Mate fidelity and breeding site tenacity in a monogamous sandpiper, the black turnstone

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We examined the relationship between mate fidelity and breeding site tenacity during a 5-year study of the black turnstone, *Arenaria melanocephala*, a socially monogamous sandpiper breeding in subArctic Alaska. We tested the predictions of several hypotheses regarding the incidence of divorce and the benefits of fidelity to mate and breeding site. Interannual return rates to the breeding grounds (88% for males, 79% for females) were among the highest yet recorded for any scolopacid sandpiper, and 88% of returning birds nested on their previous year's territory. The annual divorce rate was only 11%, and mate fidelity was significantly linked to fidelity to territory but independent of sex and year. Males arrived in spring significantly earlier than their mates and interannual fidelity was influenced by the relative timing of arrival of pair members. Reunited pairs had significantly higher fledging success than new pairs formed after death or divorce. The incidence of divorce was unrelated to reproductive success the previous year, although birds nested significantly further away after failure than after a successful nesting attempt. Sightings of marked individuals suggested that members of pairs do not winter together, and breeding site tenacity provides a mechanism through which pair members can reunite. We reject the 'incompatibility' hypothesis for divorce in turnstones, and our data contradict predictions of the 'better option' hypothesis. Alternatively, we propose the 'bet-hedging' hypothesis to explain the occurrence of divorce, which transpires when an individual pairs with a new mate to avoid the cost of waiting for a previous mate to return. Such costs can include remaining unmated, if the former mate has died, or experiencing lower reproductive success because of delayed breeding.

Mate fidelity provides benefits that contribute to increased individual fitness in many species of birds. These include improving coordination between mates in hatching or rearing young, prolonging parental investment and reducing an individual's cost of mate sampling (see review in Black 1996). The incidence of mate fidelity in a species is hypothesized to be dependent on several factors, including longevity and migratory habit (Rowley 1983). Species in which mates migrate long distances to separate wintering grounds are thought to be least likely to maintain pair bonds between breeding seasons because of high mortality rates and the uncertainty of their mate's survival (Rowley 1983).

Insights into the benefits of mate fidelity in monogamous species have been gained by comparing reproductive success of pairs that reunited with success of those that changed mates because of either divorce or death of former mates. Several hypotheses have been proposed to

explain why pair members would sever their pair bond rather than reunite for a subsequent breeding attempt. In a recent review of the theoretical framework of divorce among birds (Choudhury 1995), two primary competing hypotheses emerged supporting divorce as an active choice to improve individual fitness. The 'better option' hypothesis (Ens et al. 1993) predicts that one partner should initiate divorce if it can improve its reproductive success; the 'victimized' member may suffer reduced success as a result. The 'incompatibility' hypothesis (Coulson 1972; Rowley 1983) suggests that members of a pair may have low reproductive success not because of their intrinsic poor quality but because of some incompatibility, and that both members should increase success by mating with new partners.

Two alternative hypotheses suggest that divorce may occur not through active choice but rather as the result of an external event. The 'accidental loss' hypothesis (Owen et al. 1988) suggests that divorce may occur through temporary loss of a partner, such as in geese through accidental separation during migration because

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of disturbance or bad weather. The 'forced divorce' hypothesis (B. Taborsky & M. Taborsky, personal communication, in Choudhury 1995) contends that divorce may be caused by the intrusion of a third bird that is dominant over and displaces the former mate. Both of these could be interpreted as subsets of the better option hypothesis if the costs of mate fidelity outweigh the benefits of divorce and some choice is exercised by one of the partners (Choudhury 1995). Several testable predictions arise from these hypotheses, which involve examination of reproductive success before and after divorce, divorce rates relative to vacancies caused by mortality, timing of pair formation and mechanisms of initiation of divorce (Choudhury 1995).

Mate fidelity is highly correlated with breeding site tenacity in many species. Because of this, breeding site tenacity has been viewed by many authors as a mechanism through which pair members that winter separately can reunite and thereby increase their reproductive success (Soikkeli 1967; Holmes 1971; Fairweather & Coulson 1995). Alternatively, mate fidelity has been hypothesized to be an ancillary consequence of breeding site tenacity, but this alternative has rarely been examined explicitly (Morse & Kress 1984).

Sandpipers of the family Scolopacidae exhibit a broad array of mating systems with an attendant array of parental care patterns (Oring & Lank 1984). The diversity of social systems in this family has stimulated much discussion on selective factors that might have shaped their evolution (e.g. Pitelka et al. 1974; Myers 1981a, b; Howe 1982; Oring & Lank 1984; Reed & Oring 1993; Whitfield & Tomkovich 1996; Reynolds & Székely 1997). The black turnstone, *Arenaria melanocephala*, is a territorial, socially monogamous scolopacid sandpiper with biparental care (Handel 1982). Both sexes incubate eggs and care for precocial young. Territories are used for nesting, feeding and brood rearing, although some feeding occurs on nearby mudflats. Territorial boundaries expand and defence diminishes as failed breeders leave the area. Black turnstones breed mainly in subArctic Alaska and migrate to wintering grounds that extend from south-coastal Alaska to Baja California, Mexico (Handel & Gill 1992; AOU 1998).

In this paper we examine the relationship between mate fidelity and breeding site tenacity in a marked population of black turnstones and how these factors are in turn related to reproductive success. We test some of the predictions of the above hypotheses that address the decisions of pair members (1) to return to former breeding territories or not and (2) to divorce or reunite with former mates for subsequent breeding attempts. We also present information on winter site tenacity to provide insights on how cross-seasonal interactions (Myers 1981b) may help shape the social system of this species.

