

Ecological correlates of mate fidelity in two Arctic-breeding sandpipers

Brett K. Sandercock, David B. Lank, Richard B. Lanctot, Bart Kempenaers, and Fred Cooke

Abstract: Monogamous birds exhibit considerable interspecific variation in rates of mate fidelity between years, but the reasons for this variation are still poorly understood. In a 4-year study carried out in western Alaska, mate-fidelity rates in Semipalmated Sandpipers (*Calidris pusilla*; mate fidelity was 47% among pairs where at least one mate returned and 94% among pairs where both mates returned) were substantially higher than in Western Sandpipers (*Calidris mauri*; 25 and 67%, respectively), despite the similar breeding biology of these sibling species. Divorce was not a response to nesting failure in Western Sandpipers, and mate change had no effect on the reproductive performance of either species. Nor were mate-fidelity rates related to differential rates of breeding dispersal, because the species did not differ in site fidelity. Reunited pairs and males that changed mates showed strong site tenacity, while females that changed mates moved farther. Differences in local survival rates or habitat are also unlikely to explain mate fidelity, since the two species did not differ in local survival rates, ϕ (Western Sandpipers: $\hat{\phi} = 0.57 \pm 0.05$ (mean \pm SE), Semipalmated Sandpipers: $\hat{\phi} = 0.66 \pm 0.06$), and they bred in the same area, sometimes using the same nest cups. Although we were able to reject the above explanations, it was not possible to determine whether mate retention was lower in Western Sandpipers than in Semipalmated Sandpipers because of interspecific differences in mating tactics, time constraints imposed by migration distance, or a combination of these factors. Western Sandpipers exhibited greater sexual size dimorphism, but also migrated for shorter distances and tended to nest earlier and more asynchronously than Semipalmated Sandpipers. Finally, we show that conventional methods underestimate divorce rates, and interspecific comparisons may be biased if breeding-dispersal and recapture rates are not considered.

Resumé : Les oiseaux monogames font preuve d'une variation interspécifique considérable de leur fidélité à un partenaire d'une année à l'autre et les causes de cette variation sont toujours mal comprises. Au cours d'une étude de 4 ans dans l'ouest de l'Alaska, les taux de fidélité au partenaire mesurés chez des Bécasseaux semipalmés (*Calidris pusilla*; 47 % des couples dont au moins l'un des partenaires est revenu et 94 % dont les deux partenaires sont revenus) se sont avérés plus élevés que ceux mesurés chez l'espèce-soeur, le Bécasseau d'Alaska (*Calidris mauri*; 25 et 67 %, respectivement), en dépit de la similitude de la biologie de leur reproduction. Le divorce n'est pas une réaction à l'insuccès de la nidification chez le Bécasseau d'Alaska et le changement de partenaire n'a pas d'effets sur la performance de reproduction, ni chez l'une, ni chez l'autre des deux espèces. La fidélité n'est pas non plus reliée à des taux différentiels de dispersion pour la reproduction, puisque les deux espèces manifestent la même fidélité à un site. Les couples reformés et les mâles qui changent de partenaire ont une fidélité tenace au site alors que les femelles qui changent de partenaire s'en éloignent. Des différences dans le taux de survie enregistré localement et l'habitat sont également des facteurs peu probables de fidélité au partenaire puisque les taux de survie enregistrés localement ne diffèrent pas chez les deux espèces (Bécasseau d'Alaska: $\hat{\phi} = 0,57 \pm 0,05$ (moyenne \pm erreur type), Bécasseau semipalmé: $\hat{\phi} = 0,66 \pm 0,06$) et que celles-ci se reproduisent dans la même région, utilisant parfois des nids posés sur le même support. Nous avons pu réfuter toutes ces explications, mais il n'a pas été possible de déterminer si la fidélité au partenaire est plus faible chez le Bécasseau d'Alaska à cause de différences interspécifiques dans les stratégies d'accouplement, à cause de contraintes temporelles imposées par la distance de migration ou à cause de ces facteurs combinés. Le dimorphisme sexuel est plus important chez le Bécasseau d'Alaska, mais cet oiseau migre aussi sur de plus courtes distances et sa période de nidification est plus hâtive et moins synchronisée que celle du Bécasseau semipalmé. Enfin, nous

Received April 13, 2000. Accepted July 19, 2000.

B.K. Sandercock.¹ Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada, and Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3110, U.S.A.

D.B. Lank and F. Cooke. Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

R.B. Lanctot. U.S. Geological Survey, Biological Resources Division, Alaska Biological Science Center, 1011 East Tudor Road, Anchorage, AK 99503, U.S.A.

B. Kempenaers. Research Center for Ornithology of the Max Planck Society, P.O. Box 1564, D-82305 Starnberg (Seewiesen), Germany.

¹Author to whom all correspondence should be sent at the following address: Centre for Applied Conservation Biology, Department of Forest Sciences, The University of British Columbia, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada (e-mail: bsandercock@interchange.ubc.ca).

démonstrons que les méthodes classiques sous-estiment la fréquence des divorces et que les comparaisons interspécifiques peuvent n'être pas valides si la dispersion de reproduction et les taux de recapture ne sont pas pris en compte.

[Traduit par la Rédaction]

Introduction

Mate fidelity from one breeding season to the next is generally found in long-lived, iteroparous animals that are socially monogamous. Extended pair bonds have been reported in all vertebrate groups, including fishes (Fricke 1986; Reavis and Barlow 1998), reptiles (Bull 1988), and mammals (Clutton-Brock 1989), but inter- and intra-specific variation in rates of mate-fidelity among birds has received the most attention (for reviews see Rowley 1983; Ens et al. 1996). A range of hypotheses have been offered to account for variation in mate-fidelity rates (Choudhury 1995; Black 1996), and these ideas can be grouped into direct and indirect explanations (termed adaptive and nonadaptive by Dhondt and Adriaensen 1994). Direct explanations predict that reproductive performance will improve subsequent to mate change, possibly because divorcing pairs were initially unsuited (termed the incompatibility hypothesis by Coulson 1972), or because one mate leaves for a better breeding situation with a higher quality individual or site (termed the better option hypothesis by Ens et al. 1993). Divorce can also be a consequence of dispersal following breeding failure (Oring and Lank 1984; Ens et al. 1996). Indirect hypotheses relate mate-fidelity rates to other features of avian life histories, including mortality rates (McNamara and Forslund 1996), habitat preferences (Haig and Oring 1988; Cézilly and Johnson 1995), and aspects of migration (Dhondt and Adriaensen 1994; Rees et al. 1996). Testing these hypotheses has proved difficult because exclusive predictions are not always possible, and because past methods used for estimating divorce rates are problematic.

Migratory birds that breed in the Arctic provide a tractable study system for investigating variation in mate-fidelity rates because reproductive decisions are time-constrained. Local breeding conditions are suitable for only a short period, and the probability of completing southward migration probably declines with later timing of departure. Thus, migration distance is likely to affect reproductive decisions, including mate choice (Myers 1981; Williams and Rodwell 1992; Rees et al. 1996). Mate fidelity may confer an advantage if it reduces the time costs of searching for and courting a mate (Slagsvold and Dale 1991; Rees et al. 1996). On the other hand, waiting for a previous partner to return may not be a viable strategy if later breeding is disadvantageous or adult mortality rates are high, and individuals risk not breeding at all if they fail to obtain a new mate early on (Olsson 1998; Bried et al. 1999). Mortality rates may have little effect on mate fidelity, however, if divorce has a substantial negative effect on reproductive performance (McNamara and Forslund 1996).

