Return rates of male and female monogamous shorebirds to their breeding grounds

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This paper summarizes available information on breeding area tenacity of males and females in 29 species of migratory shorebirds. Of these, return rates were male-biased in 25 species. However, the difference between the sexes was often relatively small, and sometimes reversed from one season to another or from one study area to another. In the four species where site tenacity was not male-biased (all single investigations), two taxa showed equal return rates and two were slightly female-biased. Among all species considered, certain of the longest-distance migrants (especially *Pluvialis squatarola, P. dominica, P. fulva, Tringa flavipes, Heteroscelus incanus, Calidris tenuirostris* and *C. canutus*) showed the greatest gender-related variation with breeding ground fidelity strongly favouring males.

INTRODUCTION

Site-faithfulness to breeding grounds may influence stability of local populations (Parr 1980, 1992; Hitchcock & Gratto-Trevor 1997), and enhance lifetime reproductive success of individuals through past experience on the nesting area (Miller 1983, Oring *et al.* 1983, Thompson & Hale 1989). Familiarity with the site and with neighbours is presumed to be highly beneficial, especially for males competing with conspecifics for nesting territories (Oring & Lank 1984). Therefore, when males in a migratory monogamous species establish territories before attracting a mate the result is likely to be male-biased site tenacity and female dispersal (Greenwood 1980). Male-biased return rates are relatively common in shorebird breeding ground studies, though intersexual differences are often relatively small and not statistically significant. Furthermore, the degree of male-bias varies widely among species, and also intraspecifically (i.e., between populations and between years in the same population). In this paper, we examine published information on male and female return rates of monogamous shorebirds in relation to the distance over which they migrate and the geographic latitude of their nesting grounds. Our intent is to provide a compilation useful to workers studying shorebird reproduction.

METHODS

The data represent a literature survey (selective for papers containing either gender-related return calculations or data from which such calculations could be derived), plus J. Klima's unpublished studies of American Golden-Plovers *Pluvialis dominica* at Churchill, Manitoba in 1999–2002 and J. R. Jehl's unpublished studies of Semipalmated Sandpipers *Calidris pusilla* from the same locality in 1993–2001. For the most part, return rates cover more than one post-banding season, and represent the ratio between the cumulative number of returnees relative to the cumulative number of marked birds (29 studies). In this approach an individual is counted in each season that it returns. Less commonly (14 studies), a returning individual is counted only once no matter how many times it returns. Such non-cumulative rates can be based on only the first post-banding year or any post-banding year. Some investigators (6 studies) have used statistical modelling (see Sandercock 2003) to estimate the apparent survival rate of each sex.

Generally, only those return rates based on more than 10 marked birds are considered in this review. Exceptions were made where small samples were in accord with other investigations as with Grey Plovers *P. squatarola* (Moitoret *et al.* 1996, Sviridova 2000), and American Golden-Plovers (Moitoret *et al.* 1996), and where relatively small numbers of individuals were observed over several years, as with Long-billed Curlews *Numenius americanus* (Redmond & Jenni 1982) and Ruddy Turnstones *Arenaria interpres* (Bergman 1946). Wherever return rates are known for more than one population of a species (or for subspecies in the case of Dunlins *Calidris alpina*), the findings are presented separately.

It is impossible to know the precise migration distances associated with the population(s) reported in the various studies. Therefore, we approximated distances by measuring probable migratory pathways. To do this, we measured on a globe the most direct orthodromic route from roughly the mid-latitude of the winter range (based on the maps in Hayman *et al.* 1986) to the location of each breeding ground study site. From these measurements, we divided most of the studies into three categories: migration over long distances (8,000–14,000 km), moderate distances (4,000–7,000 km), and relatively short distances (<4,000 km). There were several studies involving populations of uncertain mobility and we placed these in a fourth category. The latter grouping consists of birds likely to be relatively sedentary or possibly migrating only a few hundred kilometres.

