52.4 (21)
1993	59.6 (47)
1994	79.6 (49)
1995	51.2 (43)

Table 3. Number of nests found and number of banded adult female and male Semipalmated Plovers (both newly banded and returned individuals) in each year at Churchill, Manitoba.

Year	Number of nests found	Number of birds banded	
		females	males
1992	21	9	14
1993	47	32	29
1994	49	43	45
1995	43	39	40

Sexual differences and effect of mate fidelity on nest site

tenacity - As nestcup locations for several of the birds

banded in 1992 were uncertain, calculations of site tenacity

are restricted to the years 1993-1994 and 1994-1995. Adult

site tenacity was evaluated with regard to pairing status,

as there could not be a difference in nest site distance

moved between the sexes for those pairs that reunited in

successive years. For those birds that changed mates, their

previous mate may have either been present (divorce) or not

present (re-pairing) the following year (Table 4). Females

that re-paired and those that divorced moved similar

distances to their new nest sites in successive years.

These groups moved significantly farther than both females

which reunited and all males regardless of marital status.

There was no significant difference in the distance between

successive nest sites in the latter groups (Table 4).

Effect of nest success on subsequent philopatry and site

tenacity - Some individuals banded in 1993 returned to the

study area in both 1994 and 1995, and would therefore

represent repeated measures. With regard to previous nest

success, there was no difference in the frequency of

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Table 4. Distance moved by Semipalmated Plovers between successive nest sites for each sex and three categories of pairing. Horizontal lines at bottom of chart indicate homogenous groupings using nonparametric multiple comparisons based on Kruskal-Wallis rank sums.

	Male			Female		
	Reunite	Re-pair	Divorce	Reunite	Re-pair	Divorce
median (m)	33.3	63.3	25.55	27.15	370	770
n*	10	9	7	16	6	7
range	11.05-46.4	1.50-130	11.00-111	2.10-62.8	117-1890	75.7-1190
mean (m)	33.3	67.5	41.6	30.3	630	564
SE of mean	3.8	16.0	13.4	3.9	274	167

*Sample sizes of reunited males and females differ; for females distance moved was independent of individual, therefore some individuals in different years are represented more than once

returning birds in 1995 with or without these repeated individuals for either males (Fisher's exact, $P=0.19$) or females ($P=0.29$). Addition of these data therefore, should not bias the ratio of return rates. Nest success in 1993 did not affect the return rate of either sex to the study area in 1994 (Table 5). This was also true of females the following year, but males which nested successfully in 1994 returned at a higher frequency than those which were unsuccessful (Fisher's exact one-tailed test, $P=0.01$; Table 5). As the power of the test may be too low to detect a significant result in 1994 due to small sample sizes, I combined the data from both years. After pooling, there was no effect of previous nest success on the subsequent rate of return for either sex of Semipalmated Plovers (Table 5).

To analyze the effect of success on subsequent site tenacity, the distance moved between the years 1993-1994 and 1994-1995 were pooled due to the low rate of nest failure in 1994. Previous success was also assessed for each category of pairing status, as tenacity differed for males and females which changed mates (see above, Table 4), although the categories of divorce and re-pairing were combined for each sex due to low sample size. For reunited pairs and

Table 5. Effect of nest success on subsequent rate of return of adult Semipalmated Plovers to the study area in Churchill.

Year of Banding	Year of Return	Nest Outcome	Males			Females		
			Return	Not return	P^*	Return	Not return	P
1993	1994	Success	13	8	0.86	13	12	0.25
		Failure	6	2		2	5	
1994	1995	Success	26	12	0.01	19	16	0.32
		Failure	1	6		3	5	
Total		Success	39	20	0.14	32	28	0.14
		Failure	7	8		5	10	

*significance tested using Fisher's exact one-tailed test.

males that changed mates, previous nest success did not significantly affect the distance moved in the subsequent breeding season (Table 6). For females that changed mates, those that had nested successfully the year before did not move as far as those whose nests had failed, although my sample size was quite small and only marginally significant $P=0.08$ (Table 6).

Effect of nest success on subsequent mate fidelity - The level of mate fidelity in this population varied between years (Table 7). For the years combined, an almost equal number of birds re-paired (17/41) as reunited with their previous mate (16/41), while half that number divorced (8/41).

If only one individual of a banded pair returns to the study area, as in the case of re-pairing, the pair does not have an opportunity to reunite. Only cases where both individuals of a pair returned (divorce and reuniting) can therefore be used to study the effect of previous nest success on mate fidelity. Unfortunately, for very few of the pairs which nested unsuccessfully in one year did both individuals return the following year (Table 8). For only

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Table 6. Effect of previous nest success on site tenacity. Data from 1994 and 1995 were not significantly different (P=0.31; Wilcoxon two-sample test) and were therefore combined.

Pairing Status	Previous Nest Outcome						P^*
	Successful			Unsuccessful			
	median (m)	range (m)	n	median (m)	range (m)	n	
Reunited pairs	30.7	2.10-46.4	10	33.6	22.85-44.4	2	0.91
Male mate change	46.9	1.50-130	17	38.4	28.15-111	4	0.89
Female mate change	246	75.7-1190	10	870	770-1890	3	0.08

*significance tested using Wilcoxon two-sample test.

Table 7. Level of mate fidelity in Semipalmated Plovers breeding in the Churchill, Manitoba study area. Data for reunitings and divorces are pairs of birds, data for re-pairing represents individuals (numbers in parentheses indicate sample size).

