Social constraints on access to mates in a high density population of New Zealand Snipe (*Coenocorypha aucklandica*)

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ABSTRACT

A colour-banded sample of New Zealand Snipe (*Coenocorypha aucklandica*) was studied on the Snares Islands over six breeding seasons. Snipe reached densities of 11.5 birds/ha; they were serially monogamous, but alpha males regained their original partner and territory at the start of the following breeding season. Up to 47% of males and 30% of females were excluded from breeding each year, although they were tolerated within breeding territories. Breeding adults were highly faithful to their territories and mates regardless of previous breeding success. About 83% of adults were seen in the study area the year after banding. No males moved to different territories, and only 11% of females moved, all to adjacent territories. Less than 9% of breeders changed partners between years if their previous mate was still present.

Territory area was not influenced by intruder density; in years of high population density a higher proportion of birds was excluded from breeding. Nonbreeding adults obtained a territory or mate only if a territorial bird died. Prior residence was an important factor in acquiring a territory both within and between breeding seasons. Mortality was density-dependent, and a relatively constant proportion of nonbreeding birds was assimilated into the breeding population each spring.

New Zealand Snipe were faithful to their natal area; 46% of fledglings were later seen in the study area. There was no sex bias in return rates, but females tended to disperse slightly further than males. About 11% of males and 57% of females bred as 1-year-olds. Previously nonterritorial birds (beta status) gained access to territories and mates when alpha status birds were caring for chicks. No inbreeding was recorded.

KEYWORDS: New Zealand Snipe, *Coenocorypha aucklandica*, territory, philopatry, natal dispersal, mate fidelity, mortality, migration, Snares Islands

INTRODUCTION

Dispersal patterns of birds and mammals are closely linked with social structure (Greenwood 1980, Oring & Lank 1984). Greenwood (1980) concluded that sex-biased dispersal was driven largely by reproductive enhancement through increased access to mates or resources and the avoidance of inbreeding. In birds, where the predominant social system involves resource defence by males, females tend to disperse further than males.

Landbirds on islands typically live at high densities (e.g. Yeaton 1974, Case *et al.* 1979, Emlen 1979, Crowell & Rothstein 1981, Arcese & Smith 1988) and may

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have contiguous territories occupying all available habitat (Grant 1968, Barlow 1974). In monogamous species that do not breed communally, territorial behaviour by socially dominant individuals may prevent subordinates from gaining territories or mates (Brown 1969, Davies 1978, Wittenberger 1981). In some dense populations, the virtual absence of 'dispersal sinks' (suboptimal habitats where mortality exceeds natality; Emlen 1979, Atwood 1980) forces nonterritorial birds to occupy territories claimed by socially dominant birds (e.g. Tompa 1964, Price *et al.* 1983). Under these circumstances, recruitment of new birds into the breeding population may be constrained by spatial and temporal patterns in territory vacancies (e.g. death or emigration of breeding birds). For species that occur at high densities in relatively uniform habitats, dispersal of new and established breeders may be determined by the availability of territories or mates, rather than factors such as habitat quality or inbreeding avoidance.

The relationship between social structure and dispersal has been studied in many species of waders in the family Scolopacidae (see review in Oring & Lank 1984). The two components of dispersal usually considered are breeding site fidelity (return rates of breeding adults to the same breeding location in successive years) and natal philopatry (the breeding of young birds near their birth place; Oring & Lank 1984, Thompson & Hale 1989). Monogamous scolopacids tend to be territorial, with high breeding site fidelity by both sexes, and low sex-biased natal philopatry, e.g., Dunlin *Calidris alpina* (Holmes 1966, Soikkeli 1970a), Western Sandpiper *C. mauri* (Holmes 1971), Semipalmated Sandpiper *C. pusilla* (Gratto *et al.* 1985), Stilt Sandpiper *Micropalma himantopus* (Jehl 1973), Long-billed Curlew *Numenius americanus* (Redmond & Jenni 1982), Whimbrel *N. phaeopus* (Skeel 1983) and Redshank *Tringa totanus* (Thompson & Hale 1989). The tendency towards slightly male biased breeding site fidelity in these species has been attributed to variation in territory fidelity of the two sexes (Oring & Lank 1984): males that change mates often retain the same territory in subsequent years, whereas females that change mates usually move to a new territory, which may be beyond the boundaries of the study area.