RESULTS

The data are summarized in Table 1. Return rates of males exceeded those of females in all but four species (Eurasian Oystercatcher *Haematopus ostralegus*, Long-billed Curlew, Marbled Godwit *Limosa fedoa*, and Red-necked Stint *C. ruficollis*) though intersexual differences were very slight in some cases. Furthermore, multiple studies of the same species (or subspecies in *C. alpina*) showed varying degrees of male-bias. Male-bias of 15% or more occurred within each of the three migration categories. However, the most striking evidence of a difference between the sexes was among long-distance migrants (8,000–14,000 km). Of these, male-bias was particularly strong (ranging from 28–67%) in Grey Plovers, American Golden-Plovers, Pacific Golden-Plovers *P. fulva*, Lesser Yellowlegs *Tringa flavipes*, Wandering Tattlers *Heteroscelus incanus*, Bristle-thighed Curlews *Numenius tahitiensis* in one of two studies, Great Knots *C. tenuirostris*, and Red Knots *C. canutus*. The return rates of several other long-distance travellers (Semipalmated Sandpipers, Western Sandpipers *C. mauri*, Red-necked Stints, and Spoon-billed Sandpipers *Eurynorhynchus pygmeus*) were substantially less biased, ranging from essentially no difference between the sexes to male-bias of 15%. In six species (Eurasian Golden-Plover *P. apricaria*, American Golden-Plover, Eurasian Oystercatcher, Common Sandpiper *Actitis hypoleucos*), Semipalmated Sandpiper, and the southern race of European Dunlin *C. a. shinzii*) there were studies in which females returned in higher proportions than males in some seasons, but multi-year averages were either male-biased or almost equal.

Across the species studied, the return rates of males and females were moderately and significantly correlated ($r = 0.55$, $p < 0.0005$). In both sexes, return rates were negatively correlated with the latitude (Table 1) of the nesting site. This influence was strong and statistically significant in females ($r = -0.59$, $p < 0.0001$, $n = 49$); weak and non-significant in males ($r = -0.19$, $p = 0.10$, $n = 49$). Similarly, return rates of both sexes were inversely related to migration distance (Table 1). Mean rates among females were 36%, 59%, and 73% for long, medium, and short distance migrants, respectively; corresponding values among males were 67%, 73%, and 80%, respectively. These rates were significantly different for females (ANOVA, $F = 11.48$, $df = 2$ and 39, $p < 0.001$); but not for males (ANOVA, $F = 1.43$, $df = 2$ and 39, $p = 0.25$).

Table 1. Records of breeding area tenacity.

Species	Mean return rates(%)						
	Males	Females	M–F	Calc.[a]	Lat.[b]	Seasons[c]	Source
Studies involving long-distance migration (8,000–14,000 km)[d]							
Pluvialis squatarola	78	17	61	c	76 EA	2	1
P. squatarola	63	0	63	c	73 EA	2	2
P. squatarola	72	44	28	c	71 EA	6	3
	53–92[e]	27–67[e]					
P. squatarola	100	33	67	nc	70 NA	4	4
P. dominica	57	0	57	nc	70 NA	4	4
P. dominica	80	15	65	c	65 NA	12	5
P. dominica	72	41	31	c	59 NA	3	6
	67–86	8–73	–6+78[e]				
P. fulva	38	0	38	nc	74 EA	1	2
P. fulva	59	8	51	c	73 EA	2	2
P. fulva	77	25	52	c	65 NA	12	5
Tringa flavipes	92	40	52	nc	61 NA	1	7
Heteroscelus incanus[f]	89	56	33	nc	61 NA	2	8
Numenius tahitiensis	81	82	–1	nc	66 NA	3	9
N. tahitiensis	100	63	37	nc	62 NA	3	9
Calidris tenuirostris	92	50	42	c	65 EA	2	10
C. canutus	63	10	53	c	76 EA	2	1
C. pusilla	68	53	15	nc	70 NA	4	4
C. pusilla	57	58	–1	c, a	59 NA	8	11
	33–82	0–100	–40+33				
C. pusilla	48	44	4	c, a	59 NA	4	12
	37–57	33–57	0–6				
C. pusilla	61	56	5	sm	59 NA	6	13
C. pusilla	73	59	14	sm	64 NA	2	14
	70–77	56–63					
C. mauri	16	6	10	c	66 EA	2	1
C. mauri	60	57	3	sm	64 NA	2	14
	57–62	55–59					
C. ruficollis	22	23	–1	c	66 EA	2	15
Eurynorhynchus pygmeus	67	64	3	c	63 EA	2	16

(continued)

(Table 1. continued)