In this paper, we examine the ecological correlates of mate fidelity in two Arctic-breeding shorebirds: Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*Calidris pusilla*). These sibling species differ substantially in divorce rates (see Results), despite their similar breeding biology. Both species are monogamous, females usually produce one clutch of four eggs, the two sexes share incubation duties,

and males provide most parental care after hatching (Gratto-Trevor 1991, 1992; Sandercock 1997; Sandercock et al. 1999). The sexes differ in their wintering range and timing of migration: males tend to winter farther north and arrive on the breeding grounds before females (Butler et al. 1987; Gratto-Trevor 1992; Harrington and Haase 1994). As in other monogamous sandpipers, pairs reunite on breeding territories (Soikkeli 1967; Miller 1979) and unmated males use aerial courtship displays to attract mates (Lanctot et al. 2000).

Two-species comparisons have been discouraged because an effective sample size of 2 offers limited inference (Garland and Adolph 1994). We have pursued this approach despite its shortcomings because our application of an identical methodology to two species facilitated controlled comparisons, and because future comparative analyses will require the demographic information presented here. Our study had three aims: to test whether such factors as prior nesting success and change in reproductive performance directly affect persistence of pair bonds, to evaluate indirect explanations based on differences in annual mortality rates, habitat, and features of migration, and last, to evaluate sources of bias associated with measuring mate-fidelity and survival rates. In many studies, non-returning birds are assumed to have died but they may not have been detected if they dispersed or eluded capture. To account for these factors and possible sexual differences, movements of banded birds were used to measure breeding-site fidelity, and mark-recapture statistics were used to determine local survival and recapture rates (Lebreton et al. 1992; Burnham and Anderson 1998).

Methods

Study area and field methods

Breeding populations of Western Sandpipers and Semipalmated Sandpipers were studied at a 4-km² study site 21 km east of Nome, Alaska (64°20'N, 164°56'W), from May to July in 1993–1996. The study area was a heterogeneous mixture of low tundra ridges, mud flats, and shallow freshwater ponds, and was part of a large continuous region of suitable habitat around Safety Sound, a large estuary formed by three river drainages.

Breeding sandpipers were captured with walk-in traps placed over the nest, and individually marked with combinations of coloured leg bands and a numbered metal band (Western Sandpipers: $N = 83$ –147 per year; Semipalmated Sandpipers: $N = 47$ –113 per year). Loss of metal bands was never observed. Breeding sandpipers were sexed by behaviour (e.g., courtship displays, copulatory position) and culmen length (Sandercock 1998a). Mist nets were also used to capture sandpipers from premigratory flocks at the end of the breeding season (Western Sandpipers: $N = 185$ –837 per year; Semipalmated Sandpipers: $N = 51$ –135 per year). These birds received a numbered metal band and a dark green flag, and provided information on migration routes and wintering areas of these populations.

To determine mate-fidelity rates, we examined mated pairs of marked birds where at least one partner returned to the study site the following year. The term mate change is used when one member of the pair returned and mated with a new individual. In this sample, mate change may have been caused by absence of a mate that died or to undetected divorce if a previous mate was not recap-

Table 1. Mate-fidelity rates among pairs of Western Sandpipers and Semipalmated Sandpipers at Nome, Alaska (N is the number of pairs).

Species and year	At least one mate returned				Both mates returned		
	% that changed mates ^a	% that divorced ^b	% that reunited ^c	N	% that divorced ^b	% that reunited ^c	N
Western Sandpiper							
1993–1994	48.3	24.1	27.6	29	46.7	53.3	15
1994–1995	74.2	3.2	22.6	31	12.5	87.5	8
1995–1996	62.9	11.4	25.7	35	30.8	69.2	13
Total	62.1	12.6	25.3	95	33.3	66.7	36
Semipalmated Sandpiper							
1993–1994	42.3	3.9	53.9	26	6.7	93.3	15
1994–1995	44.4	3.7	51.9	27	6.7	93.3	15
1995–1996	70.6	0	29.4	17	0	100	5
Total	50	2.9	47.1	70	5.7	94.3	35

^aOne bird returned and mated with a new individual.

^bBoth members of a pair returned and each mated with a new individual.

^cBoth members of a pair returned and reunited.

tured. The terms divorced and reunited are used to describe pairs where both members returned but each mated with different or the same individual, respectively. Within-season mate-fidelity rates were not considered because renests were rare (0.6%, or 2 of 345 nests in 1993–1995).

To assess the reproductive performance of sandpipers, nests were located by observing sandpipers that flushed or used distraction behaviour. Nest locations were plotted on high-resolution aerial photographs (scales 1:1250 – 1:1600) in relation to microtopographical features; the accuracy of this method was ± 5 m. The date of clutch initiation was calculated by back-dating from egg laying (0.8 eggs/day), stage of incubation (20 or 21 days), or date of hatching (Sandercock 1998b). For nests found during laying, clutch size was determined by revisiting the nest until the egg number remained unchanged. Egg length (L) and breadth (B) were recorded with calipers; egg volume (V) was estimated using $V = 0.47LB^2$ (B.K. Sandercock, unpublished data). Nests were visited every 6–7 days during incubation, and daily around the expected date of hatching. Nest fate was defined as either successful, when at least one chick was observed to have left the nest, or unsuccessful, when the eggs were abandoned or disappeared before the expected hatching date, often with signs of predation (Sandercock 1998b). After the young left the nest, locations of the nest cups were marked with small sticks to allow comparison of nest sites from year to year.

Statistical analyses

In analyses of mate fidelity, pairing events in different years were considered to be independent because the sexes winter at different latitudes and reunite anew each spring. To explore the proximate causes of divorce, mate fidelity was examined in relation to the success of first nests, or second nests if a pair renested. Precocial sandpiper young were mobile and highly cryptic, and it was not possible to determine survival of nestlings until fledging. To investigate the influence of mate fidelity on reproductive performance, years were pooled, one record was selected at random for each individual with respect to pair status, and reproductive information was compared among first nesting attempts. Timing of clutch initiation varied annually, but modal clutch size and egg volume did not (Sandercock et al. 1999). Thus, in analyses of breeding performance following mate change, clutch-initiation dates were adjusted by subtracting the median annual laying date specific to each species. Analyses of egg size were based on mean egg volume per clutch because eggs laid by individual females were not independent observations.

Most statistical analyses were performed with SAS procedures (version 6.12; SAS Institute Inc. 1990). Data were tested for normality, and contingency or nonparametric tests were used where appropriate. Single-classification nonparametric tests were calculated using χ^2 approximations (Proc NPARIWAY). All tests were two-tailed and considered significant at probability levels < 0.05 ; all means are presented ± 1 SE.

Mark–recapture statistics were used to calculate survival rates for the two species of sandpipers. Limited data precluded the use of multistate models that incorporated information on nesting success or pair-bond status. Instead, individual capture histories were coded using two criteria: captured as a breeder attending a nest (1) or not detected (0). In general, the probability of capturing a returning bird was the product of the true survival rate (S), the rate of site fidelity (ψ), the probability of breeding (γ), the probability of finding a nest (ω), and the probability of capture (c) once a nest was detected. Local survival ($\phi = S \cdot \psi$, also termed apparent survival) and recapture rates ($p = \gamma\omega c$) were estimated separately for each species with the program MARK (version 1; White 1999), following the information–theoretic approach discussed by Burnham and Anderson (1998).