METHODS

Study Area and Field Methods

We studied the breeding ecology of a colour-banded population of black turnstones nesting on coastal graminoid meadows at the mouth of the Tutakoke River (61°10′N, 165°40′W) on the central Yukon-Kuskokwim Delta, Alaska. Coastal meadows are less than 1 m in relief, dissected by numerous tidal sloughs and shallow (<1 m), brackish ponds, and bordered by the mud and sand flats of Angyoyaravak Bay, which extend approximately 5 km at low tide. Vegetation on coastal meadows consists primarily of sedges, grasses and a few dwarf shrubs, including predominantly *Carex rariflora*, *C. ramenskii*, *Calamagrostis deschampsioides*, *Salix ovalifolia*, and *Empetrum nigrum* (Kincheloe & Stehn 1991). We arrived in late April or early May before turnstones did in 1978–1980 and remained until mid-September in 1978–1979, well after all adults and young had departed. In 1981–1982 we arrived after turnstones had begun to nest and in 1980–1982 we left in late June or early July before all young had fledged.

We attempted to capture all black turnstones nesting on a 20-ha study plot and monitor their breeding success. We searched for nests daily by observing turnstone behaviour from 3-m tall blinds and we rechecked them every 1–2 days. We monitored survival of broods by methodically searching the area from observation towers and on foot every 1–2 days posthatch for colour-banded adults tending chicks. We captured a total of 32 males and 43 females during incubation using modified bow-traps and marked each with a U.S. Fish and Wildlife Service metal band and a unique combination of one to three coloured leg bands. We assumed there would be no effect of capture and colour-banding on either resighting rates or nesting success, based on results of a similar shorebird study (Redmond & Jenni 1982). We determined the sex of most banded adults on the basis of the position during copulation. For a few, we determined sex on the basis of plumage characteristics and gender-exclusive behaviours (male aerial display flights). We verified the accuracy of these sexing criteria by examining gonads of 18 males and 20 females collected with a shotgun off the main study area under a U. S. Scientific Collecting Permit in conjunction with an auxiliary study of food habits (unpublished data). We banded 150 newly hatched chicks from 1978–1981 with a metal band, 102 of which were also given a single coloured leg band denoting year of hatch. We searched the study plot every 1–2 days and a surrounding 175-ha area less frequently throughout the nesting season to determine annual return rates and nesting status of previously marked birds. Each season after birds departed we mapped locations of nests and measured distances between subsequent nesting attempts of marked individuals.

Statistical Analysis

To assess differences in interannual return rates to the study area and to individual territories in relation to sex, year, and interactions between sex and year, we tested the fit of a series of hierarchical logit loglinear models using likelihood-ratio tests (Fienberg 1991). The statistical significance of individual factors was tested using Z values. For those marked birds that returned to nest, hierarchical loglinear models (Fienberg 1991) were used to test the

independence of territorial fidelity, mate fidelity, sex and year. We tested for differences in arrival dates between marked pair members using a *t* test for paired comparisons (Sokal & Rohlf 1981). Most pairs were represented by a single observation but, to increase sample sizes, we included observations for two different years for five pairs after determining there was no interannual correlation.

We estimated nesting and fledging success by calculating a daily survival rate (DSR) for the laying and incubation period (27 days) and brood-rearing period (27 days) using the maximum-likelihood estimation method (Bart & Robson 1982). We used orthogonal contrasts of DSRs (Sauer & Williams 1989) to test whether a pair's experience with each other or with a territory was related to reproductive success. To do this, we compared DSRs during both the nesting and brood-rearing periods by mate status (reunited with mate from previous year versus nesting with new mate) and by territory experience (both new to the territory versus one or both experienced on the territory). An individual was considered experienced on its territory if it had nested during the previous year in the same area relative to the nests of neighbouring pairs. For pairs with multiyear histories, we randomly selected a single year's reproductive data to avoid problems of pseudoreplication. We excluded results from 1978 because the previous year's histories were unknown and those from 1982 because reproduction was almost a complete failure due to heavy predation by Arctic foxes, *Alopex lagopus* (unpublished data). We made the assumption that reproductive success in a given year provided a relative measure of lifetime fitness but realize that other factors outside the breeding season could have strongly affected fitness.

We used two-way analysis of variance (ANOVA) to test whether the distance a returning adult moved to nest in a subsequent year was related to its hatching success the previous year or current pair status. Distances were transformed to ranks because of non-normal distributions and nonhomogeneous variances. We used the Mann–Whitney *U* test to determine whether distances pairs moved between renesting attempts within a season differed from distances that birds moved between years. We also used Mann–Whitney *U* tests to compare distances moved by males and females that nested with new mates after success or failure the previous year. For birds with a multiyear history we randomly selected a single year to avoid problems of nonindependent samples. For those marked birds that nested for 3–5 years, we used Kruskal–Wallis ANOVA to test for differences among individuals and we used multivariate analysis of variance (MANOVA) of the ranked data to test for temporal trends in median distances moved in sequential years.

RESULTS

Return Rates

Interannual return rates of colour-marked males to the study area ranged from 84 to 93% over the 5 years (Fig. 1), with an overall return rate of 88% (*N*=90 records of 31 individuals). Among marked females, interannual return
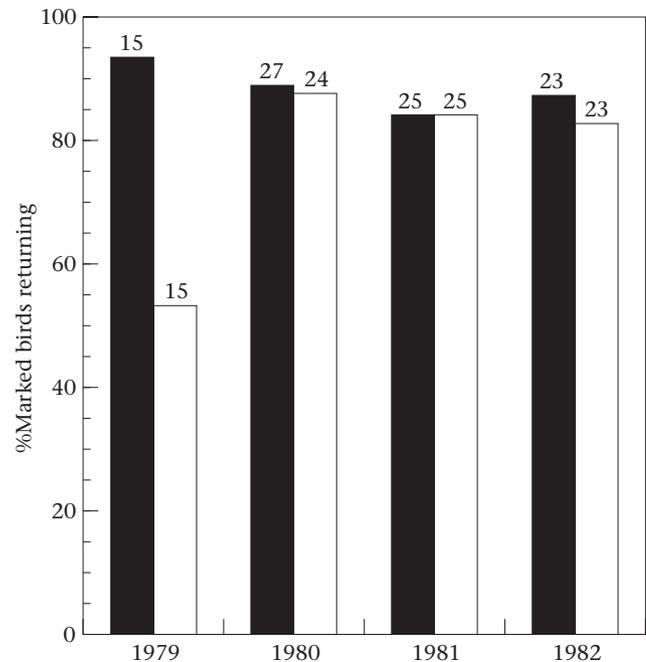