Species	Mean return rates(%)						
	Males	**Females**	**M–F**	**Calc.[a]**	**Lat.[b]**	**Seasons[c]**	**Source**
Studies involving medium-distance migration (4,000–7,000 km)							
Charadrius hiaticula	100	79	21	nc	56 EA	1	17
Ch. semipalmatus	59	41	18	nc	59 NA	5	18
	41–80	36–50	3–30				
Ch. semipalmatus	71	71	0	sm	59 NA	7	19
N. phaeopus	87	68	19	c	61 EA	2	20
Limosa limosa	78	69	9	nc	53 EA	7	21
C. mauri	58	49	9	c, r	62 NA	2	22
	46–68	38–60					
C. minutilla	65	38	27	nc	44 NA	1	23
C. maritima	60	54	6	nc	79 EA	**7**	24
C. alpina sakhalina	77	62	15	c	66 EA	2	25
Studies involving short-distance migration (<4,000 km)							
Ch. melodus	75	56	19	c	50 NA	3	26
N. americanus	67	73	–6	c, a	42 NA	4	27
L. fedoa	96	96	0	sm	51 NA	2	28
Arenaria melanocephala	88	79	9	c	61 NA	4	29
	84–93	53–88	0–40				
C. ptilocnemis	79	68	11	c	66 EA	2	25
C. alpina shinzii	77	72	5	c	62 EA	7	30
	64–84	63–93	–9+22				
C. a. shinzii	89	77	12	c	55 EA	5	31
	83–92	71–90	–1+17				
C. a. shinzii	67	65	2	c, a	54 EA	5	32
Studies of populations with uncertain mobility							
P. apricaria[g]	74	69	5	c	57 EA	15	33
	0–100	0–100	–33+35				
Haematopus ostralegus	90	90	0	c	52 EA	14	34
	82–98	84–96	–5+4				
Tringa totanus[h]	76	71	5	nc	54 EA	3	35
T. totanus	42	35	7	c, r	54 EA	2	36
	40–44	33–37					
T. totanus	75	72	3	sm, r	54 EA	12	37
Actitis hypoleucos	64	58	6	c	53 EA	12	38
	35–83	33–75	–25+40				
Ar. interpres	87	70	17	c	60 EA	2–4	39

[a] Return rate calculations varied among studies (see Methods): c = cumulative, nc = non-cumulative, sm = statistical modelling in which results depend both on observed return rates and on the statistical model used; a = rate calculated from data contained in the paper cited; r = identification of individuals required recapture in post-banding years and the influence of this method on return rates is uncertain.

[b] Latitude (in degrees north) of the research site, and whether in Eurasia (EA) or North America (NA).

[c] Post-banding seasons (i.e., the number of seasons during which the study site was monitored for returnees).

[d] See Methods.

[e] Ranges shown where studies include sufficient data and interyear variation exceeds 10%. Variability in M–F percentages are given for studies that detail year-by-year return rates for each sex.

[f] This study was conducted in Alaska, and it was uncertain whether birds were from wintering grounds along the Pacific coast of North and South America (±5,000 km), from Oceania (±8,000 km), or both.

[g] Data are from a population in decline that ultimately disappeared from the study site.

[h] Nesting in this species is semi-colonial and non-territorial, how this might affect return rates is uncertain.

Sources:

1. Tomkovich & Soloviev 1994; 2. Sviridova 2000; 3. Ryabitsev 2000; 4. Moitoret *et al.* 1996; 5. Johnson *et al.* 2001a; 6. J. Klima, unpubl. data; 7. Tibbitts & Moskoff 1999; 8. Gill *et al.* 2002; 9. Marks *et al.* 2002; 10. Tomkovich 1996, 2002; 11. J. R. Jehl unpubl. data; 12. Gratto-Trevor *et al.* 1985; 13. Sandercock & Gratto-Trevor 1997; 14. Sandercock *et al.* 2000; 15. Morozov & Tomkovich 1986; 16. Tomkovich 1994a; 17. Pienkowski 1984; 18. Flynn *et al.* 1999; 19. Badzinski 2000; 20. Grant 1991; 21. Jonas 1979; 22. Holmes 1971; 23. Miller 1983; 24. Payne & Pierce 2002; 25. Tomkovich 1994b; 26. Haig & Oring 1988; 27. Redmond & Jenni 1982; 28. Gratto-Trevor 2000; 29. Handel & Gill 2000; 30. Soikkeli 1970; 31. Jönsson 1991; 32. Heldt 1966; 33. Parr 1992; 34. Safriel *et al.* 1984; 35. Grosskopf 1959; 36. Thompson & Hale 1989; 37. Thompson & Hale 1993; 38. Holland & Yalden 1991; 39. Bergman 1946.