Years	% Reunite	% Re-pair	% Divorce
1993-1994	33.3 (6)	50.0 (9)	16.7 (3)
1994-1995	43.4 (10)	34.8 (8)	21.7 (5)

Table 8. Effect of nest success on subsequent mate fidelity. Re-pairings omitted as only those cases where both individuals of a pair returned can be used to assess mate fidelity.

| Year | Previous Nest Outcome | | | | P^a |
| | Successful | | Unsuccessful | | |
	Reunite	Divorce	Reunite	Divorce	
1993-1994	5	1	2	1	0.92
1994-1995	10	5	0	0	**
Combined	15	6	2	1	0.66

*significance tested using Fisher's exact one-tailed test
**unable to calculate frequencies

three unsuccessful pairs did both sexes return, but this is

due more to the low rate of nest failure in 1994 rather than

to non-return of reproductively unsuccessful individuals.

When the sampling years were pooled, previously unsuccessful

individuals were as likely to reunite with their former

partners (66%) as were successful individuals (71%).

Intrayear mate and site fidelity - Renesting attempts

following nest failure were infrequent in the Churchill

study area. The major cause of nest failure was predation

(mainly from red fox *Vulpes vulpes* and Herring Gulls *Larus*

argentatus), although two nests in 1994 failed due to

abandonment by adults (causes unknown) and two were lost to

high tides. In 1994 nest success was very high (79.6%), and

only one renesting attempt was recorded; in 1995 five

renesting attempts were recorded. For those pairs which

renested, predation of the original attempt occurred 1.5 to

12 days ($\bar{x}$ =5.75 days, SE=1.43) after nest initiation, and

the last egg was laid for the second nest 10 to 13 days ($\bar{x}$

=10.58, SE=0.49) later. In all six instances, there was no

change in mate between the original nest and the renest in

the same year. The distance moved between the original and

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second nest cups was low ($\bar{x}$ =37.04m, SE=7.75), and was not

significantly different from pairs that reunited between

years (Mann-Whitney U test, U=37.5, P=0.45).

*Effect of mate change on subsequent nest initiation date and

nest success* - In 1994, the date of nest initiation was not

significantly different between reunited pairs and those

which had changed mates and formed a new pair bond (re-

pairing and divorce combined, Table 9). In 1995, those

individuals that reunited with their mate of the previous

year nested significantly earlier than those forming a pair

bond with a new individual. Although the range in

initiation dates was similar for the two years, the mean

nest initiation date was three days earlier in 1994 ($\bar{x}$ = day

161.4, SD=2.86) than in 1995 ($\bar{x}$ = day 164.4, SD=2.52). In

1994 the weather at the beginning of the nesting period was

extremely favourable, with above 0°C temperatures consistent

after day 146 (Fig 2). In 1995 the weather was not more

variable during the nest initiation period (days 145 to 165;

F=1.09, P=0.85), but above zero daily means were not

consistent until after day 151. Similar to above, in 1994

those individuals which had kept their mate of the previous

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Table 9. Date of nest initiation (day of year) for Semipalmated Plovers which reunited or changed mates in successive years. Change of mate could occur through re-pairing or divorce.

Year of nesting	Pairing Status						P^*
	Reunite			Change mate			
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	
1994	160.5	1.0	6	160.8	0.4	17	ns
1995	163.0	0.5	10	165.5	0.6	19	0.002

*significance tested using Student's t-test, ns = not significant
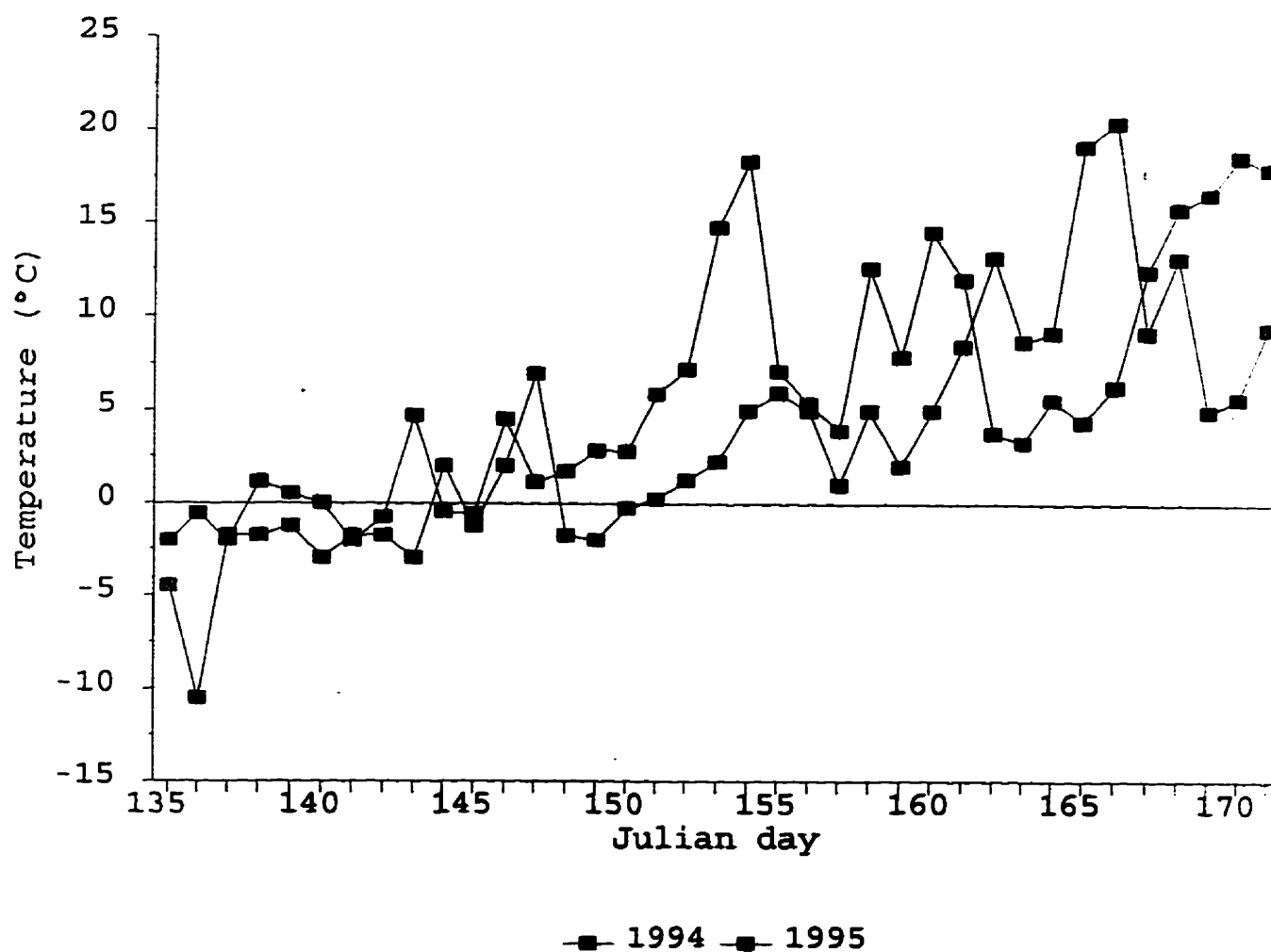
Figure 2. Daily mean temperatures in Churchill, Manitoba for
1994 and 1995. Measurements were taken at the Churchill
Weather Office and were supplied by the Atmospheric
Environment Service of Environment Canada. Daily mean
represents the arithmetic mean of daily maximum and daily
minimum temperatures (day 135 = 15 May in each year)