Figure 1. Percentage of colour-marked male (■) and female (□) black turnstones returning to the breeding grounds each year, 1979–1982. Numbers above bars denote sample sizes.

rates varied from 53 to 88%, with an overall return rate of 79% (*N*=87 records of 38 individuals). Return rates did not differ significantly between sexes (logit loglinear analysis, likelihood ratio test: *Z*= − 0.41, *P*=0.63) or among years (all |*Z*|<1.90, all *P*>0.058); combined, 84% of the marked adults returned to the study area each year. True differences may have existed in return rates between sexes or between years but it is unlikely they were large. Given our sample sizes, the power to detect large, medium, or small deviations from hypothesized uniform return rates (effect sizes sensu Cohen 1988, page 224) was 0.99, 0.93 and 0.59, respectively. Fidelity to individual territories was also high each year. Among all birds that returned to the study area and whose territory we were able to determine, 88% of males (*N*=75 returns, interannual range 83–96%) and 87% of females (*N*=63, interannual range 77–94%) returned to the territory that they had occupied the previous year. There were no significant differences in territorial fidelity rates between sexes (*Z*=1.01, *P*=0.31) or among years (all |*Z*|<1.41, all *P*>0.15). Among the 14 cases in which neither banded mate returned to the territory the following season, six (43%) of the territories were absorbed by adjacent pairs, five (36%) remained unoccupied and three (21%) were occupied by new pairs.

Mate Fidelity

The rate of interannual mate fidelity was high and linked to the rate of fidelity to territory (Fig. 2). Most returning males (66%) and females (77%) reunited with mates from the previous year on the same territory. Only three (6%) of 50 reunited pairs nested on a new territory.
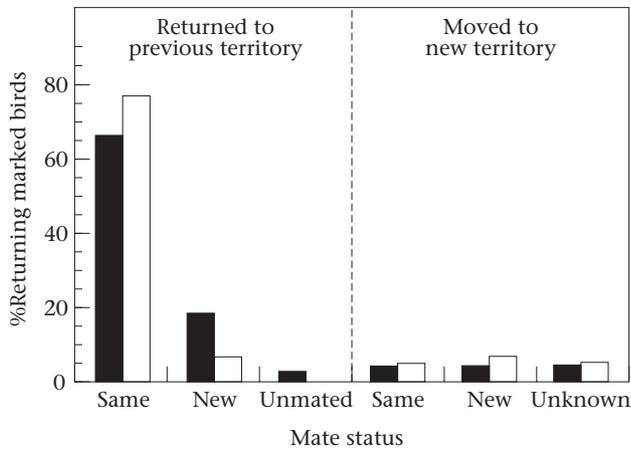
Figure 2. Percentage of male (■; *N*=71) and female (□; *N*=61) black turnstones that returned and reunited with the same mate, paired with a new mate, remained unmated, or had unknown breeding status. Mate status is shown in relation to territory tenacity. Unknown status includes birds that were known to be alive but whose breeding status that year was undetermined.

Fidelity to previous year's mate and fidelity to territory were statistically related to each other, but were both independent of sex of the individual and year (loglinear model goodness of fit: χ^2_3=4.64, *P*=0.20). Because survival rates and mate fidelity were so high, the incidence of pairs remaining together for several years was relatively high. Among the pairs in which both members were banded, 53% (21 of 40 pairs) reunited the year after they were marked, 35% (13 of 37) were together for 3 years, 35% (11 of 31) reunited for a fourth year and 33% (5 of 15) remained together for all 5 years.

Three per cent of returning males and no females were recorded unmated (Fig. 2). The nesting status of three males and three females was undetermined; we knew that these birds did not reunite with previous mates or nest on the previous year's territory, but they could have remained unmated. These included two females that were not observed at all during an intervening year, one of which returned to her former territory and one of which nested on a new territory the subsequent year.

Newly Formed Pairs

Birds nesting with new mates included both those whose former mates did not return (and presumably had died) and those that were divorced. The returning bird's fidelity to territory and its subsequent mate status depended both on its sex and also on whether it had been divorced or widowed (Fig. 3). The annual divorce rate among 56 pairings in which both members were known to be alive the following year was 11% (6 pairs). None of the divorced birds of either sex returned to their previous year's territory to nest with a new, unfamiliar mate (Fig. 3). One divorced male remained unmated all season on his territory and two others paired with neighbouring females that had been widowed. The remaining three divorced males all moved to a new territory, two of which were known to nest with new females. In contrast to the
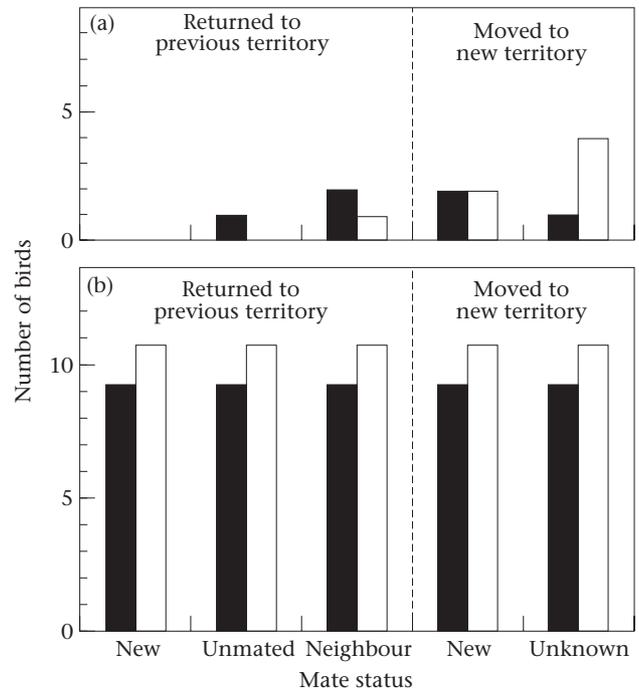