First, a global model that included sex and annual variation in ϕ and p was developed (i.e., the Cormack–Jolly–Seber model, $\phi_{\text{sex} \times t}, p_{\text{sex} \times t}$). Age structure was not included because the age of sandpipers was usually unknown. Goodness of fit to this global model was calculated using a bootstrap method that generated a distribution of expected deviances under the assumptions of no heterogeneity and full independence ($N = 1000$ simulations). This procedure tested whether or not our data met the assumptions of mark–recapture methods. An overdispersion factor (\hat{c}) was calculated by dividing the observed deviance of the global model by the mean expected deviance. Second, reduced models were constructed with the logit-link function. Relative model fit was assessed with a modified version of Akaike's Information Criterion (AIC) that included correction factors for overdispersion and small sample size (quasi-AICc (QAICc)). Models were equally parsimonious if the difference in QAICc from the best fit model was ≤ 2 . To obtain annual estimates of $\hat{\phi}$ and \hat{p} , model parameters were weighted by Akaike weights (w), and model averaging was used to calculate parameters and an unconditional variance that included model uncertainty (Burnham and Anderson 1998). To obtain overall estimates of $\hat{\phi}$ and \hat{p} , a variance-components procedure was applied to the global model ($\hat{\beta}$). The program CONTRAST (Hines and Sauer 1989) was used to make post-hoc comparisons of these parameters.

Table 2. Coefficients of variation (CV) in laying dates of Western Sandpipers and Semipalmated Sandpipers at Nome, Alaska (Julian date 139 = May 20).

Year	Western Sandpiper			Semipalmated Sandpiper			P^a	
	Median laying date (range)	CV	N	Median laying date (range)	CV	N	Median	Variance
1994	139.5 (134–159)	3.65	54	149.0 (138–158)	3.63	54	<0.001	>0.7
1995	143.0 (132–165)	5.16	49	147.0 (138–162)	4.62	53	<0.02	>0.5
1996	142.0 (134–155)	3.87	62	148.5 (144–156)	1.83	22	<0.001	<0.001

Note: Values in parentheses are ranges.

^aSignificance of medians and variances tested using Mann–Whitney U tests and variance-ratio tests.

Table 3. Change in breeding performance of Western Sandpipers and Semipalmated Sandpipers in relation to pairing status (mean \pm SE or frequency).

Pairing status	Western Sandpipers			N	Semipalmated Sandpipers			N
	Change in residual laying date (days) ^a							
Male changed mate	–0.3 \pm 0.9			35	–1.0 \pm 0.9			23
Female changed mate	–1.4 \pm 1.0			36	–0.2 \pm 2.0			12
Pair was reunited	–0.1 \pm 1.3			18	–0.2 \pm 1.1			26
	Change in clutch size (%)							
	–1 egg	0 eggs	+1 egg		\leq –1 egg	0 eggs	+1 egg	
Male changed mate	5.3	84.2	10.5	38	25.0	62.5	12.5	24
Female changed mate	2.6	92.3	5.1	39	14.3	64.3	21.4	14
Pair was reunited	0.0	94.4	5.6	18	10.7	71.4	17.9	28
	Change in mean egg size (cm ³)							
Male changed mate	–0.00 \pm 0.10			38	–0.15 \pm 0.13			24
Female changed mate	–0.00 \pm 0.04			39	0.02 \pm 0.05			14
Pair was reunited	0.14 \pm 0.09			18	–0.07 \pm 0.06			28

^aThe residual laying date was calculated by subtracting the mean laying date specific to each species. Positive values indicate that laying date advanced or egg size increased.

Results

Mate-fidelity rates

In pairs where at least one mate returned, Semipalmated Sandpipers retained mates at higher rates (range of annual rates 29.4–53.9%) than did Western Sandpipers (22.6–27.6%; Table 1). The difference between the species was significant (logistic analysis, species: $\chi^2_1 = 6.2$, $P < 0.02$), and the proportion of pairs that changed mates or divorced did not vary annually (year: $\chi^2_2 = 1.7$, $P > 0.4$; interaction: $\chi^2_2 = 1.8$, $P > 0.4$). However, mate change among pairs where one bird returned could have resulted from either the death or the absence of a mate, or by divorce. If the sample was restricted to pairs where both members were known to have returned, Semipalmated Sandpipers still had significantly higher mate-fidelity rates (93.3–100.0%) than Western Sandpipers (53.3–87.5%; species: $\chi^2_1 = 3.9$, $P < 0.05$). The proportion of reuniting pairs did not vary annually (year: $\chi^2_2 = 0.9$, $P > 0.6$; interaction: $\chi^2_2 = 0.9$, $P > 0.6$). In this sample, mate change was by divorce only.

Reproductive performance

Western Sandpipers and Semipalmated Sandpipers bred sympatrically at Nome, Alaska. Nests of the two species were interspersed throughout the study area, and were found on low tundra ridges adjacent to foraging areas on the margins of shallow freshwater ponds. Semipalmated Sandpipers started nesting significantly later than Western Sandpipers in

all years, and the difference in timing averaged 4–10 days (Table 2). Semipalmated Sandpipers tended to nest more synchronously than Western Sandpipers, although the difference was significant in only 1 of 3 years.

Interseason divorce was observed in 12 of 36 pairs of Western Sandpipers and 2 of 35 pairs of Semipalmated Sandpipers (Table 1). Breeding failure was not the proximate cause of divorce in Western Sandpipers. Contrary to our expectation, divorcing pairs had rates of nesting success in the previous year that were higher (90.9%, $N = 11$) than those of pairs that eventually reunited (62.5%, $N = 24$), although the difference was not significant (Fisher's exact test, $P = 0.12$).

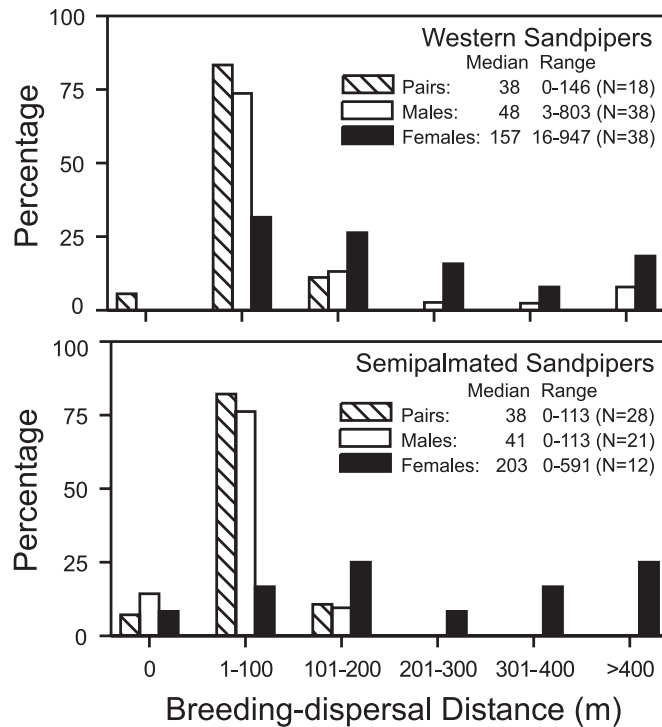
Direct hypotheses accounting for mate fidelity could be supported if birds changing mates had earlier laying dates, bigger clutches, or larger eggs. However, the mean change in laying dates of birds that switched mates was not significantly different from that of pairs that reunited (matched-pairs ANOVA, pairing status: $F_{[2,144]} = 1.6$, $P > 0.1$; species: $F_{[1,144]} = 1.9$, $P > 0.1$; interaction: $F_{[2,144]} = 0.3$, $P > 0.7$; Table 3). Clutch size was significantly more variable in Semipalmated Sandpipers than Western Sandpipers, with a greater number of individuals laying fewer or more eggs than in their previous clutch (logistic analysis, species: $\chi^2_2 = 10.3$, $P < 0.01$; see also Sandercock et al. 1999). Nonetheless, changes in clutch size were not related to either pairing status ($\chi^2_2 = 1.5$, $P > 0.8$) or an interaction between status and species ($\chi^2_4 = 1.0$, $P > 0.9$; Table 3). Finally, differences between mean egg size in pairs that changed mates were not

Table 4. Quasi-Akaike Information Criterion (QAIC_c) values for maximum-likelihood models of local survival (ϕ) and probability of recapture (p) of Western Sandpipers ($N = 152$ females and 144 males) and Semipalmated Sandpipers ($N = 122$ females and 108 males).