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year were no more successful than those with novel mates, but in 1995 reunited pairs had higher nesting success than individuals with a new mate, although this trend was only marginally significant (Table 10).

Relative quality of pre- and post-divorce sites and mates - Semipalmated Plovers breeding at Churchill were sexed on the basis of plumage colouration and body size; females were larger than males and male plumage was darker than that of females (Table 11). For those birds that were known to have divorced, the difference in quality between the previous and current mate and nest site were compared. For neither males nor females was there any significant difference in the body condition or plumage colouration between the mate prior to and following a divorce (Table 12). In addition, the characteristics of a nest site did not differ significantly for either males or females in the year following a divorce (Table 13).

Table 10. Effect of new pair bond on subsequent success. Change of mate could occur through either re-pairing or divorce. Some individuals banded in 1993 returned in 1994 and 1995; they are represented more than once as an individual's pairing status was independent of year ($P>0.05$).

| Year of Nesting | Pairing Status | Nest Outcome | | P^* |
		Success	Failure	
1994	Reunite	4	2	0.27
	Change Mate	15	2	
1995	Reunite	10	0	0.03
	Change Mate	11	8	

*significance tested using Fisher's exact one-tailed test

Table 11. Average body size and plumage characteristics for adult male and female Semipalmated Plovers.

Characteristic	Male			Female		
	x̄	SE	n	x̄	SE	n
mass (g)	46.2	0.4	47	48.4	0.4	50
tarsus (mm)	22.99	0.11	49	23.19	0.15	50
wing chord (mm)	124.33	0.37	49	125.84	0.43	50
mass:tarsus	2.02	0.02	47	2.09	0.02	50
black:total culmen length (mm)	0.56	0.01	48	0.61	0.01	50
supercilium length (mm)	6.52	0.39	48	10.70	0.55	49
black crown depth (mm)	6.55	0.14	47	5.13	0.14	50
# brown feathers in breast	2.7	0.5	48	13.0	0.8	50
# brown feathers in crown	0.9	0.2	48	5.4	0.5	50

Table 12. Comparison of size and colour characteristics of (1) female observed in first and second years (old mate - new mate; male divorce) and (2) male observed in first and second years (old mate - new mate; female divorce).

Character	Male divorce			Female divorce		
	x̄ (SE) difference in character	P*	n	x̄ (SE) difference in character	P	n
mass(g)	0.86 (0.87)	0.36	7	-1.38 (0.86)	0.17	6
tarsus length(mm)	-0.44 (0.61)	0.52	7	0.39 (0.70)	0.60	6
mass:tarsus	0.06 (0.04)	0.19	7	-0.09 (0.06)	0.18	6
wing chord(mm)	2.80 (1.29)	0.10	5	-0.92 (1.54)	0.58	6
black:total culmen length(mm)	-0.05 (0.07)	0.40	5	0.00 (0.02)	0.97	6
supercilium length(mm)	-2.12 (2.58)	0.46	5	2.83 (1.73)	0.16	6
black crown depth(mm)	0.28 (0.87)	0.74	5	0.31 (0.63)	0.65	6
# of brown feathers in breast	0.20 (2.31)	0.94	5	-1.67 (1.33)	0.27	6
# of brown feathers in crown	-1.75 (1.03)	0.19	4	-0.33 (0.84)	0.71	6

* significance tested using two-tailed paired t-test

Table 13. Comparison of nest site characteristics of (1) male nest site in first and second years (old site - new site; male divorce) and (2) female nest site in first and second years (old site - new site; female divorce). For nesting area mean and SE, n=18.

Site Characteristic	x̄ (SE)	Male divorce			Female divorce		
		x̄ (SE) difference in character	P*	n	x̄ (SE) difference in character	P	n
Horizontal visibility(%)							
at 5 m	94.9 (2.0)	-5.0 (5.0)	0.37	5	-8.1 (6.7)	0.31	4
at 10 m	81.4 (3.5)	-2.5 (4.8)	0.63	5	-10.6 (10.8)	0.40	4
at 15 m	56.0 (3.4)	-7.5 (6.5)	0.31	5	-6.3 (11.3)	0.62	4
at 25 m	28.1 (3.5)	5.0 (10.9)	0.67	5	-7.5 (12.4)	0.59	4
Distance to foraging area (m)	27.3 (6.3)	-26.4 (15.4)	0.16	5	-27.0 (13.3)	0.13	4

* significance tested using two-tailed paired t-test

DISCUSSION

Returning to a breeding area is presumed to be advantageous in terms of familiarity with food and mate availability, territory acquisition, and predator avoidance (Greenwood and Harvey 1982). However, if many related individuals repeatedly return to the same area, there is a possibility of inbreeding in the population. Inbreeding is generally assumed to be harmful (Greenwood and Harvey 1982, Shields 1983), and in an avian population with a relatively high rate of adult philopatry, avoidance of inbreeding is mainly achieved through natal dispersal (Greenwood and Harvey 1982). If adult philopatry is male-biased, natal philopatry may be similarly male biased; if only males are close relatives, inbreeding will be reduced.