Figure 3. Number of (a) divorced and (b) widowed black turnstones that paired with new, unbanded mates, remained unmated, mated with banded neighbours, or had unknown breeding status. ■: Males; □: females. Mate status is shown in relation to territory tenacity.

males, all six of the divorced females moved off their previous territory the year of the divorce. Two of these females nested with new mates, the nesting status of two was not confirmed, and the other two were not seen until the following year.

Fidelity to territory among both widowed males and widowed females was much higher than that among divorced birds (Fig. 3). Composition of new mates, however, differed between the sexes. In 12 of 14 cases (86%), widowed males returned to their previous year's territory. Ten of the 12 (83%) that returned nested with new mates and one remained unmated all summer on his old territory. Only one widowed male paired with a neighbouring female, which had divorced her mate and not been seen the previous year. Of the two widowed males that moved to new territories, one nested with a new mate and the other's nesting status was undetermined. Three of four widowed females (75%) also returned to nest on their previous year's territory. Only one of these (33%), however, nested with a new male; the others paired on combined territories with neighbouring males that had been divorced or widowed.

Timing of Arrival of Returning Birds

In 1979 and 1980, when we were able to record the arrival of marked birds, females returned an average of 2 ± 0.8 days (range -3–13 days) later than their marked mates (paired *t* test: t_{22}=2.32, *P*<0.05). We examined fidelity and mate status in relation to arrival dates for
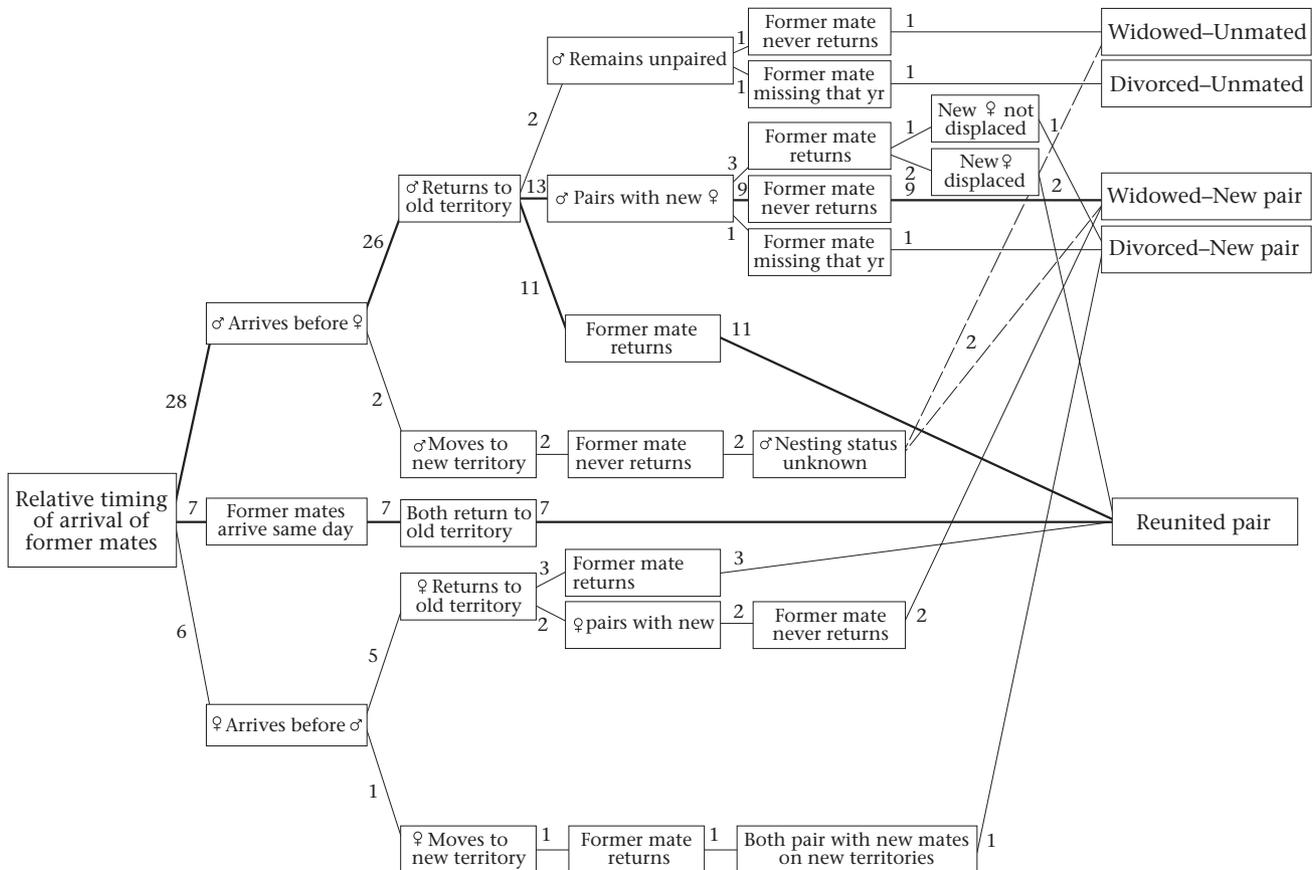
Figure 4. Relationship between the timing of arrival on the breeding grounds of previously paired black turnstones and their subsequent mating status that season. Analysis includes 41 pairs for which both members had been marked the previous season and arrival dates of returning birds were obtained. Numbers indicate the number of birds that followed each pathway. Heavy lines indicate primary pathways (>15% of outcomes). Dashed lines indicate possible pathways where final outcome was uncertain.