All the studies listed above deal with migratory scolopacids breeding in the Northern Hemisphere; no published studies have described breeding dispersal by the 18% of scolopacid species that are non-migratory. Most non-migratory members of the family breed in the Southern Hemisphere (Hayman *et al.* 1986). The New Zealand Snipe (*Coenocorypha aucklandica*) is a non-migratory wader that is now confined to four small oceanic island groups, each with an endemic subspecies (Hayman *et al.* 1986, Judd 1998). New Zealand Snipe on the Snares Islands live at high densities and many birds are unable to obtain a territory or mate (Miskelly 1990a). This paper describes social structure, dispersal patterns and mortality rates in a colour-banded sample of New Zealand Snipe on the Snares Islands, focusing on factors that limit access to mates. Differences in breeding dispersal patterns between New Zealand Snipe and other scolopacids are discussed with regard to the constraints imposed by a sedentary habit and intense competition for mating opportunities.

STUDY AREA & METHODS

A colour-banded sample of New Zealand Snipe was studied at Snares Islands Nature Reserve (48°02'S, 166°36'E) during all breeding seasons from 1982/83 to 1987/88. Fieldwork was carried out between September and March, which encompassed all egg-laying, and rearing of all but the latest-hatching chicks (Miskelly 1990a). A total of 541 days of observations was made, including 64 days by G.J. Eller in 1983/84, when I was absent from the island.

The study area was situated just north of the Biological Station on Main (North East) Island and was marked out in a 20 m grid. During the first two field seasons the study area was about 4 ha, but it was extended to 7.5 ha in 1984/85. About 61% of the study area was under a tight 6 - 10 m canopy of *Olearia lyalli*, with some *Brachyglottis stewartiae*; 28% was open, and 12% was under a 2 - 4 m canopy of *Hebe elliptica*. Ground cover was a mosaic of bare peat (32%) and tussock (29%, mainly *Poa tennantiana*), with smaller areas of fern (13%, mainly *Polystichum vestitum*), swards of *Callitriche antarctica* and *Crassula moschata* (10%), bare rock (6%), mud (5%), and *Stilbocarpa robusta*, penguin colonies and open water (2% each).

Adult snipe were captured by handnet during the day, or by spotlight and handnet at night. All 21 - 64 adult snipe resident in the study area each year were individually colour-banded (total = 93) and assigned to one of five social classes (see Results) on the basis of intraspecific interactions. Adults were sexed by measurements and sex-specific displays (Higgins & Davies 1996). Locations of marked birds were recorded on the grid during daily surveys of the study area. Territory boundaries were identified by observing territorial disputes and by plotting sightings of calling males during the courtship and incubation stages of the breeding cycle. Territory areas (and the area of zones of overlap between years for each male's territory) were estimated with a polar planimeter (mean of three replicates from each of two pole positions). Pairs were identified by prolonged consorting, courtship feeding, mating or attendance at the same nest.

Forty-five nests were found in the study area (Miskelly 1990a). Chicks were banded in the nest (n = 29) or while accompanying an adult (n = 69). An adult was considered to have failed if its dependent chick disappeared prematurely (the adult was seen three or more times unaccompanied by a chick, and the chick was not seen subsequently). Areas of suitable habitat in a band 400 m wide around the study area were searched regularly (every 2 - 3 days) for snipe with leg bands. Snipe seen by expedition members elsewhere on the island (maximum of 2.3 km from the study area) were routinely checked for bands.

Measurements are given as mean ± s.d. unless otherwise stated.

RESULTS

Social structure

Territory defence by New Zealand Snipe was performed solely by males. At the start of each breeding season the study area was divided into contiguous, non-

TABLE 1 - Density of snipe (birds/ha) in the study area 1982/83 to 1987/88. For each season, densities were calculated for only those birds whose entire territory or home range was contained within the artificial boundaries of the study area, hence total areas given in the table are slightly less than for the full study area, i.e. 4 ha for 1982-84 and 7.5 ha for 1984-88.