In the case of the population of Semipalmated Plovers I studied, adult philopatry is not male biased, and is relatively high. An overall adult return rate of 45% (60 of 132 marked birds returned; Table 1) must be considered a minimum survival rate for this species. Several closely related species have annual adult mortality rates of approximately 45% (Little Ringed Plover (*C. dubius*), Ringed

Plover (*C. hiaticula*), Kentish Plover (*C. alexandrinus*);

Boyd 1962). These mortality rates are calculated as the

number of individuals that return in year *i* that were known

to be present in year *i* - 1 (Smith and Houghton 1984), and

they presuppose a strong tenacity to the breeding area.

These estimates are supported by a study of the fidelity of

adult Semipalmated Plovers to a fall migration stopover area

which also indicated an annual mortality rate of 44%,

although the authors estimated a lower rate of mortality

(30%) when band loss and reduced search effort were

accounted for. With these mortality rates, it appears that

the majority of adult Semipalmated Plovers in my study that

survive return to the Churchill area in successive years to

breed. With this relatively high rate of adult return, the

low rate of natal philopatry that I found is predicted from

the model of Greenwood and Harvey (1982), although a high

rate of juvenile mortality cannot be excluded as a

contributing factor to low natal return.

Although the ultimate cause of natal dispersal may be

inbreeding avoidance, several proximate causes have been

proposed by others. One explanation for a low rate of

juvenile return in shorebirds is saturation of the breeding

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territories with established conspecifics (Groen 1993). I

find this hypothesis unlikely in Churchill, as some sizeable

areas occupied by successful pairs in one year were not

utilized the next, and therefore the study area did not

appear saturated. Soikkeli (1967) argued that changes in

the climate of central and northern Europe contributed to

lower winter mortality of Dunlin, and that milder spring and

fall weather can account for the observed expansion of the

breeding range of this species in Finland. He also claimed

that when adult philopatry was high, colonization of new

breeding grounds was most likely by birds breeding for the

first time.

If juvenile mortality is high and first year

individuals are no more likely to return to their natal area

than to any other area with suitable habitat, I would expect

a low rate of juvenile return to my study area. Although

posthatch mortality is difficult to observe in precocial

species, data from the 1995 breeding season in Churchill

suggest that juvenile survival from hatch to fledge is

approximately 60% in Semipalmated Plovers (E. Nol unpubl.

data). In other shorebirds, juvenile survival from hatch to

fledge can range from 39-42% in Snowy Plovers

(*C. alexandrinus nivosus*, Warriner *et al.* 1986) to 64% in

Dunlin (Soikkeli 1967), to 82% in Piping Plovers (Haig and

Oring 1988) and 83% in Spotted Sandpipers (Reed and Oring

1993). As annual mortality is higher for young,

inexperienced individuals during their first migration and

winter than it is for adults (Kus *et al.* 1984; Moore and

Sandberg 1994), an expected return rate of 27% (hatch to

fledge survival x adult overwinter survival; 0.60 x 0.45)

for juvenile Semipalmated Plovers banded at hatch might be

high.

Many species of shorebirds exhibit rates of natal

philopatry which are much lower than this, including

Semipalmated Plovers (Appendix 2; Thompson *et al.* 1994).

Several factors may have contributed to an underestimation

of natal return in this study. First, some juveniles banded

in 1988 could have returned in succeeding years but not been

observed as there was a gap in censusing from 1989-1991,

although calculation of natal return for 1992-1995 only is

even lower (0%), so this is unlikely to be a significant

effect. Second, some shorebirds do not migrate north in

their first spring, but instead oversummer and begin

breeding as two year olds (Thompson *et al.* 1994). Although

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age at first breeding is not known for Semipalmated Plovers, two sister species have a median age of first breeding of one year (Ringed Plover, Pienkowski 1984; Piping Plover (*C. melodus*), Wilcox 1959). Even if Semipalmated Plovers do not begin breeding until age two, some birds that had hatched in 1992 and 1993 should have been seen in 1994 and 1995 respectively.

Third, most population studies are necessarily conducted within a finite study area, and the longer the dispersal distance of a juvenile, the less likely that its breeding site will fall within the study area (Baker *et al.* 1995). My study area was bounded to the north by Hudson Bay and to the south by bog and boreal forest, both considered unsuitable nesting and foraging habitat for Semipalmated Plovers. Dispersal would therefore take place primarily in an east/west direction. The maximum observed interyear nest site distance moved by an adult Semipalmated Plover was 1.9 km; almost all possible movements of less than 2 km would result in dispersal to a censused area. Although the study area was restricted to a coastal strip, movements greater than a few kilometers would be more likely to go undetected, and a juvenile need not disperse much farther

than an adult to be missed in censusing. Of the three

possible explanations for the low rate of natal return, high

juvenile mortality and dispersal from the study area are

likely the most influential in my study.

In Semipalmated Plovers, both parents desert the brood

before fledging is complete, and juveniles flock together

before migrating (E. Nol, unpubl. data). It is not known

whether the fall migration, overwintering, and spring

migration occur in family groups, but it appears unlikely.

Spring migration flocks may consist of both experienced and

novel breeders; if the adults are returning to a known area

to breed, the first year individuals migrating with them may

breed there as well. While not familiar with the area, the

new individuals would at least be assured that both suitable

breeding habitat and potential mates are present.

Recruitment into the Semipalmated Plover population at

Churchill is therefore likely by first time breeders, but

not necessarily those hatched in the area.