41 cases in which at least one member of a marked pair returned (Fig. 4). Fidelity to mates and territories depended on when birds arrived in relation to their former mates and whether unpaired alternative mates were available to either of them.

In all cases when former mates arrived on the same day (N=7), they reunited and nested on their previous territory. More commonly, however, males returned before their former mates (28 of 41 pairs). Almost all of these early-arriving males returned to their old territories (N=26) and a large number reunited with their former mates as soon as the females returned (N=11). An almost equal number, however, paired with new females (N=13). In most of these new pairings, the male's former mate never returned and he was apparently widowed (N=9). Similarly, among the few females that arrived before their former mates (6 of 41 pairs), half reunited with former mates on their old territories (N=3).

New pairings resulting in divorce occurred in three sequences. In one case, a female that had returned well before her former mate arrived (>10 days) moved to a new territory; both individuals subsequently paired with new, unmarked mates on new territories. In the other two scenarios, early-arriving males paired with marked, widowed females on adjacent territories. In one case the male's former mate was not observed until the following

season. In the other case, the widowed female was the first to arrive, followed by the adjacent male and then by the male's former mate. The former mate was observed only briefly on the territory and the male nested with the adjacent widowed female after his former mate left.

Twice, a potential divorce was thwarted when a late-returning female displaced a new female. In each case, a marked male was closely associating and exchanging in nest scrapes with an unmarked female 1–2 days after he had arrived. This association continued for 3–5 days, until the male's former mate returned. After the marked female returned, the former mates immediately reunited and the unmarked female was not seen again.

Two males remained unmated all season on their old territories, one apparently widowed and one whose former mate was still alive but not seen until the following year. Two other widowed males moved to new territories but their subsequent nesting status was not determined. No unmated females were ever observed.

Fidelity within Years

Five marked females laid replacement clutches in a new nest after their first clutches were preyed upon. Seven additional nests were suspected of being second attempts, based on territorial associations of the marked birds and

Table 1. Reproductive success of black turnstones during 1978–1981 in relation to mate status and previous experience on territory

Stage	Factor tested	Status	Number observed	Number unsuccessful	Total days observed*	Daily survival rate Mean±SD	Cumulative success Mean (95% CI)	χ^2	P
Nesting	Mate status	Reunited	21	10	417.0	0.9763±0.0074	52 (33–73)	1.29	NS
		New pair	10	3	245.5	0.9879±0.0070	72 (44–94)		
	Experience on territory	Experienced	22	11	455.5	0.9761±0.0071	52 (33–72)	0.08	NS
		Both new	18	10	366.0	0.9730±0.0084	48 (28–70)		
Brood rearing	Mate status	Reunited	13	2	177.0	0.9888±0.0079	74 (41–97)	5.95	<0.025
		New pair	7	6	37.5	0.8517±0.0556	1 (0.01–19)		
	Experience on territory	Experienced	14	4	159.5	0.9752±0.0122	51 (22–84)	0.96	NS
		Both new	8	4	74.5	0.9477±0.0254	23 (4–68)		

Cumulative reproductive success is hatching or fledging success over the 27-day nesting or brood-rearing period, respectively. Experienced pair had one or both pair members nesting on the territory in a previous year. Daily survival rates were calculated by methods of Bart & Robson (1982) and statistical comparisons were made using orthogonal contrasts following Sauer & Williams (1989). Each chi-square test has a single degree of freedom.
*Total number of days all nests and broods in each group were observed.

Table 2. Reproductive success before and after divorce for six individual pairs

	Fate of breeding attempt*				
Before divorce	After divorce		Change in success†		
Pair	Male	Female	Male	Female	
Failed	Failed	Unknown	0	0 or +	
Failed	Failed	Unknown	0	0 or +	
Failed	Successful	Not seen	+	0 or +	
Failed (H)	Unknown	Unknown	0 or +	0 or +	
Successful	Unmated	Not seen	−	− or 0	
Successful	Unknown	Successful	− or 0	0	

*Failed: failed to hatch or fledge young; failed (H): hatched but failed to fledge young; successful: successfully raised young that were still alive (10–16 days old) when we departed; unknown: fate of breeding attempt unknown; unmated: male defended territory all season but did not nest; not seen: female not seen all season but observed following year.
†Known or possible change in success before and after divorce: +: improved; 0: no change: −: worse. Note that after failure, reproductive fate could only stay the same or improve; after success, fate could only stay the same or worsen.

the date on which clutches were completed. In all cases the females remained paired with their original mates on their original territories for the second nesting attempt. There were no instances of second clutches after a brood successfully fledged.

Mate Status, Territorial Experience and Reproductive Success

Nest survival rates did not differ significantly by either mate status or experience on the territory (Table 1). Reunited pairs, however, had significantly higher daily brood survival rates (0.9888 ± 0.0079) than those of newly formed pairs in which at least one member had previously occupied the same territory (0.8517 ± 0.0556) ($\chi^2_1=5.95$, $P<0.025$). Brood survival rates (measured up to 27 days posthatch) did not differ significantly between pairs in which both members were new to the territory and pairs in which one or both members had previous experience on the territory. To confirm that these conclusions were not biased by small sample sizes resulting from excluding multiple-year records of the same individuals, we repeated the tests including all records. The conclusions of all tests remained unchanged.