Model for ϕ	Western Sandpipers					Semipalmated Sandpipers				
	$s \times t$	$s + t$	s	t	c	$s \times t$	$s + t$	s	t	c
$s \times t$	12	9.9	7.8	7.8	5.8	9.9	7.8	5.9	5.7	3.8
$s + t$	10.2	6.2	4.3	4.2	2.3	8	3.9	2.1	1.9	0.0
s	9.1	5.3	3	3.2	1	7	2.9	10.6	0.8	8.7
t	8.2	4.2	2.7	3.3	1.2	8.6	5.1	4.3	6.9	5
c	7.3	4.2	1.5	2.3	0	8.1	4.6	13.1	5.7	13.6

Notes: QAIC_c values include correction terms for small sample size and overdispersion (Western Sandpipers: $\hat{c} = 1.56$, Semipalmated Sandpipers: $\hat{c} = 1.00$), and are expressed as deviations from the best fit model. Best fit ($\Delta\text{QAIC}_c = 0$) and equally parsimonious models ($\Delta\text{QAIC}_c \leq 2$) are shown in boldface type; s is sex effects, t is time or annual variation, c is a constant, \times denotes a model with interaction, and $+$ denotes an additive or main-effects model.

Fig. 1. Distribution of distances between nesting attempts in consecutive years for pairs of Western Sandpipers and Semipalmated Sandpipers that reunited, males that changed mates or divorced, and females that changed mates or divorced.



significantly different from those in reuniting pairs (matched-pairs ANOVA, pairing status: $F_{[2,155]} = 0.9, P > 0.4$), nor did the differences vary between sandpipers (species: $F_{[1,155]} = 2.2, P > 0.1$; interaction: $F_{[2,155]} = 0.7, P > 0.4$; Table 3).

Breeding-site fidelity

Years were pooled to examine the effects of pairing status on breeding-dispersal distance. Pairing status had a significant effect on the distances moved by sandpipers in consecutive years (Kruskal–Wallis test, Western Sandpipers:

$\chi^2_2 = 20.4, P < 0.001$; Semipalmated Sandpipers: $\chi^2_2 = 11.0, P < 0.005$). Females that changed mates or divorced moved significantly farther than those that reunited with the same mate, whereas males that changed mates or divorced did not move farther than reuniting pairs (Fig. 1). When pairing status was controlled for, breeding-dispersal distances did not differ between the species (Mann–Whitney U test, reuniting pairs: $\chi^2_1 = 0.34, P > 0.5$; females that changed mates: $\chi^2_1 = 0.03, P > 0.8$; males: $\chi^2_1 = 1.64, P > 0.2$).

The strongest breeding-site fidelity observed was the reuse of nest cups in consecutive years, usually by a remating pair or by a male returning the following year (Fig. 1). One male Semipalmated Sandpiper mated with three different females in 3 consecutive years and reused the same nest cup each time. Another male Semipalmated Sandpiper reused a nest cup after breeding 70 m away during an intervening year. Nest cups were also used by different pairs of Western Sandpipers ($N = 4$), different pairs of Semipalmated Sandpipers ($N = 3$), and in one case by a pair of Western Sandpipers that used a nest cup previously occupied by a pair of Semipalmated Sandpipers ($N = 1$).

Local survival rates and probabilities of recapture

A total of 296 Western Sandpipers and 230 Semipalmated Sandpipers were captured as breeding adults during the 4 years of this study. Two parents were captured on most nests (86.8%), but occasionally a clutch was depredated before both birds had been captured (one parent only: 11.2%; neither parent: 2.0%; $N = 446$ nests in 1993–1996).

Goodness-of-fit tests based on bootstrap simulations indicated that the model $\phi_{\text{sex} \times t}, p_{\text{sex} \times t}$ was an acceptable global model for both species (Western Sandpipers: $P > 0.05$; Semipalmated Sandpipers: $P > 0.4$), and that overdispersion rates were low (Western Sandpipers: $\hat{c} = 1.56$; Semipalmated Sandpipers: $\hat{c} = 1.00$). The best fit model in Western Sandpipers was one where local survival rate (ϕ) and probability of recapture (p) collapsed to constants (Table 4). However, equally parsimonious models included sex or time dependence in ϕ and sex dependence in p . In Semipalmated Sandpipers, the best fit model included annual variation and a constant difference between the sexes in local survival rates

Table 5. Local survival rates ($\hat{\phi}$) and probabilities of recapture (\hat{p}) among Western Sandpipers and Semipalmated Sandpipers breeding at Nome, Alaska, in 1993–1996.

	Sex	Year	Western Sandpipers	Semipalmated Sandpipers
Local survival rate ^a	Females	1993–1994	0.592±0.067	0.558±0.079
		1994–1995	0.548±0.070	0.631±0.096
	Males	1993–1994	0.616±0.064	0.702±0.067
		1994–1995	0.574±0.067	0.767±0.077
Recapture rate	Pooled	Pooled	0.565±0.046	0.659±0.059
		Females	1993–1994	0.801±0.073
		1994–1995	0.795±0.078	0.658±0.085
	Males	1993–1994	0.819±0.069	0.668±0.067
		1994–1995	0.813±0.069	0.668±0.073
		Pooled	Pooled	0.801±0.060

Note: Annual estimates were calculated via model averaging (mean ± unconditional SE), and pooled estimates were calculated by applying a variance-components method to the global model $\phi_{\text{sex} \times \text{time}}$ (*i.e.*, mean ± SE of β).

^aLocal survival was nonestimable for 1995–1996 because additional information would have been required in order to estimate the probability of recapture for this transition.

and a constant probability of recapture. Models that included annual variation in p but not always in ϕ were also equally parsimonious.

Model averaging and a variance-components approach were used to calculate parameters for both species. Parameter estimates averaged across the best fitting (*i.e.*, constrained) models indicated that the local survival rate of Western Sandpipers was higher in 1993–1994 than in 1994–1995, whereas the opposite was true for Semipalmated Sandpipers (Table 5). In both species, males had higher local survival rates than females, whereas the probability of capture was relatively constant. Overall, Semipalmated Sandpipers had local survival rates that were 10% higher than those of Western Sandpipers, but the difference was not significant ($\chi^2_1 = 1.6$, $P > 0.2$; Table 5). Conversely, the probability of recapture was 13% higher among Western Sandpipers but the difference between the species was not significant ($\chi^2_1 = 2.7$, $P > 0.1$).

Migration routes

Twenty Western Sandpipers banded at Nome, Alaska, were resighted during fall migration at locations on the Pacific coast from British Columbia to southern California, and in Nevada (Butler et al. 1996). Two Western Sandpipers were resighted as wintering birds at Ensenada, Mexico (31°52'N, 116°37'W), and four were recaptured at Chitré, Panama (7°58'N, 80°26'W). Two Semipalmated Sandpipers banded at Nome were sighted during fall migration in Oklahoma and Texas, and two individuals banded at Salinas, Ecuador (2°13'S, 80°58'W), were resighted at the field site in western Alaska.