An advantage of returning to a site would be

familiarity with the area in terms of food resources and

protection from predators. When breeding for the first

time, an individual will only be familiar with areas it

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occupied as a juvenile, and the further it breeds from its natal site, the fewer advantages there will be as a result of familiarity. For Ringed Plovers breeding in Scotland, chicks generally moved no farther than 4 km from their nest site during the fledging period (Jackson 1994). In the following year, 78.9% of those chicks that returned nested less than 4 km from their natal site.

In Churchill, Semipalmated Plover chicks generally moved less than 4 km from their nest site in the 35 days following hatch, although one was observed 9 km and another 12.8 km away (E. Nol, unpubl. data). For juveniles, it would seem that any familiarity with areas further from the nest site must be gained after fledging. Post-fledging dispersal may be highly advantageous in migrants, as time and energy constraints are likely lower at this time than in the following spring (Morton 1992). Habitat variables may also be more accurately assessed during the post-fledging period, especially in sub-arctic and arctic regions such as Churchill, where breeding areas are often covered by snow or water in late May and early June when Semipalmated Plovers begin to arrive (pers. obs.).

Adult philopatry and site tenacity - The dispersal of

offspring from their natal site is often explained as an

inbreeding avoidance mechanism, even though direct evidence

of inbreeding depression is limited in avian systems

(Greenwood *et al.* 1978, van Noordwijk and Scharloo 1981,

Shields 1982, Keller *et al.* 1994). Inbreeding avoidance is

further used as an explanation for sex differences in adult

dispersal, even though it does not provide much insight into

the direction of the bias. If inbreeding avoidance is the

only mechanism maintaining dispersal in juveniles and

adults, then the sex subject to the highest costs of

inbreeding should be the most likely to disperse. In

polygamous mating systems these costs may vary, but in

monogamous species, inbreeding costs should be relatively

similar for males and females (Greenwood 1980).

Except for the Anatidae (which generally have a mate-

defense mating system), in most avian species exhibiting a

monogamous mating system males defend a resource important

to the acquisition of a mate. If familiarity with a

breeding site aids in acquisition, then the costs of male

dispersal should be fairly high, and female biased dispersal

should be the norm (Greenwood 1980, Greenwood and Harvey

1982). In this way sex-biased philopatry is a mechanism for inbreeding avoidance, and the direction of the bias is determined by the mating system (Redmond and Jenni 1982).

Adult Semipalmated Plovers returned to the Churchill study area at rates similar to other socially monogamous shorebirds (Appendix 3). These studies support Greenwood's hypothesis of female biased dispersal, although many report no significant difference in return rates between the sexes (but see Miller 1977, Skeel 1983). A sexual bias not large enough to be seen in return rates of Semipalmated Plovers was observed in the distance moved between successive nest sites. A number of other studies have also found a male bias in nest site tenacity but not philopatry for monogamous shorebirds with a male resource defence system (Holmes 1971, Gratto et al. 1985, Haig and Oring 1988). In these species, females that took a new mate (either through re-pairing or divorce) dispersed significantly farther than males, even though they returned to the general area at similar rates. Oring and Lank (1982) suggest that this greater female movement is caused by usurpation of previous breeding areas and mates by other females. They recognize that this ursurpation may also apply to males, but propose that while

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returning males may face one aggressor on a former

territory, females may face two residents: their former

partner and an ursurping female. This may be one explanation

for the male bias in site tenacity but not philopatry in

Semipalmated Plovers, because although males and females

appeared to arrive at the Churchill study area at the same

time, males were observed on the breeding territories before

females.

In cases where breeding areas are unstable or disturbed

between years, both males and females may not have an

opportunity to return to a study area or previous breeding

site in successive years. In addition, the value of

territory familiarity diminishes with an increase in the

alteration of the site (Jackson 1994). Although the nesting

sites used by Semipalmated Plovers in the Churchill area

were extremely stable from year to year, in two cases nest

sites were heavily disturbed. Construction on gravel roads

around the Churchill Northern Studies Centre in the fall of

1994 destroyed the nestcups and graded the surrounding area

of two pairs of plovers. Although suitable undisturbed

nesting substrate was available within a 300 m radius and

traffic on the roads was no greater than before, none of the

four individuals were resighted in the study area in 1995.

Two species of plovers habitually breed in unstable or unpredictable areas: Piping Plovers breed on ephemeral sand dunes (Haig and Oring 1988) and Ringed Plovers may breed on cropland (Jackson 1994). In these species, nest site destruction was followed by a higher dispersal frequency and greater dispersal distance the following year, but individuals were no less likely to return to the same general breeding area. In the case of Semipalmated Plovers, it is possible that when a traditionally stable nesting area is radically altered, normally philopatric and tenacious individuals will be too disturbed to breed at any site within the study area.

In a relatively stable environment, an individual may increase its chances of reproductive success if it returns to a site where it has previously bred successfully (Darley et al. 1977, Harvey et al. 1979, Gratto et al. 1985, Thompson et al. 1988, Jackson 1994). Few unsuccessful pairs of Semipalmated Plovers returned to the study area, but this was due mainly to the high rate of nest success in 1994. In my study, previous breeding success did not increase the probability of return, nor did it increase the level of site

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tenacity in this species. This appears to be consistent with results for only some shorebirds; in stable environments, previous success affects return rates or site tenacity in many shorebird species (Redmond and Jenni 1982, Gratto et al. 1985, Thompson et al. 1988, Groen 1993, Oring and Lank 1993, Jackson 1994), but not in others (Gratto et al. 1985, Schamel and Tracy 1991, Jackson 1994).