Year	Area (ha)	Males				Females			Total
		Gamma	Beta	Alpha	Total	Beta	Alpha	Total	
1982/83	3.91	0.77	1.28	2.56	4.60	0.77	1.79	2.56	7.16
1983/84	3.91	-	0.77	2.81	3.58	0.51	1.28	1.79	5.37
1984/85	5.59	0.18	0.89	3.04	4.11	0.72	2.15	2.86	6.98
1985/86	5.59	0.54	2.68	3.58	6.80	1.25	3.40	4.65	11.45
1986/87	5.28	0.38	1.14	3.79	5.30	0.38	3.98	4.36	9.66
1987/88	5.16	0.19	0.58	3.68	4.46	0.39	3.88	4.26	8.72

overlapping territories of 0.08 - 0.63 ha (0.27 ± 0.12 ha, n = 82). Males defended their territories by Loud Calling (Miskelly 1990b, 1999, Higgins & Davies 1996) and, occasionally, by fighting (Miskelly 1984, Higgins & Davies 1996). Those males that maintained exclusive territories at the start of a breeding season (November) were defined as alpha males, and comprised 53 - 83% of the resident males each year (Table 1).

Territory ownership by a male was a prerequisite for obtaining a mate, but 7 of 82 alpha males (9%) did not have mates for one breeding season. The remaining alpha males were behaviourally monogamous, with the exception of one simultaneously polygynous male in each of four years (Miskelly 1989a & 1990a). All mates of alpha males at the start of a breeding season were defined as alpha females, and comprised 70 - 91% of the resident females each year (Table 1). The remaining 9 - 30% of females were referred to as beta females.

During courtship and incubation, alpha males defended their territories against all other Loud Calling males. Silent males (and all females) fed unchallenged within any territory, although alpha males guarded their mates before incubation commenced by chasing any male which approached within 2 m of the alpha female. Forty-four different nonterritorial males were seen within alpha males' territories on 641 occasions; on 68 occasions the intruder was seen within 10 m of the resident alpha male. Alpha males attacked or chased 14 intruders that called, plus a further two that approached the alpha female; 52 intruders were ignored or displayed to, without being attacked or chased from the territory.

Following hatching, males cared for the first chick to leave the nest, and females cared for the second (final) chick (Miskelly 1990a). Any bird that lost a dependent chick attempted to obtain a new mate while its original mate cared for the surviving chick. Alpha males with newly-hatched chicks attempted to maintain their territory, but most were unable to evict other Loud Calling males, and after 1 - 2 days devoted all their time to chick-rearing. Only one alpha male successfully defended his territory while raising a chick (the simultaneously polygynous male in 1986/87; Miskelly 1989a). Territories of the remaining 24 alpha males with dependent young were usurped by one or more previously nonterritorial males, each of which then maintained an exclusive territory. A male that did not hold a territory in November, but who challenged an alpha male and/or claimed a territory while the previous owner was raising a chick, was classified as a beta male. All beta males that obtained territories late in the season had home ranges that had overlapped with the previous owner's territory within a breeding season.

Beta males comprised 13 - 40% of the resident male population each year (Table 1). After obtaining a territory, beta males courted any resident female that did not have a dependent chick - either an alpha female that had lost her chick (n = 5), or a beta female (n = 5). One beta male in 1985/86 and another in 1986/87 obtained mates that subsequently laid; both females were alpha females whose original mates were still raising a chick.

The remaining 0 - 17% of males each year, termed gamma males, did not have fixed home ranges and did not attempt to gain territories (Table 1).

Alpha males that lost their dependent chick, immediately reclaimed their former territory (n = 16) and courted any resident female that did not have a dependent chick - usually their previous mate (n = 12, six of which laid again), but occasionally another alpha female (one, which laid) or a beta female (two, one of which laid). The remaining failed alpha male was unsuccessful in attracting a second mate.

Movement between social classes and age of first breeding

Movement between social classes occurred in one direction only, although 25 - 33% of the beta status birds of both sexes retained that status for two breeding seasons (Table 2). All ten gamma males were presumed to be 1-year-olds; two birds were of known age (banded as chicks) and none remained a gamma male for more than one season. The beta male class was comprised of almost equal numbers of 1- and 2-year-olds. All males aged 3 years or older were alpha males. Two 1-year old males defended territories at the start of the breeding season (alpha male status) but neither obtained a mate.