Discussion

Western Sandpipers and Semipalmated Sandpipers are sibling species that have similar breeding biology, demography, and annual life-cycles. Nonetheless, Semipalmated Sandpipers had mate-fidelity rates that were substantially higher than those of Western Sandpipers (1.9 times greater if at least one mate returned or 1.4 times greater if both mates returned; Table 1). The mate-fidelity rates of these two species are

within the range of values reported for other socially monogamous shorebirds (Table 6), but most of the variation in these rates remains unexplained. Below we examine direct and indirect explanations for inter- and intra-specific variation in mate-fidelity rates, and then discuss methodological problems in estimating mate fidelity.

Direct explanations for variation in mate-fidelity rates

Direct explanations for variation in mate-fidelity rates include potential changes in reproductive performance, the opportunities for additional matings, and variation in breeding-site fidelity. We found no support for hypotheses that explain divorce by suggesting that animals change mates to improve their reproductive performance (Choudhury 1995; Ens et al. 1996). Timing of laying, clutch size, and egg size were unaffected by mate change in sandpipers. Some authors have reported that faithful sandpiper pairs nest early relative to the rest of the population (Soikkeli 1967; Pierce 1997), but most analyses did not control for potential effects of female age (Sandercock et al. 1999). Several bird species are known to divorce or disperse following nest failure (Oring and Lank 1984; Ens et al. 1996; Flynn et al. 1999), but this was not true for Western Sandpipers and some other small monogamous shorebirds (Gratto et al. 1985; Haig and Oring 1988; Pierce 1997). It is unlikely that nesting success affected the mate-fidelity rates of Semipalmated Sandpipers because divorce was quite rare (<10%; see also Table 6). Survival of young until fledging was not measured but we expected loss of eggs to have a greater effect on mate fidelity because one or both parents usually abandon sandpiper young before they can fly (Gratto-Trevor 1991; Pierce 1997; B.K. Sandercock, personal observation).

The observation that mate change does not appear to affect reproductive performance suggests that in sandpipers the costs of searching for a new mate may be low. However, our analyses of mate fidelity were based only on breeding birds, and a hidden cost of divorce may be failure to find a new mate. Stilt Sandpipers (*Calidris himantopus*) and Purple Sandpipers (*Calidris maritima*) without returning partners sometimes fail to nest (Jehl 1973; Pierce 1997). Nonbreeding

Table 6. Mate-fidelity rates of socially monogamous shorebirds where both members of mated pairs returned in 2 consecutive years (*N* is the number of pairs).

	% reuniting	Sources
Intracontinental migrants		
Piping Plover (<i>Charadrius melodus</i>)	33.3 (30); 45.5 (11)	Haig and Oring 1988; Wiens and Cuthbert 1988
American Avocet (<i>Recurvirostra americana</i>)	44.8 (29)	Robinson and Oring 1997
Dunlin (<i>Calidris alpina</i>)	72.1 (43)	Soikkeli 1967
Common Redshank (<i>Tringa totanus</i>)	78.8 (151)	Hale and Ashcroft 1982
Eurasian Oystercatcher (<i>Haematopus ostralegus</i>)	92.0 (515)	Harris et al. 1987
Purple Sandpiper (<i>Calidris maritima</i>)	92.3 (13)	Pierce 1997
Willet (<i>Catoptrophorus semipalmatus</i>)	95.0 (20)	Howe 1982
Transcontinental migrants		
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	58.3 (48)	Flynn et al. 1999
Western Sandpiper (<i>Calidris mauri</i>)	61.5 (13); 66.7 (36)	Holmes 1971; this study
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	81.0 (79); 94.3 (35)	Gratto et al. 1985; this study
Least Sandpiper (<i>Calidris minutilla</i>)	96.8 (31)	Cooper 1993

Semipalmated Sandpipers have been reported in Manitoba (Gratto-Trevor 1991), and our mark-recapture analyses suggest that they are present at Nome as well. Semipalmated Sandpipers tended to have lower probabilities of recapture than Western Sandpipers (Table 5). The difference was not due to our ability to capture sandpipers because the two species were trapped on the nest with equal success. The nests of Semipalmated Sandpipers may have been less detectable because this species had higher rates of nest failure than Western Sandpipers (Sandercock 1998b). However, a difference in recapture rates could also indicate variation in the number of nonbreeders. Thus, Semipalmated Sandpipers might have higher mate-fidelity rates if switching mates imposes a greater risk of failing to obtain a new breeding partner in this species.

Western Sandpipers might have lower mate-fidelity rates than Semipalmated Sandpipers if individuals of either sex were abandoning their mate to obtain additional matings. The opportunities for such tactics seem limited because most females produce just one clutch (>98%), breeding seasons are short and synchronous (80% of nests are initiated in 1–2 weeks; Sandercock et al. 1999), and biparental care during incubation is obligate, at least in Western Sandpipers (Erckmann 1981). Moreover, monogamous sandpipers have relatively small testes (Cartar 1985) and short sperm (Johnson and Briskie 1999). Rates of extrapair fertilization are low in Western Sandpipers (<5%, *N* = 137 nestlings from 55 broods; D. Blomqvist and B. Kempnaers, unpublished data) and other monogamous shorebirds (<5%; Heg et al. 1993; Pierce and Lijfeld 1998; Zharikov and Nol 2000). On the other hand, Western Sandpipers exhibit greater sexual size dimorphism than Semipalmated Sandpipers (Sandercock 1998a). If sexual selection is indeed stronger in Western Sandpipers, females may be more discriminating, and hence more likely to divorce, because competition for mates is stronger, or because signals of male quality or male contributions to parental care show greater variation.

A migratory bird faces two important decisions when returning to its breeding ground: should it return to the same site as in the previous year, and if so, should it reunite with the same partner? In monogamous species where the sexes

winter at separate locations, site fidelity may determine mate fidelity by influencing the likelihood of relocating a mate. Here, interspecific differences in breeding dispersal could not explain variation in mate-fidelity rates because both sandpiper species showed strong fidelity to their nesting areas (Fig. 1). Breeding dispersal was female-biased in both species, as it is in other monogamous, male-territorial shorebirds (Soikkeli 1967; Gratto et al. 1985; Flynn et al. 1999) and passerines (Clarke et al. 1997).

Indirect explanations for variation in mate-fidelity rates

Indirect explanations for variation in mate-fidelity rates include differences in breeding habitat, annual survival rates, and aspects of migration. Breeding-habitat characteristics are unlikely to account for the difference in mate-fidelity rates between Western Sandpipers and Semipalmated Sandpipers because the two species nested together in the same habitat, and even used the same nest cups. Mate- and site-fidelity rates are thought to be low in Piping Plovers (*Charadrius melodus*) and American Avocets (*Recurvirostra americana*) because these species breed in ephemeral habitats where environmental perturbations make the availability of nesting sites unpredictable (Table 6; Haig and Oring 1988; Robinson and Oring 1997). In contrast, the arctic habitats used by sandpipers are relatively stable, and aerial photographs indicate that the microhabitat features of our tundra study area have remained unchanged for at least 30 years (B.K. Sandercock, unpublished data).