For species breeding in ephemeral or patchy habitats, the effect of success is similarly equivocal (Haig and Oring 1988, Wiens and Cuthbert 1988, Jackson 1994). One explanation for returning to a breeding territory despite previous failure there is that there may be a lack of suitable alternatives, either spatially or temporally. Another is that as the main cause of nest failure is predation, dispersal to a new territory may not decrease the chance of predation enough to balance the cost of unfamiliarity with the new site (Gratto et al. 1985). In addition, Thompson and Hale (1989) suggest that greater philopatry or site tenacity in previously successful birds may be an artifact of better quality individuals having both higher breeding success and higher survival rates.

Although only marginally significant, female

Semipalmated Plovers that changed mates exhibited greater site tenacity if they had been successful than if they had been unsuccessful. Females of several species exhibit a greater tendency to move following reproductive failure (Redmond and Jenni 1982, Thompson and Hale 1989). A tendency for female-biased dispersal following an unsuccessful nesting attempt is not surprising in a species exhibiting male resource-defence. If there are benefits to site tenacity and costs of dispersal are high, these costs would be greater for males, who should be less likely to move regardless of reproductive success.

Since male Semipalmated Plovers exhibited nest site tenacity regardless of pairing status, females would only reunite with their previous mate if they also exhibited high site tenacity. In this way, site tenacity is thought to promote mate fidelity in many migratory species (Soikkeli 1967, Morse and Kress 1984, Gratto et al. 1985, Bradley et al. 1990, Jackson 1994). If the breeding range or suitable breeding habitat covers a relatively large geographical area (as is the case for Semipalmated Plovers), strong breeding site tenacity by both sexes would increase the opportunity for mate fidelity. When males and females arrive on the

breeding grounds synchronously, it can be difficult to determine whether or not a return to a former site is simply a consequence of pairing with a former mate. Experimental destruction of burrows in Leach's Storm-Petrels revealed that mate fidelity was rare when individuals did not have their former burrow as a common reference site (Morse and Kress 1984). Another study showed that pair bond renewal in shags (*Phalacrocorax aristotelis*) was dependent on the female's ability to locate the male on the breeding grounds, and that this was a function of how far the male had moved (Aebischer *et al.* 1995), indicating that mate retention is indeed strongly site dependent.

Mate fidelity - In many species of long-lived monogamous birds, both members of a breeding pair are likely to survive to the next season and the same individuals will often reunite with each other in successive seasons (Coulson 1966, Brooke 1978, Bradley *et al.* 1990). In these cases, biparental care is common, and co-operation between the breeding partners can have considerable influence on the reproductive success of the pair. An increase in the reproductive success of a pair can be attributed to a

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combination of increased age and breeding experience of each individual, as well as increased duration of the pair bond (Coulson 1966, Bradley *et al.* 1990).

In shorter-lived migratory species the annual mortality rate is generally higher, and therefore both members of a pair are less likely to survive to the next breeding season. However, in many species, including Semipalmated Plovers, when both members of a pair are found in the same study area the following year, they are more likely to reunite than divorce. Studies of this phenomenon have shown that when both members of a pair return, the rate of reunion was 67% in Semipalmated Plovers (this study), 62% in Western Sandpipers (Holmes 1971), 72% in Dunlin (Soikkeli 1967), 81% in Semipalmated Sandpipers (Gratto *et al.* 1985), 95% in Willets (Howe 1982), and 100% in Stilt Sandpipers (Jehl 1973). Several of these authors suggested that a high rate of mate fidelity reflects strong site tenacity, and that the adaptive significance is that individuals are more familiar with their territories and mates, facilitating pair formation and nesting. A study of Caspian Terns reported that winter storms and fluctuating water levels result in a low interyear stability of the nesting habitat of this

species. The author suggested that the low annual rate of mate retention (25%) in this species was due to an inability of pairs to return to their previous nesting site (Cuthbert 1985).

If individuals generally reunite with their previous mates, there must be some advantage to doing so. Rowley (1983) argued that advantages can include facilitation of pair bond formation leading to earlier nest initiation and increased hatching success, and a certainty that both members will have at least some breeding experience. Coulson (1966) found that in Kittiwake Gulls, a change of mate led to a later date of nest initiation. This was true even of experienced individuals breeding with novel but equally experienced mates, so the delay in laying was not due to the lack of cumulative breeding experience. A change of mate in kittiwakes also resulted in lower fledging success. This effect was found in individuals that changed mates because their former partner was not present as well as those individuals which divorced; lower success therefore appears (at least in this species) to be a result of the change of mate and not a function of the method of change.

Dunlin that retained their previous mates nested

earlier and had greater survival of chicks after hatch than did pairs that changed mates (Soikkeli 1967). Short-tailed Shearwaters had a decrease in hatch success with novel mates (Bradley et al. 1990), and in one of four years, reunited Semipalmated Sandpiper pairs nested significantly earlier than remated or divorced pairs (Gratto et al. 1985).

In my study, reunited pairs of Semipalmated Plovers had earlier nest initiation and higher hatching success in 1995 but not in 1994. Some studies have found that low mean temperatures or high variability in the weather at the breeding grounds can delay nest initiation (Soikkeli 1967, Cowardin et al. 1985, North and Ryan 1988); this might further retard pair formation between unfamiliar individuals. Mean daily temperatures at Churchill were generally higher in 1994 from time of arrival through the laying period, but the weather during this time was not any less variable in 1994 than in 1995.

Soikkeli (1967) noted that in Finland, there was a distinct rise in mean daily temperature of 6-9°C a few days before the commencement of egg-laying. In 1994, the mean day of the start of egg-laying at Churchill was day 156 for both reunited pairs and new mate pairs. Prior to that,

there were five consecutive days of mean temperatures greater than 5°C. In 1995, of the five days prior to commencement of egg-laying in reunited pairs (day 158) and new mate pairs (day 160.5), only one had a mean temperature greater than 5°C. It is possible that if the weather just prior to egg-laying is favourable, there may be no delay in initiation for novel pairs of Semipalmated Plovers, and that a selective advantage to reunited pairs will only be apparent in years with less than optimal weather during the initiation period.