The youngest male recorded breeding was a 1-year old beta male; the same bird also bred as an alpha male at 2 and 3 years old. The only other known-age male breeders were a beta male at 2 years old and an alpha male at 3 years old.

Females bred younger than males: 71% were paired at 1-year old (Table 2). The beta female class was comprised of similar numbers of 1- and 2-year-olds. All females aged 3 years or older were alpha females.

Once a bird of either sex attained alpha status, it retained that status until it disappeared from the study area (presumed dead).

Four of seven 1-year old females bred (57%), compared with one of nine 1-year old males (11%) (Fisher's exact test, P = 0.106). Three females first bred as 2-year-olds, and two as 3-year-olds.

TABLE 2 – Movement of snipe through social classes. Social status in the first year (Year N) is given across the top of each column; social status in the following year (Year N + 1) is given in each row. For example, social status was determined for 12 one-year-old males that had been banded as chicks: 2 were gamma males, 8 were beta males and 2 were alpha males.

A. Males			Year N		
		Chick	Gamma	Beta	Alpha
	Gamma	2	-	-	-
Year N + 1	Beta	8	1	6	-
	Alpha	2	2	18	76

B. Females			Year N	
		Chick	Beta	Alpha
	Beta	4	3	-
Year N + 1	Alpha	10	6	65

Natal philopatry, dispersal and inbreeding

In birds, natal philopatry is usually estimated by banding a large number of chicks, then recording the number of each sex subsequently found as breeders in the study area (Oring & Lank 1984). If natal dispersal is low, an estimate of natal philopatry may simply reflect sexual differences in pre-breeding survival. However, pre-fledging mortality in shorebirds is usually very high (e.g. Green 1988, Thompson & Hale 1989), therefore the age at which chicks are marked greatly influences estimates of natal philopatry and survival to breeding age (Thompson & Hale 1989).

Of 98 snipe chicks handled on the Snares Islands, 29 were banded on the day of hatching (usually within the nest bowl) and 69 were banded at 1 - 78 days old. Three (10.3%) chicks banded in the nest were recovered in or near the study area at breeding age (1+ years old); 26 (37.7%) chicks banded away from the nest were recovered at breeding age. Chicks banded away from the nest were more likely to be recovered in subsequent years than chicks banded on the day of hatching ($\chi^2 = 7.32$, $P = 0.007$), because most nestling mortality occurred within a day of hatching (Miskelly 1990a and Table 3). Late-hatching chicks were just as likely to be recovered in subsequent years as early-hatching chicks (Miskelly 1990a). About 46% of fledglings were found as 1-year-olds.

The 29 1-year-olds recaptured in or near the study area were divided equally by sex: 14 males (14% of chicks banded) and 15 females (15%). Natal dispersal distances of the sexes was estimated by measuring the distance between the centres of natal and first own-territories for 17 known-age snipe. Nine females moved 202 ± 87 m (range 80 - 350 m), significantly further than eight males (113 ± 86 m; range 0 - 260 m) ($t_{15} = 2.14$, $P = 0.049$). Note that territories averaged about 58 m in diameter.

Sex-biased natal dispersal is often claimed to be an inbreeding avoidance mechanism (Bischof 1975, Packer 1979, Greenwood 1980). Although natal disper

TABLE 3 – Sightings of known-age adult snipe in or near the study area in relation to age of last capture (or sighting) as a chick. Recovery rates at 1-year old did not differ for early- and late-hatching chicks (Miskelly 1990a).

Age at last capture (days)	No. of chicks captured	No. recovered at age 1+ years	% recovered
0 (in nest)	16	1	6.3
1 - 20	20	4	20.0
21 - 40	16	6	37.5
41 - 60	23	7	30.4
61 - 80	11	5	45.5

sal distances of male and female snipe overlapped, sibling-sibling inbreeding was unlikely due to the low probability of two siblings of opposite sex surviving to breeding age (about 1.4%) combined with the low probability of the members of an alpha pair both dying at the time when the two siblings were attempting to obtain their respective territories (about 2.2%). Parent-sibling inbreeding was also unlikely due to the low probability of an alpha status bird dying the same year that its same-sex offspring was looking for a territory (about 2.4% for males and 1.9% for females).