Interspecific variation in mate-fidelity rates has been related to annual survival rates in both empirical (Rowley 1983; Ens et al. 1996) and theoretical studies (McNamara and Forslund 1996). However, we found an almost twofold difference in mate-fidelity rates even though differences in local survival rates between adult Western Sandpipers and Semipalmated Sandpipers were small and nonsignificant (Table 5). Interspecific variation in mate-fidelity rates could be due to sex differences in survivorship if the decision to reunite or divorce depends on the availability of alternative mates. Male Semipalmated Sandpipers had higher local survival rates than females (Tables 5 and 6; see also Sandercock and Gratto-Trevor 1997), and our population may have had a

male-biased sex ratio, like birds in northern Manitoba (Gratto-Trevor 1991). If females' decisions to stay together or divorce were related to the operational sex ratio, divorce should have been more common in Semipalmated Sandpipers than in Western Sandpipers. In fact, the opposite pattern was found.

In general, the importance of survival rates for explaining differences in mate-fidelity rates seems overstated. Rowley (1983) argued that there should be little selection for mate fidelity in short-lived birds because it is unlikely that both mates will survive to return to the breeding grounds. However, Ens et al. (1996) were unable to detect a relationship between divorce and "survival" rates in a comparative analysis of divorce rates for 76 species of birds. Their analysis may have been flawed because they did not control for breeding dispersal or recapture rates (see below), but it is clear that long-lived birds often have markedly different mate-fidelity rates. For example, Greater Flamingos (*Phoenicopterus ruber*; Cézilly and Johnson 1995) and Barnacle Geese (*Branta leucopsis*; Forslund and Larsson 1991) both have high local survival rates ($\hat{\phi} = 0.92\text{--}0.93$), but also have mate-fidelity rates of 1.7 and 97.6%, respectively.

Aspects of migration could be relevant as indirect explanations of variation in mate-fidelity rates. Resightings of sandpipers marked at Nome during migration were limited but are consistent with migration routes proposed for Alaskan populations of these species: Semipalmated Sandpipers are at the westernmost edge of their breeding range and use central flyways to reach wintering areas on the west coast of South America (Harrington and Morrison 1979; Lank 1983; Morrison 1984; Gratto-Trevor and Dickson 1994), whereas Western Sandpipers use Pacific flyways to reach more northerly wintering areas in North and Central America (Butler et al. 1996; Warnock and Takekawa 1996; this study). Thus, the mate-fidelity rates of Semipalmated and Western Sandpipers at Nome covary positively with migration distance. Comparisons with other populations are also consistent with this observation (Table 6). Semipalmated Sandpipers at Nome had mate-fidelity rates that were significantly higher than those reported by Gratto et al. (1985) for a more southerly population in Manitoba (94.3 vs. 81.0%, G test, $G_1 = 3.90$, $P < 0.05$). Conversely, returning pairs of Western Sandpipers at Nome had mate-fidelity rates that were not significantly different from those of another population studied by Holmes (1971) elsewhere in Alaska (66.7 vs. 61.5%, $G_1 = 0.11$, $P > 0.7$). While migration distance affects shorebird mating systems (Myers 1981) and potentially the mate-fidelity rates of our two study species, it presently does not appear to be a general explanation for variation in mate-fidelity rates of the monogamous species studied thus far (Table 6).

Migration could influence mate-fidelity rates through effects on either the timing or the synchrony of arrival (Williams and Rodwell 1992; Rees et al. 1996; Bried et al. 1999). For example, passerine land birds that winter in equatorial regions migrate later and more synchronously than species departing for breeding areas from northern temperate sites (Hagan et al. 1991). In this study, Western Sandpipers arrived and began displaying before Semipalmated Sandpipers (B.K. Sandercock, personal observation), and initiated their clutches, on average, 4–10 days earlier. Local environmental conditions were more variable in the early season, and Western Sandpipers

may have had lower mate-fidelity rates because late snow-fall or freezing events led to changes in territory quality that affected pair formation. Later breeding could have led to greater time constraints among Semipalmated Sandpipers, and it may have been beneficial for an individual to stay with a partner if it reduced the energy or time investment in courtship. Observations of the behaviour of Western Sandpipers support this idea, because faithful males spent less energy on pair-bonding displays than did males with new mates (Lanctot et al. 2000). However, this argument only holds if the two partners arrive on the breeding grounds at around the same time. If not, an individual may be forced to forgo breeding if its mate does not return and it fails to attract a new mate early on.

Thus, synchrony in the timing of arrival of the sexes may also be important. Differential arrival of previously paired birds has been proposed as a partial explanation for divorce rates of tits (Dhondt and Adriaensen 1994) and penguins (Olsson 1998; Bried et al. 1999). Soikkeli (1967) reported that 8 of 12 cases of divorce in Dunlins (*Calidris alpina*) were due to "preemption" (cf. Ens et al. 1996); late-arriving birds found that their previous mates were already paired. Quantitative observations of timing of arrival of sandpipers at our study site were not available, but could be relevant, given that males winter farther north and precede females to the breeding grounds during spring migration (Butler et al. 1987; Gratto-Trevor 1992; Harrington and Haase 1994). Timing of arrival and laying are correlated in other arctic-breeding shorebirds (Hildén and Vuolanto 1972; Soikkeli 1967; Jönsson 1987), and a tendency towards less variation in the laying dates of Semipalmated Sandpipers may indicate that timing of arrival was more synchronous in this species. If so, synchronized arrival may have facilitated relocation of a previous mate and led to higher mate-fidelity rates. Annual variation in the mate-fidelity rates of Western Sandpipers was not consistent with this prediction, however, because rates of reuniting in pairs where both mates returned were actually lowest in years when laying was synchronous (Tables 1 and 2). Further tests of the effect of migration distance on mate-fidelity rates in monogamous shorebirds await better data on the timing and synchrony of arrival and application of comparative methods (cf. Dubois et al. 1998).

Methods for calculating mate-fidelity rates

Interspecific comparisons of mate-fidelity rates have traditionally been based on estimates from studies that report the percentage of pairs that changed mates, divorced, or reunited. Return rates yield biased estimates of survival because they fail to correct for recapture and emigration rates (Lebreton et al. 1992). Calculations of mate fidelity are subject to the same problems, a point not discussed in recent reviews (Choudhury 1995; Black 1996; Ens et al. 1996). The probability of capturing one male (m) or female (f) is the product of true survival rate (S), the site-fidelity rate (ψ), the probability of breeding (γ), the probability of finding a nest (ω), and the probability of capture (c) once a nest is detected. Thus, the probability of recapturing a returning pair is

$$\text{Pr}(\text{pair}) = S_m S_f \psi_m \psi_f \gamma_m \gamma_f \cdot \omega^x \cdot c_m c_f$$

where x is the number of nests.

A ratio of probabilities for reuniting and divorcing pairs gives an indication of the potential bias in conventional estimates of divorce rates. We illustrate this point using approximate values of the above parameters based on this study. If survival rate ($S_m = S_f \approx 0.6$), breeding propensity ($\gamma_m = \gamma_f > 0.6$), and capture rate ($c_m = c_f > 0.9$) are not related to mate fidelity, these probabilities cancel each other when reuniting and divorcing pairs are compared. In both sandpiper species, breeding dispersal covaried with sex and mate-fidelity rate: males and reuniting females moved short distances (79–90% moved <200 m; Fig. 1) relative to the size of the study area (4 km²; $\psi_f = \psi_m \approx 1$), whereas females that divorced or changed mates moved distances (68–75% moved >200 m) that could have taken them off the study area ($\psi_f \approx 0.7$). Shorebird eggs are cryptic, and some nests were likely missed each year ($\omega \approx 0.9$). Hence, the probability of detecting both members of a reuniting pair was at least 1.6 times greater than the probability of detecting a divorcing pair (ratio of $\psi_m \psi_f \omega^x = (1 \cdot 1 \cdot 0.9^1) \cdot (1 \cdot 0.7 \cdot 0.9^2)^{-1}$).