Occasionally, Semipalmated Plover pairs which lost their nests early in the season renested with the same mate in the same area as the original nest. In these cases, an unsuccessful nesting attempt did not precipitate pair divorce or a decrease in site tenacity within a season. It has been suggested that intrayear mate fidelity provides for rapid renesting and higher reproductive success; individuals do not have to invest time in acquiring new sites and mates (Soikkeli 1967, Haig 1987). Piping Plovers that retained their mates renested sooner and had higher hatching and fledging success than birds which chose new mates. In this species intrayear territory switching was common, likely due

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to the creation of new territories because of storms and evaporation of lakes (Haig and Oring 1988). The frequency of mate change is also low in renesting Kentish Plovers in Hungary, although intrayear dispersal is high, possibly due to the ephemeral nature of the breeding sites (Szekely and Lessells 1993).

I suggest that intrayear site and mate retention in Semipalmated Plovers is obligatory, and reflects a shortage of time and lack of opportunities for acquisition of a new mate or site in the middle of the breeding season. Few unpaired males or females were observed on the breeding areas in Churchill after the first week of incubation, and as nest losses did not occur synchronously, the opportunity for mate switching was low. It is difficult to assess whether suitable alternative nesting sites were available, but territories were not lost to storms or flooding, and no new suitable areas were created through evaporation of ponds or lakes, as was the case for the Piping Plovers.

Divorce - Even though annual reuniting is common among Semipalmated Plovers nesting at Churchill, divorce does occur between almost one-third of all pairs in every year.

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Given that, at least in some years, mate fidelity provides an advantage in terms of hatching success, it is interesting to examine the conditions under which both individuals of a pair return to the breeding area but do not reunite. Some studies have suggested that when reproductive failure occurs, active pair-bond termination may be used to enhance future reproductive success. Divorce is more prevalent among pairs that were previously unsuccessful in Piping Plovers (Haig and Oring 1988; Wiens and Cuthbert 1988), Redshanks (Thompson et al. 1988), Short-tailed Shearwaters (Bradley et al. 1990), Kittiwake Gulls (Coulson 1966), and Manx Shearwaters (Brooke 1978).

In my study, there was no such tendency for unsuccessful pairs to divorce the following year, but as nesting success was very high in 1994, the sample size for unsuccessful nesting is too small for meaningful analysis. In one other study of sub-arctic breeding shorebirds, there was no effect of nesting success on subsequent mate fidelity (Semipalmated Sandpiper, Gratto et al. 1985). It may be possible that in species with temporally constrained breeding seasons, an individual will return to a previous mate if it is present regardless of prior success, as it

would at least be assured of some breeding experience and a certain level of compatability (i.e. at least initiated a nest in the previous year).

A pair may not necessarily have had to experience breeding failure for divorce to be selectively advantageous if an individual can be assured that its new mate or site is of higher quality than its old one. Other than knowledge of previous reproductive success, morphological characteristics are a good measure of mate quality, because in an environment where time for mate assessment is brief, a choice must be made according to information which is instantly assessable (Sullivan 1994). Assessment of site quality is difficult, but horizontal visibility has been shown to be important for species with precocial young (Sullivan Blanken 1996).

Few studies have directly compared the pre- and post-divorce quality of mates and sites. Jones and Montgomerie (1991) found that interyear fidelity in Least Auklets was related to male, but not female ornamentation; males with larger facial plumes were more likely to reunite than males with smaller plumes. They suggested that female auklets were divorcing males on the basis of plumage or some other

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character with which plumage was associated, but the authors
did not compare the relative improvement in a female's
choice of mate. Morse and Kress (1984) reported that
Leach's Storm-Petrels were more likely to divorce following
experimental burrow destruction between breeding seasons.
However, this mainly indicates that mate retention is highly
site-dependent, and does not necessarily signify that the
new site is of higher quality than the old, undisturbed
site.

Semipalmated Plovers were not more likely to gain a
mate or site of higher quality following a divorce.
However, when both individuals of a pair return to the
breeding area, it is likely that reproductive decisions are
made on the basis of current quality. Therefore a
comparison of the pre-divorce mate or site in the previous
year to the post-divorce mate or site in the current year
may not be the most accurate indicator of relative
improvement in quality. Although not available, an analysis
of current quality of both pre- and post-divorce mates and
sites might reveal an increase in quality. However, this
seems unlikely as there was no detectable difference in the
plumage or body condition of an individual from year to

year, nor did I observe much difference in the quality of site chosen by an individual between years.

In some species, pair divorce may be a result of differential arrival times on the breeding grounds (Soikkeli 1967). Arrival of Semipalmated Plovers at Churchill appeared relatively synchronous, but as time between arrival and laying of the first egg was relatively short, a delay in arrival of even a day or two by one partner could conceivably result in divorce of the pair. Waiting for the potential non-return of a dead mate may mean lost opportunities for re-pairing, particularly in short-lived species (Rowley 1983). It is also possible that an individual may actively divorce to avoid reuniting with a mate that previously engaged in extra-pair copulations (male divorcing a female) or withheld a portion of parental care to become bigamous (female divorcing male; Linden 1991). Although no incidences of bigamy were ever observed in Churchill, extra-pair copulations between banded individuals were seen on two occasions. The former could be tested by rigorous behavioural observations and the latter through genetic analysis of parental investment.

CONCLUSIONS

In the area around Churchill, Manitoba, the majority of adult Semipalmated Plovers that survived migration and overwinter returned to the area in successive years to breed. Greenwood's (1980) theory of sex-biased dispersal states that in a species with a male resource defence mating system, dispersal should be female-biased. Similar to most monogamous shorebirds, there was no evidence for this in return rates of Semipalmated Plovers, although males did return at slightly higher rates. In his review of mating systems and dispersal, Greenwood did not make a distinction between philopatry and site tenacity. Indeed some of his examples of dispersal are given in terms of territory-widths moved, a measurement often equated with site tenacity in the literature. On this scale, as with most other shorebirds, Semipalmated Plovers provide support for Greenwood's theory; male Semipalmated Plovers, whether with the same or a new mate, return to the same nest site in successive years, whereas females which re-pair or divorce disperse a significantly greater distance. Females, but not males, also have a tendency to move following reproductive failure.