No instances of inbreeding were recorded during the six years of this study. However, only two pairings were recorded where both birds were of known parentage, along with 15 pairings where one bird was of known parentage. Adults of unknown parentage were either raised outside the study area (n = 40) or were adults when the study began (n = 35).

Breeding dispersal and survival of adults

Alpha males and alpha females that held territories within the study area were never subsequently found on territories outside the study area. Estimated breeding site fidelity (Table 4) is probably an accurate estimate of the mean annual survival rates of breeding males and females. A few nonbreeders (beta and gamma status) banded in the study area were later found on territories up to 180 m outside the study area (see Natal philopatry), but recovery rates of these birds (Table 4) are also considered accurate estimates of between-year survival. No snipe of any age was seen further than 350 m from where it was banded.

Social status had no effect on the probability of a bird being recovered in the subsequent year (Table 4). Mean adult breeding site fidelity (= survival) was 83.3%.

Territory and mate fidelity

Alpha males never lost their territory-holding status between seasons (n = 76; Table 2). To determine whether alpha males changed territory location between seasons, I compared territory overlap between consecutive years. If a male retained the same territory in consecutive years, overlap would be 100%; if a male

TABLE 4 – Sightings of adult snipe of known breeding status in or near the study area one year after banding. Birds were counted more than once if present in the study area for three or more years. All between group comparisons of return rates were nonsignificant (P > 0.05).

	No. present Year N	No.present Year N+1	%	χ^2	P
Alpha male	78	64	82.1	0.16	0.69
Beta & gamma males	43	34	79.1		
Alpha female	64	56	87.5	0.21	0.65
Beta female	18	15	83.3		
Total male	121	98	81.0	1.10	0.30
Total female	82	71	86.6		
Total	203	169	83.3		

moved to a new part of the study area, overlap would be zero. Territory maps for the same male in consecutive years were obtained for 23 different males (1 - 3 cases each, total = 44 cases). Mean percent overlap between consecutive years was 53.1 ± 19.1% (range 9.9 - 94.7%). Once a male obtained a territory, he always retained at least 10% of that territory in the subsequent year; no male shifted his territory entirely during the six years of the study.

There were 50 cases where the mates of territorial males were known in two consecutive seasons. Of 47 cases where both members of the pair were still present in the study area in the second season, 43 (91.5%) males retained the same partner they had at the start of the previous breeding season, and four (8.5%) had new mates. The four females that changed mates all moved to adjacent territories; three had bred successfully the previous year.

Breeding success the previous year did not affect mate fidelity. There were 39 cases where both members of a pair were alive in the subsequent season, and where it was known whether the pair had succeeded in raising at least one chick to a minimum age of five days old. Eighteen of 21 successful pairs, and 17 of 18 failed pairs remained together for the second season (χ^2 = 0.803, n.s.). One pair that failed for three consecutive years was still together the following year.

A female whose mate disappeared between breeding seasons either paired with the male that claimed the vacant territory (n = 8) or moved to an adjacent territory (n = 2).

Effect of population density on territory size

If territory size is determined by intruder pressure, there should be a strong negative correlation between the density of potential territory holders and territory area (Krebs 1971, Myers *et al.* 1979). In contrast, if a territory holder defends an area that contains sufficient resources (e.g. space, food, nest sites) to obtain a mate and raise young, then territory area should vary independently of intruder pressure (Hinde 1956). A third possibility is that minimum territory size is set by