This simple example demonstrates that most estimates of divorce rates, including those in this study, are likely to underestimate true divorce rates. Furthermore, it implies that interspecific comparisons of mate-fidelity rates should be made with caution if data on breeding dispersal and capture rates are unavailable. This problem was avoided here because rates of breeding-site fidelity did not differ between the two species. Undetected breeding dispersal cannot explain the lower mate-fidelity rates of Western Sandpipers, unless it is on a much larger spatial scale than that of our study.

Conclusion

In this study, direct and indirect explanations for a large difference in mate-fidelity rates between sympatric populations of Western and Semipalmated Sandpipers were evaluated. Since they are from an observational study that considers only two species, our data are a relatively weak test of these competing hypotheses (Garland and Adolph 1994). Here, mate fidelity was not related to prior nesting success nor did it lead to changes in reproductive performance, although a greater risk of failure to breed might select for fidelity in Semipalmated Sandpipers. Indirect explanations based on interspecific differences in annual survivorship or breeding habitat could not explain the difference in behaviour. Differential mate fidelity was not an artifact of differential rates of breeding dispersal, although we have shown that dispersal can affect interspecific comparisons of mate-fidelity rates. Although we were able to reject the above explanations, it was not possible to determine whether mate retention was greater in Semipalmated Sandpipers than in Western Sandpipers because of differences in mating tactics, differences in time constraints imposed by migration distance, or a combination of these factors. It would be profitable for future investigations to include focal behavioural observations during pair formation, and to evaluate potential variation in mating tactics and timing of arrival within these and other species.

Acknowledgments

S.A. Cullen, L.M. Edwards, S. Hall, L. Imbeau, N. Imbeault, R.S. Mulder, P.D. O'Hara, K.M. O'Reilly, C.A. Schuppli, C.

St. Pierre, and S.A. Wyshynski provided capable assistance with fieldwork. The Sitnasauk Native Corporation generously permitted access to their lands for this research project. K. Bey, R.E. Gill, Jr. (Alaska Biological Science Center, U.S. Geological Survey), R. Harris (National Parks Service), M. and C. Thomas, and W. Stephensen (Marine Mammal Management) provided logistical support. A. Jaramillo, P.D. O'Hara, N. Warnock, and other bird-watchers kindly reported sightings of banded birds. G. Barlow, S.R. Beissinger, D. Blomqvist, B. Ens, E. Nol, F.A. Pitelka, N. Warnock, T.D. Williams, and anonymous reviewers provided constructive criticism on previous drafts of the manuscript. B.K. Sandercock was supported by fellowships from Queen's University and Simon Fraser University, a National Science Foundation grant (DEB-9503194) to S.R. Beissinger, and a Killam Postdoctoral Fellowship from The University of British Columbia during preparation of the manuscript. Research was supported by funds from the Canadian Wildlife Service (CWS), the CWS/NSERC Research Chair in Wildlife Ecology, a Dean's Grant for Doctoral Field Travel (Queen's University), the Konrad Lorenz Institute for Comparative Ethology, the Northern Studies Training Program, a Natural Sciences and Engineering Research Council of Canada Operating Grant (to F. Cooke), the U.S. Geological Survey (Alaska Biological Science Center), and awards from the Frank M. Chapman, John K. Cooper, and Jennifer Robinson memorial funds. Capture and banding of sandpipers was conducted under permits from the U.S. Fish and Wildlife Service, the Alaska Department of Fish and Game, and Animal Care Committees at Queen's University and Simon Fraser University.

References

- Black, J.M. 1996. Pair bonds and partnerships. In *Partnerships in birds: the study of monogamy*. Edited by J.M. Black. Oxford University Press, Oxford. pp. 3–20.
- Bried, J., Jiguet, F., and Jouventin, P. 1999. Why do *Aptenodytes* penguins have high divorce rates? *Auk*, **116**: 504–512.
- Bull, C.M. 1988. Mate fidelity in an Australian lizard *Trachydosaurus rugosus*. *Behav. Ecol. Sociobiol.* **23**: 45–49.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Butler, R.W., Kaiser, G.W., and Smith, G.E.J. 1987. Migration chronology, length of stay, sex ratio, and weight of Western Sandpipers *Calidris mauri* on the southern coast of British Columbia. *J. Field Ornithol.* **58**: 103–111.
- Butler, R.W., Delgado, F.S., de la Cueva, H., Pulido, V., and Sandercock, B.K. 1996. Migration routes of the Western Sandpiper. *Wilson Bull.* **108**: 662–672.
- Cartar, R.V. 1985. Testis size in sandpipers: the fertilization frequency hypothesis. *Naturwissenschaften*, **72**: 157–158.
- Cézilly, F., and Johnson, A.R. 1995. Re-mating between and within breeding seasons in the Greater Flamingo *Phoenicopterus ruber roseus*. *Ibis*, **137**: 543–546.
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Anim. Behav.* **50**: 413–429.
- Clarke, A.L., Sæther, B.-E., and Røskaft, E. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos*, **79**: 429–438.
- Clutton-Brock, T.H. 1989. Mammalian mating systems. *Proc. R. Soc. Lond. B Biol. Sci.* **236**: 339–372.