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Whether or not this movement of female Semipalmated Plovers is due to the active choice of a new site or mate is difficult to determine from this study. Neither females nor males appeared to significantly improve the quality of their site or mate following divorce, and my sample size was not large enough to discover if either sex enhanced its reproductive success after divorce. Determination of the costs and benefits of both mate fidelity and divorce is needed for a full understanding of why divorce occurs; this may require experimental studies employing mate removal to create vacancies and increase intrasexual competition, reduction or enhancement of clutch size to alter perceived reproductive success, or manipulation of mate and/or site quality. This information is likely to be both species-specific and dependent on the particular life-history of the population (Choudhury 1995).

Information on site and mate fidelity in shorebirds is considerable, but due to the generally prohibitive cost of work in the North, most research to date has been on temperate nesting species. The sub-arctic breeding habitat of Semipalmated Plovers may impose additional temporal constraints on reproductive decisions. In many species of

shorebirds, reproductive failure is associated with an
increased rate of pair divorce as well as a decrease in site
tenacity. The lack of this association in Semipalmated
Plovers may be a result of temporal pressure; time between
arrival and nest initiation is very short. Individuals may
return to a familiar territory rather than expend time
establishing a novel one, and to a familiar mate as time for
assessment of a new one is limited. Mate quality may
instead be improved through extra-pair copulations during
the nest initiation period (Sullivan 1994).

Some research on shorebird site and mate fidelity has
been initiated due to habitat loss or disturbance, and
consequent decline of the populations concerned (Piping
Plover, Haig and Oring 1988, Wiens and Cuthbert 1988; Black-
tailed Godwit *Limosa l. limosa*, Groen 1993; Lapwing *Vanellus
vanellus*, Thompson *et al.* 1994). Although the breeding
habitat of Semipalmated Plovers at Churchill, Manitoba is
currently relatively stable, the additive stress of a large
scale disturbance may be considerable when this species is
already subject to temporal pressures. Disturbances such as
loss of migratory staging areas, climatic change, and
development of northern natural resources are not

inconceivable.

Studies of dispersal, such as this one, are important
not only because they may allow us to predict some of the
consequences of habitat change, but also because they
contribute to a greater understanding of the parameters that
provide stimuli to and control of dispersal. This is
fundamental to the definition of a population, and can
influence a wide range of other research, including areas
such as ecological genetics and speciation, evolution in
Mendelian populations, and metapopulation dynamics.

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Appendix 1. Regression equation ($R^2=0.86$) for estimating
hatch date of a Semipalmated Plover nest from egg specific
gravity (S. Board, unpubl. data).

Index of specific gravity of an egg:

$$ISG = \frac{mass}{(length)(width)^2}$$

Estimation of hatch date for a nest:

mean ISG = 4.38 + 0.0261 days to hatch

SE=0.013

Appendix 2. Return rates of juvenile shorebirds (Charadriiformes) to the area in which they were banded. All studies are of three or more years duration (after Thompson et al. 1994).

Species	Number banded	Number returned	Percent returned	Source
Charadrius hiaticula	42 *	24	57.1	Pienkowski 1984
C. melodus	979 *	34	3.5	Wilcox 1959
	90 *	11	12.2	Haig and Oring 1988
C. alexandrinus	1220	68	5.6	Rittinghaus 1956
C. montanus	229	2	0.9	Graul 1973
C. semipalmatus	259	1	0.4	This study
Pluvialis apricaria	54 *	31	57.4	Parr 1980, 1992
Vanellus vanellus	481 *	208	43.2	Thompson et al. 1994
	90 *	20	22.2	Thompson et al. 1994
Calidris pusilla	770	35	4.5	Gratto 1988
C. mauri	185	7	3.8	Holmes 1971
C. temminckii	328	25	7.6	Hilden 1979
	134	8	6.0	Breiehagen 1989

C. alpina	448	16	3.6	Heldt 1966
	511	57	11.2	Soikkeli 1970
	144	24	16.7	Jonsson 1991
Limosa limosa	243	0	0	Jonas 1979
Numenius phaeopus	135	2	1.5	Skeel 1983
N. americanus	270	11	4.1	Redmond and Jenni 1982, 1986
Tringa totanus	754	24	3.2	Grosskopf 1959, 1968
Actitis hypoleucos	457	19	4.2	Holland and Yalden 1991
A. macularia	256 •	27	10.5	Oring *et al.* 1983
	263 •	44	16.7	Alberico *et al.* 1992
Phalaropus tricolor	149	10	6.7	Colwell *et al.* 1988
P. lobatus	108	10	9.3	Hilden and Vuolanto 1972
	555	28	5.0	Reynolds and Cooke 1988
	323	32	9.9	Schamel and Tracy 1991

• chicks banded as fledglings

Appendix 3. Return rates of socially monogamous adult shorebirds (Charadriiformes) to the area in which they were banded in the year following banding.

Species	%Return		n	Reference
	Female	Male		
Charadrius melodus	56	75	57	Haig and Oring 1988
C. semipalmatus	40	51	132	This study
Vanellus vanellus	55	65	300	Thompson et al. 1994
Numenius phaeopus	38	59	51	Skeel 1983
N. americanus	69	71	43	Redmond and Jenni 1982
Tringa totanus	69	71	192	Grosskopf 1959
Calidris himantopus	50	50	42	Jehl 1973
C. alpina	71	77	323	Soikkeli 1970a, 1970b
C. pusilla	44	47	522	Gratto et al. 1985
C. mauri	40	50	105	Holmes 1971
C. minutilla	38	65	50	Miller 1977