There was no apparent relationship between the incidence of divorce and the pair's reproductive success the previous year, although sample sizes were small and fates of chicks past 10 days of age were difficult to ascertain (Table 2). Three of six divorced pairs had hatched young the previous season and two of these had raised chicks that were still alive when we departed (aged 13 and 16 days). Two females were not observed at all during the year of the divorce, but were seen the following year. One of these had lost her nest during incubation but the other had successfully raised chicks to at least 16 days of age. The latter was the female that returned to her former territory after a year's absence and mated with the neighbouring widowed male.
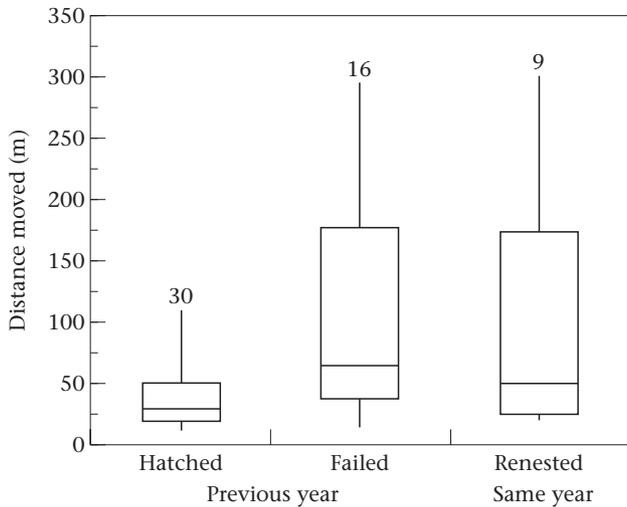
Figure 5. Distance moved between sequential nesting attempts in relation to previous hatching success. Groups include turnstones whose nests had successfully hatched young the previous year, those whose nests had failed the previous year, and pairs that renested after loss of their first clutch in the same season. The middle line in the box plot represents the median; the lower and upper bounds of the box represent the 25th and 75th percentiles, respectively. Vertical lines span from the 10th to 90th percentile. Sample sizes are indicated above each plot.

We found no significant improvement in production of young after divorce among five divorced pair members for which we knew the reproductive fate the subsequent year (Table 2). Only one successfully raised young after failing the previous year; three birds had no change in reproductive success; and one male remained unmated after having successfully raised young the previous year. We were unable to determine the change in breeding success for any of the mates of these birds. However, when we considered all possible combinations of subsequent outcomes within these pairs, we found that the probability of both members improving their success after divorce, as predicted by the incompatibility hypothesis, was only 13%. The probability of at least one member improving success after divorce, as predicted by the better option hypothesis, was 46%.

Movement Between Nesting Attempts

Marked adults nested a median distance of only 30 m (range 5–224 m, $N=30$) from their previous year's nest site if they had successfully hatched young the first year. They nested significantly further away (median 65 m, range 0–323 m, $N=16$) if they had failed the previous year (Fig. 5). This held true regardless of whether they reunited with their former mates or nested with new mates because of death or divorce, and subsequent mate status did not influence how far they moved (two-way ANOVA of ranked distances: fate: $F_{1,42}=5.92$, $P=0.02$; mate status: $F_{1,42}=0.14$, $P=0.71$; interaction: $F_{1,42}=0.80$, $P=0.38$). The distances birds moved to renest after failure within a season did not differ significantly from interannual distances birds moved after failure the previous year (Fig. 5;

Mann–Whitney U test: $U=64$, $N_1=9$, $N_2=16$, $P=0.65$). There was no significant difference between males and females nesting with new mates in how far they moved after a successful year (Mann–Whitney U test: $U=17$, $N_1=9$, $N_2=4$, $P=0.88$). Sample sizes were too small to test for differences between the sexes after failure the previous year.

The distance that a failed bird moved to a new nest site within or between seasons differed significantly among individuals for which we had three to five successive nest locations. These individual differences were exhibited by both males (Kruskal–Wallis ANOVA: $\chi^2_9=19.39$, $P=0.02$) and females ($\chi^2_6=16.25$, $P=0.01$). Among the six pairs that reunited with each other three times after successive failures, there was no significant temporal trend in distances moved after controlling for differences among individual pairs (MANOVA of ranked distances: $F_{1,11}=0.88$, $P=0.37$). Individual variation was not significant for either sex among birds that had successfully hatched young the previous year (Kruskal–Wallis ANOVA: males: $\chi^2_9=13.18$, $P=0.15$; females: $\chi^2_7=9.53$, $P=0.22$).

Fidelity to Wintering Grounds

Four turnstones marked on the breeding grounds were resighted at wintering sites in California from Bodega Bay south to Laguna Beach, a distance of over 700 km. Repeated sightings suggested that fidelity to wintering sites was high and that pair members did not winter together. One banded male was resighted repeatedly on the same stretch of beach in Laguna Beach for four consecutive winters and another male was seen in Monterey during two consecutive winters; no mate of either male was ever observed although the females were known to be alive (Gill et al. 1983; unpublished data). One adult female was seen two consecutive winters on a beach in San Luis Obispo. A colour-banded young was observed at Bodega Bay, once in its first winter and twice in its second winter.