- Cooper, J.M. 1993. Breeding biology of the Least Sandpiper (*Calidris minutilla*) on the Queen Charlotte Islands, British Columbia. M.Sc. thesis, University of Victoria, Victoria, B.C.
- Coulson, J.C. 1972. The significance of pair bond in the Kittiwake, *Rissa tridactyla*. Proc. Int. Orn. Congr. **15**: 423–433.
- Dhondt, A.A., and Adriaensen, F. 1994. Causes and effects of divorce in the Blue Tit *Parus caeruleus*. J. Anim. Ecol. **63**: 979–987.
- Dubois, F., Cézilly, F., and Pagel, M. 1998. Mate fidelity and coloniality in waterbirds: a comparative analysis. Oecologia, **116**: 433–440.
- Ens, B.J., Safriel, U.N., and Harris, M.P. 1993. Divorce in the long-lived and monogamous Oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? Anim. Behav. **45**: 1199–1217.
- Ens, B.J., Choudhury, S., and Black, J.M. 1996. Mate fidelity and divorce in monogamous birds. In Partnerships in birds: the study of monogamy. Edited by J.M. Black. Oxford University Press, Oxford. pp. 344–401.
- Eckmann, W.J. 1981. The evolution of sex-role reversal and monogamy in shorebirds. Ph.D. thesis, University of Washington, Seattle.
- Flynn, L., Nol, E., and Zharikov, Y. 1999. Philopatry, nest-site tenacity, and mate fidelity of Semipalmated Plovers. J. Avian Biol. **30**: 47–55.
- Forslund, P., and Larsson, K. 1991. The effect of mate change and new partner's age on reproductive success in the Barnacle Goose, *Branta leucopsis*. Behav. Ecol. **2**: 116–122.
- Fricke, H.W. 1986. Pair swimming and mutual partner guarding in monogamous butterflyfish (Pisces: Chaetodontidae): a joint advertisement for territory. Ethology, **73**: 307–333.
- Garland, T., Jr., and Adolph, S.C. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiol. Zool. **67**: 797–828.
- Gratto, C.L., Morrison, R.I.G., and Cooke, F. 1985. Philopatry, site tenacity and mate fidelity in the Semipalmated Sandpiper. Auk, **102**: 16–24.
- Gratto-Trevor, C.L. 1991. Parental care in Semipalmated Sandpipers *Calidris pusilla*: brood desertion by females. Ibis, **133**: 394–399.
- Gratto-Trevor, C.L. 1992. Semipalmated Sandpiper (*Calidris pusilla*). In The birds of North America No. 6. Edited by A. Poole, P. Stettenheim, and F. Gill. The Academy of Natural Sciences (The American Ornithologists' Union), Washington, D.C. pp. 1–20.
- Gratto-Trevor, C.L., and Dickson, H.L. 1994. Confirmation of elliptical migration in a population of Semipalmated Sandpipers. Wilson Bull. **106**: 78–90.
- Haig, S.M., and Oring, L.W. 1988. Mate, site, and territory fidelity in Piping Plovers. Auk, **105**: 268–277.
- Hagan, J.M., Lloyd-Evans, T.L., and Atwood, J.L. 1991. The relationship between latitude and the timing of spring migration of North American landbirds. Ornith. Scand. **22**: 129–136.
- Hale, W.G., and Ashcroft, R.P. 1982. Pair formation and pair maintenance in the Redshank *Tringa totanus*. Ibis, **124**: 471–490.
- Harrington, B.A., and Haase, B. 1994. Latitudinal differences in sex ratios among nonbreeding Western Sandpipers in Puerto Rico and Ecuador. Southwest. Nat. **39**: 188–189.
- Harrington, B.A., and Morrison, R.I.G. 1979. Semipalmated Sandpiper migration in North America. Stud. Avian Biol. **2**: 83–100.
- Harris, M.P., Safriel, U.N., Brooke, M.D.L., and Britton, C.K. 1987. The pair bond and divorce among Oystercatchers *Haematopus ostralegus* on Skokholm Island, Wales. Ibis, **129**: 45–57.
- Heg, D., Ens, B.J., Burke, T., Jenkins, L., and Kruijt, J.P. 1993. Why does the typically monogamous Oystercatcher (*Haematopus ostralegus*) engage in extra-pair copulations? Behaviour, **126**: 247–289.
- Hildén, O., and Vuolanto, S. 1972. Breeding biology of the Red-necked Phalarope *Phalaropus lobatus* in Finland. Ornith. Fenn. **49**: 57–85.
- Hines, J.E., and Sauer, J.R. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery rate estimates. U.S. Fish Wildl. Serv. Fish Wildl. Tech. Rep. No. 24.
- Holmes, R.T. 1971. Density, habitat and the mating system of the Western Sandpiper (*Calidris mauri*). Oecologia, **7**: 191–208.
- Howe, M.A. 1982. Social organization in a nesting population of eastern Willets (*Catoptrophorus semipalmatus*). Auk, **99**: 88–102.
- Jehl, J.R., Jr. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bull. **85**: 114–117.
- Jönsson, P.E. 1987. Sexual size dimorphism and disassortive mating in the Dunlin *Calidris alpina schinzii* in southern Sweden. Ornith. Scand. **18**: 257–264.
- Johnson, D.D.P., and Briskie, J.V. 1999. Sperm competition and sperm length in shorebirds. Condor, **101**: 848–854.
- Lancot, R.B., Sandercock, B.K., and Kempnaers, B. 2000. Do male breeding displays function to attract mates or defend territories? The explanatory role of mate and site fidelity. Waterbirds, **23**: 155–164.
- Lank, D.B. 1983. Migrating behavior of the Semipalmated Sandpiper at inland and coastal staging areas. Ph.D. thesis, Cornell University, Ithaca, N.Y.
- Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. **62**: 67–118.
- McNamara, J.M., and Forslund, P. 1996. Divorce rates in birds: predictions from an optimization model. Am. Nat. **147**: 609–640.
- Miller, E.H. 1979. Functions of display flights by males of the least sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia. Can. J. Zool. **57**: 876–893.
- Morrison, R.I.G. 1984. Migration systems of some New World shorebirds. In Shorebirds: migration and foraging behavior. Edited by J. Burger and B.L. Olla. Plenum Press, New York. pp. 125–202.
- Myers, J.P. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. Behav. Ecol. Sociobiol. **8**: 195–202.
- Olsson, O. 1998. Divorce in King Penguins: asynchrony, expensive fat storing and ideal free mate choice. Oikos, **83**: 574–581.
- Oring, L.W., and Lank, D.B. 1984. Breeding area philopatry, natal philopatry and social systems of sandpipers. In Behavior of marine animals, current perspectives in research. Edited by J. Burger and B.L. Olla. Plenum Press, New York. pp. 125–148.
- Pierce, E.P. 1997. Monogamy in the Purple Sandpiper (*Calidris maritima*) in Svalbard: sex roles, fidelity, and parentage. Ph.D. thesis, Zoological Museum, University of Oslo, Oslo, Norway.
- Pierce, E.P., and Lijfeld, J.T. 1998. High paternity without paternity-assurance behavior in the Purple Sandpiper, a species with high paternal investment. Auk, **115**: 602–612.
- Reavis, R.H., and Barlow, G.W. 1998. Why is the coral-reef fish *Valenciennesa strigata* (Gobiidae) monogamous? Behav. Ecol. Sociobiol. **43**: 229–237.
- Rees, E.C., Lievesley, P., Pettifor, R.A., and Perrins, C. 1996. Mate fidelity in swans: an interspecific comparison. In Partnerships in birds: the study of monogamy. Edited by J.M. Black. Oxford University Press, Oxford. pp. 118–137.
- Robinson, J.A., and Oring, L.W. 1997. Natal and breeding dispersal in American Avocets. Auk, **114**: 416–430.
- Rowley, I. 1983. Re-mating in birds. In Mate choice. Edited by P. Bateson. Cambridge University Press, Cambridge. pp. 331–360.
- Sandercock, B.K. 1997. Incubation capacity and clutch size deter-

- mination in two calidrine sandpipers: a test of the four-egg threshold. *Oecologia*, **110**: 50–59.
- Sandercock, B.K. 1998a. Assortative mating and sexual size dimorphism in Western and Semipalmated Sandpipers. *Auk*, **115**: 786–791.
- Sandercock, B.K. 1998b. Chronology of nesting events in Western and Semipalmated Sandpipers near the Arctic circle. *J. Field Ornithol.* **69**: 235–243.
- Sandercock, B.K., and Gratto-Trevor, C.L. 1997. Local survival in Semipalmated Sandpipers *Calidris pusilla* breeding at La Pérouse Bay, Canada. *Ibis*, **139**: 305–312.
- Sandercock, B.K., Lank, D.B., and Cooke, F. 1999. Seasonal declines in the reproductive effort of arctic-breeding sandpipers: different tactics in two birds with an invariant clutch size. *J. Avian Biol.* **30**: 460–468.
- SAS Institute Inc. 1990. SAS user's guide: statistics, version 6. SAS Institute Inc., Cary, N.C.
- Slagsvold, T., and Dale, S. 1991. Mate choice models: can cost of searching and cost of courtship explain mating patterns of female Pied Flycatchers? *Ornis Scand.* **22**: 319–326.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). *Ann. Zool. Fenn.* **4**: 158–198.
- Warnock, S.E., and Takekawa, J.Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis*, **138**: 160–167.
- White, G.C. 1999. Analysis of marked animal encounter data. <<http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>>.
- Wiens, T.P., and Cuthbert, F.J. 1988. Nest-site tenacity and mate retention of the Piping Plover. *Wilson Bull.* **100**: 545–553.
- Williams, T.D., and Rodwell, S. 1992. Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni penguins. *Condor*, **94**: 636–645.
- Zharikov, Y., and Nol, E. 2000. Copulation behavior, mate guarding, and paternity in the Semipalmated Plover. *Condor*, **102**: 231–235.