DISCUSSION

In all species with multiple data sets, there were wide-ranging differences in return rates between years and among populations (Table 1). Additional studies would probably reveal similar patterns in other shorebirds. Factors likely to influence this variation include: 1) winter survival, which in well-studied European populations is known to be highly variable (Peach *et al.* 1994, Goss-Custard *et al.* 1996); 2) unfavourable changes (sometimes human-caused) in local habitats that can prevent nesting (Thompson *et al.* 1988, Hitchcock & Gratto-Trevor 1997, Flynn *et al.* 1999); 3) late snowmelt (especially critical at high latitudes where the nesting period is short) that can render habitat unavailable and displace returning birds (Sviridova 2000, Johnson *et al.* 2001a); 4) previous nesting success which is often directly related to the number of birds returning the next season (Gratto *et al.* 1985, Haig & Oring 1988, Flynn *et al.* 1999, Ryabitsev 2000); 5) location of the study site as return rates may be generally higher in core parts of the breeding range (Tomkovich & Soloviev 1994); 6) weather during migration and the early arrival period (Holland & Yalden 1991); 7) physiological conditioning (i.e., was there sufficient pre-migratory fattening on wintering grounds and refuelling at stopovers?); 8) the timing of fieldwork (especially delayed arrival of observers in the spring) that may skew apparent return rates (Johnson *et al.* 2001a).

Male-bias was especially evident among long-distance migrants on breeding ranges in the far north (Grey Plover, American Golden-Plover, Pacific Golden-Plover, Lesser Yellowlegs, Wandering Tattler, Bristle-thighed Curlew (in one of two studies), Great Knot, and Red Knot; Table 1). Of these taxa, studies involving sizeable numbers of marked Pacific Golden-Plovers (Johnson *et al.* 2001b, 2004) and Bristle-thighed Curlews (Marks *et al.* 2002) indicate similar mortality rates for males and females. Such findings suggest that strongly male-biased return rates in shorebirds do not result from differential mortality, but instead reflect divergent benefits of site-tenacity for each sex. Presumably, a male benefits by returning to a familiar territory that he can reclaim with minimal conspecific hostility, whereas the benefits for a female (less engaged in territorial behaviours than the male) are fewer. If a returning female finds her former mate on a territory that is mostly unusable because of lingering snow-cover and/or meltwater, she may react by moving on and pairing with a different male (quite possibly at considerable distance from the study site) that has a territory more suitable for nesting (Tomkovich & Soloviev 1994, Johnson *et al.* 1997). Aside from snow and meltwater considerations, there are at least two other factors that might in some instances preclude the reunion of former partners. A female may arrive on breeding grounds only to find that her previous mate is already paired (Johnson *et al.* 2001a), or that a new male less attractive to her has claimed the territory. As with unusable territories, either of these situations could cause a female to disperse far enough that she would go undetected by investigators. Finding her former mate already paired would most likely result from asynchronous spring arrival of previous partners, however there is also the possibility that at least some new pairs form either during stopovers en route to breeding grounds or pre-departure from wintering grounds (Oring & Lank 1984, Connors *et al.* 1993, Tomkovich & Soloviev 1994, Sviridova 2000, Johnson *et al.* 2001a).

Of the 12 long-distance migrants listed in Table 1, there are four taxa (Semipalmated Sandpipers, Western Sandpipers, Red-necked Stints, and Spoon-billed Sandpipers) that do not conform to the pattern of strong male-bias just outlined. Eleven of the 12 species nest exclusively on tundra (the exception being the Lesser Yellowlegs, a bird that nests primarily in forested or brushy habitats, rarely on tundra; see Tibbitts & Moskoff 1999). Gender-biased site tenacity varied widely in the medium- and short-distance groups (Table 1). Among the species listed, Purple Sandpipers *C. maritima* breeding on high latitude tundra showed weak male-bias of 6%, whereas Least Sandpipers nesting much further south in sand dune habitat were more strongly male-biased at 27%. Notably, three of four studies involving the closely allied charadriids (Ringed Plover *Charadrius hiaticula*, Semipalmated Plover *Ch. semipalmatus*, and Piping Plover *Ch. melodus*) indicate similar male-biased fidelity (18–21%, Table 1) despite marked differences in migration distances and breeding habitats. The Ringed and Semipalmated Plovers are arctic and sub-arctic breeders, whereas Piping Plovers nest in mid-continental and east coast regions of North America.

Although general conclusions about a species' breeding area tenacity may remain the same with any method of calculation, actual numbers will, of course, vary. For example, the male and female return rates of Pacific Golden-Plovers at study sites in western Alaska were 77% and 25% according to cumulative counts whereas non-cumulative rates were 75% and 17%; comparable figures for American Golden-Plovers at the same sites were 80% and 15% vs. 73% and 9% (Johnson *et al.* 2001a). Ideally, comparisons of fidelity between regions should involve studies using the same methods. Because intersexual differences in return rates can be substantial (Table 1), we urge investigators to provide separate records for males and females whenever possible.

ACKNOWLEDGEMENTS

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