DISCUSSION

Breeding Ground Return Rates

The interannual return rates of adult black turnstones to the breeding grounds (88% for males, 79% for females) are among the highest yet recorded among scolopacid sandpipers. They are similar to those recorded for ruddy turnstones, *Arenaria interpres*, breeding in Finland (87% for males, 70% for females; calculated from data in Bergman 1946) and exceeded only by those of the great knot, *Calidris tenuirostris* (92% for males, 50% for females; Tomkovich 1996). Return rates above 80% are typical of larger-bodied sandpipers such as whimbrels, *Numenius phaeopus* (Grant 1991; Skeel & Mallory 1996), long-billed curlews, *Numenius americanus* (Redmond & Jenni 1986), and black-tailed godwits, *Limosa limosa* (Groen 1993). Return rates for smaller-bodied sandpipers such as turnstones, however, are generally below 80% for males and

70% for females (cf. Gratto et al. 1983, 1985; Oring & Lank 1984; Morosov & Tomkovich 1986; Thompson & Hale 1989; Reed & Oring 1993; Tomkovich 1994; Tomkovich & Soloviev 1994; Hitchcock & Gratto-Trevor 1997). Although the difference in return rates between male and female black turnstones was not statistically significant, the higher return rate among males conforms to the pattern found among most species of sandpipers (see Oring & Lank 1984; Gratto et al. 1985; Thompson & Hale 1989; Tomkovich & Soloviev 1994; Skeel & Mallory 1996). This difference has been hypothesized to result from dispersal of a small percentage of females from former breeding territories after failing to regain former territories or mates (Oring & Lank 1984). A study of dunlin, *Calidris alpina*, and common redshanks, *Tringa totanus*, confirmed that adult females do have higher rates of dispersal than males away from their previous year's nest site (Jackson 1994).

The high interannual return rates of black turnstones (84%) to their breeding grounds are probably close to their interannual survival rates. Survival rates for ruddy turnstones from three wintering ground studies were similar (85% in northeastern England, Evans & Pienkowski 1984; 86% in Scotland, Metcalfe & Furness 1985). The two female black turnstones that had not been observed during an intervening year might have nested elsewhere (considered unlikely) or perhaps had not returned at all to the breeding grounds that year. Small numbers of nonbreeding turnstones have been found during June throughout their wintering range (AOU 1998; unpublished data). Delayed maturation has been documented in many species of shorebirds (Myers 1981b) and most, but perhaps not all, nonbreeding turnstones are probably first-year birds.

Breeding Site Tenacity and Mate Fidelity

Tenacity to particular breeding territories was very high among both male (88%) and female (87%) black turnstones but comparisons with other sandpipers are difficult. Most studies have measured tenacity in terms of mean distance moved rather than location of territories relative to those of marked neighbours (cf. Gratto et al. 1985). Ruddy turnstones, however, show similarly high return rates for both males (92%) and females (88%) (calculated from data in Bergman 1946).

The strong association we found between high breeding site tenacity and high interannual mate fidelity has been documented in several other species of sandpipers (Bergman 1946; Soikkeli 1967; Holmes 1971; Howe 1982). Findings of our study support the hypothesis that for black turnstones breeding site tenacity provides a mechanism for members of a pair to reunite for subsequent breeding attempts. Sightings of marked turnstones on the wintering grounds suggest that members of reuniting pairs do not winter together and the staggered arrival of males and females confirms that pair formation generally occurs on the breeding territory. This conforms to the pattern that has been documented for many other species of shorebirds (e.g. Jehl 1973; Myers 1981a; Miller 1983; Gratto-Trevor 1992; Warnock & Gill 1996; Oring

et al. 1997). Furthermore, the incidence of some turnstone pairs reuniting on new territories on the study area refutes the alternative hypothesis (Morse & Kress 1984) that mate fidelity is simply a consequence of nest site fidelity.

The higher fledging success among reunited pairs of black turnstones adds to the growing body of evidence that mate fidelity generally increases fitness, particularly among long-lived monogamous birds (see reviews in Ryder 1980; Rowley 1983; Black 1996). The only other study that has examined the effect of mate retention on reproductive success in a monogamous sandpiper found no difference in hatching success between mate-faithful pairs and newly formed pairs, but fledging success was not measured (Gratto et al. 1983).

How might mate fidelity contribute to increased fledging success? The critical period for survival of turnstone young is the first 5 days after hatch, during which over half of the broods are lost each year (unpublished data). Studies of seabirds have suggested that hatching success increases among reunited pairs because of better coordination of incubation duties between older, experienced pair members and increased foraging efficiency of the nonincubating adult (Coulson 1966; Coulson & Thomas 1983; Emslie et al. 1992). Evidence suggests that efficiency in parental care of young chicks may be an important determinant of fledging success among sandpipers in general. In several species with biparental care of precocial young, brood survival has been linked to the contributions of the parents to care of the young chicks, when they are most susceptible to death through exposure and predation (Soikkeli 1967; Byrkjedal 1987; Székely & Williams 1995). If predation pressure has been an important factor in shaping shorebird parental care systems (Larsen et al. 1996), then the coordinated behavioural response of pair members to predators may be an important factor influencing their reproductive success. Examining seasonal mortality rates of eggs and young in relation to seasonal timing of mate desertion among different species of shorebirds may offer some insights on this hypothesis.

Response to Reproductive Failure

The relationship between poor reproductive success in one year and the subsequent incidence of divorce is variable among monogamous birds (Ryder 1980; Rowley 1983; Black 1996). In black turnstones, the incidence of divorce was not related to reproductive failure the previous year. The response of turnstones to nesting failure was to remain together, usually within the same territory, and move further away from their previous nest site. This pattern differs somewhat from that reported for other sandpipers, but many factors appear to be involved. Among semipalmated sandpipers, *Calidris pusilla*, neither divorce rates nor distances moved for subsequent nesting attempts were related to fate of the previous nest (Gratto et al. 1983). Rates of dispersal away from former nest sites for female dunlin, however, were significantly higher after nesting failure than success (Jackson 1994). In the polyandrous spotted sandpiper, *Actitis macularia*, which is

strongly territorial and often has biparental care of the female's terminal clutch, both males and females move away from a breeding area more often after failure than after success (Reed & Oring 1993). Divorce rates in common redshanks appear to be influenced variably by the previous year's success and the amount of overwinter mortality, and only females with new mates move nests further after failure than after success (Thompson & Hale 1989).

Predation was the major cause of nest failure of black turnstones, which breed in high densities along the coast in close association with predatory mew gulls, *Larus canus*, glaucous gulls, *Larus glaucescens*, and Sabine's gulls, *Xema sabini* (unpublished data). Black turnstones aggressively mob avian predators, often crossing territorial boundaries and joining with neighbours to do so (unpublished data). Moving away from an unsuccessful nest site but remaining in the same territory would potentially reduce the risk of another loss while retaining the benefits of fidelity to mate and territory.

Why Change Mates?

No turnstones changed mates within a season, and most of the turnstones that changed mates between seasons did so because their former mates failed to return. Within Scolopacinae, the interannual divorce rate among black turnstones (11%) is second only to that of willets, *Catoptrophorus semipalmatus* (6%; Howe 1982); sandpiper divorce rates typically range from 18 to 25% (Bergman 1946; Soikkeli 1967, 1970; Gratto et al. 1983; Groen 1993). Assuming a constant minimum annual survival rate of 84%, an adult black turnstone breeding for the first time would have an average further life expectancy of 6.2 years, and over 20% of the adults would live to be 10 years old. Species with long life spans are expected to gain the most from reuniting (Rowley 1983).

The incompatibility hypothesis (Coulson 1972; Rowley 1983) predicts that divorce should occur more frequently after reproductive failure and that success of both pair members should increase with new mates (Choudhury 1995). In long-lived species, one might expect younger individuals to sample a variety of mates before choosing a compatible lifetime partner (Rowley 1983). Our data do not support this hypothesis for turnstones, because there was no apparent relationship between the incidence of divorce and a pair's reproductive success the previous year, nor was there the predicted subsequent increase in success for both pair members. Our measure of reproductive success, however, was limited by our ability to monitor chick survival and a more direct measure of recruitment might have revealed some relationship to the incidence of divorce.

Support for the better option hypothesis (Ens et al. 1993) is somewhat equivocal. One of the predictions of this hypothesis is that divorce should occur more often after a winter of high mortality of one sex, since higher-quality mates (or mates with better territories) should become more available. Although 47% of the females failed to return the second year of our study, presumably due to high overwinter mortality, none of the returning females divorced to pair with one of the returning widowed males. A second prediction is that one member should increase reproductive success after divorce, sometimes at the expense of the former mate's subsequent success. Our data also failed to support this prediction.

The most evident mechanism operating in divorce among turnstones was related to the differential arrival of pair members. Because of higher reproductive success among reuniting pairs, the best option for a returning adult is to return to its former territory and pair with its former mate. If the bird's former mate fails to return, then the 'better option' may be to pair with a new bird rather than to risk remaining unpaired, which occurred with some males. Males, which generally return before their mates, may choose to pair with any female they can attract. Displacement of such inexperienced females by late-returning females was probably driven by the benefits accrued by reuniting with former mates, and could have been the result of either male choice or dominance of the former female mate. The single divorce documented among highly mate-faithful willets was thought to have occurred because of disparate spring arrival times of pair members (Howe 1982). One instance of female mate-displacement was also described for willets; this suggests that similar social forces may be operating in the two species.

If females arrive before their former mates, it is likely that the males will not return. Thus, the 'better option' for females would be to pair with a new male rather than to risk remaining unpaired. The only divorced males that nested on their former territories were those that paired with widowed females that had returned before they did. Thus, divorce may have been instigated by the male, exercising the 'better option' of pairing early with a familiar, experienced female or by the widowed female, exercising the 'better option' of pairing with a familiar, experienced male and ousting his former female mate. The latter could also be construed as supporting the forced divorce hypothesis (B. Taborsky & M. Taborsky, personal communication, in Choudhury 1995), in which divorce is caused by the intrusion of a third bird that is dominant over and displaces the former mate. The fact that the widowed females arrived before either of the divorcing birds, however, argues for active mate choice by the divorcing male and victimization of the divorcing female. In this case, the better option hypothesis is supported more strongly than the forced divorce hypothesis.

The accidental loss hypothesis was invoked by Owen et al. (1988) to explain divorce that occurs through temporary loss of a partner, such as accidental separation during migration, among pairs that normally remain together year-round. This hypothesis is not supported for turnstones because pair members did not winter together. The basic operating mechanisms may be similar, however, because the late-returning mates may have been delayed by some external event, such as bad weather.

The main characteristic of divorce in turnstones is that adults choose to pair with new mates when there is uncertainty about the return of their former partners. We propose the 'bet-hedging' hypothesis to explain this

phenomenon, in which an individual should pair with a new mate to avoid the cost of waiting for a possibly dead mate to return (Soikkeli 1967; Rowley 1983). One potential cost would be remaining unmated, which we recorded only for males. A second potential cost would be lower reproductive success because of delayed breeding with a late-returning mate. This idea is supported by the fact that fledging success was significantly lower for second breeding attempts later in the season (unpublished data). Because replacement clutches are only attempted if the first clutch is lost during the first few days of incubation, success of second attempts most closely simulates the effect that might have occurred if birds had waited longer for late-returning mates. In the bet-hedging strategy, both sexes return to former breeding territories, a male courts all females until paired, and a female pairs with the unattached male closest to her previous territory if her former mate fails to return. This strategy has also been recorded for Adélie penguins, *Pygoscelis adeliae*, and macaroni penguins, *Eudyptes chrysolophus* (Davis & Speirs 1990; Williams & Rodwell 1992). Williams & Rodwell (1992) contended that male macaroni penguins aimed primarily to retain their old nest sites rather than former mates, but our data show that reproductive success of turnstones increases as a result of reuniting with their former mates rather than retaining their former territories.

Acknowledgments

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