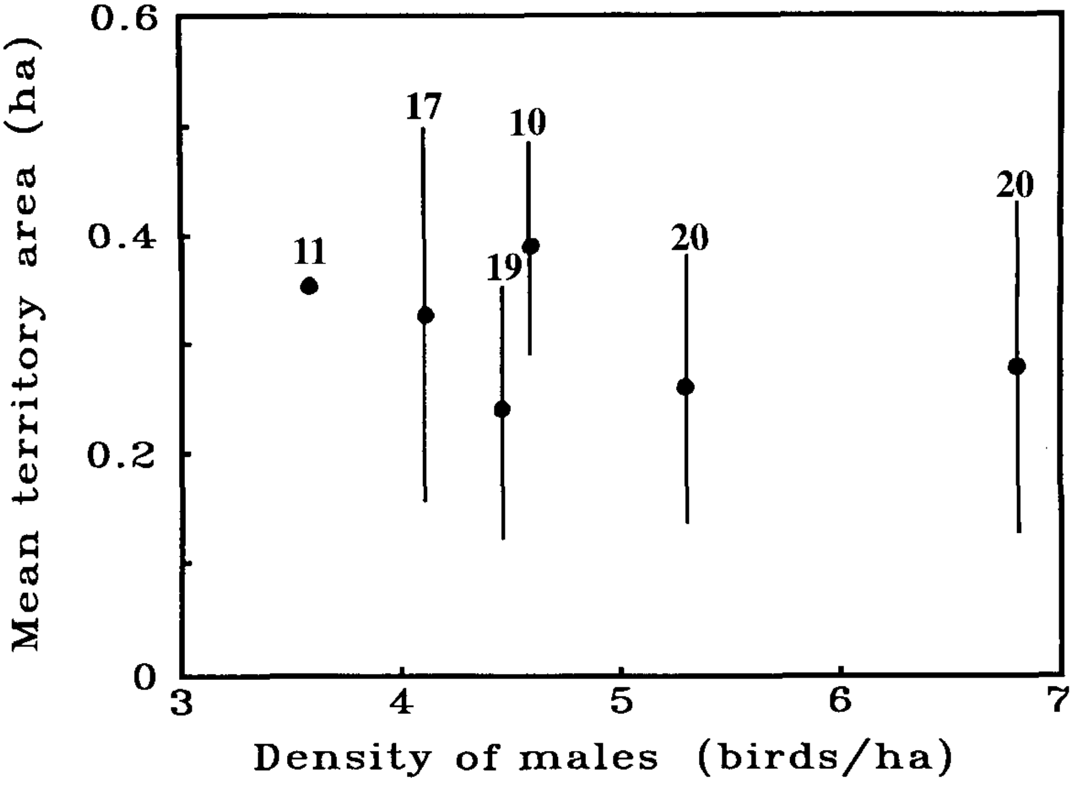

FIGURE 1 – The relationship between total male density and mean territory area. Error bars represent one standard deviation of the mean. Numbers above each estimate give the number of territories that the estimate was based on. Territory boundaries were not determined accurately in 1983/84, and so the mean territory area was calculated by dividing the total area occupied by the number of alpha males present, hence there was no estimate of variability for that year.

resource abundance, but at low intruder pressures territory holders may defend as large an area as possible (Verner 1977, Parker & Knowlton 1980).

There was no clear relationship between the density of male snipe in the study area and mean territory area (Fig. 1). Although there was a slight tendency towards larger territories at low male densities (r_4 = -0.102, n.s.), it appears that territory size was not controlled solely by intruder pressure. Mean territory area did not drop below 0.24 ha, which suggests that a minimum resource requirement determines territory size at high male densities. In other words, during years of high male densities, beta and gamma males should find it harder to obtain a territory than in years of low male density.

How males obtained territories

There were three potential ways that beta or gamma males could obtain a territory between breeding seasons: 'replacement' of an alpha male that died, 'eviction' of an alpha male by fighting, or by forming a new territory between two or more previously contiguous territories ('intercalation'). As already noted, every alpha male retained his territory until he disappeared (presumed dead); eviction was never observed. However, if alpha males were killed or severely injured during

TABLE 5 - How new alpha males obtained their territories. "Eviction" = the previous territory owner was forced to abandon the territory. "Replacement" = the previous owner disappeared (probably died). "Intercalation" = the new territory was formed between existing territories, i.e. neighbours shifted their territory boundaries to accommodate the new territory.

Years of prior residence as a beta male	How the territory was obtained		
	Eviction	Replacement	Intercalation
0	0	6	0
1	0	6	4
2	0	0	2
Total	0	12	6

fights with beta males, it would be impossible to distinguish eviction from replacement without observing the conflict. One fight between an alpha and beta male continued for over 63 min, but all 'pre-hatch' contests seen were won by alpha males. One alpha male was found dead (within his territory), but I was unable to determine the cause of death. As no vanquished alpha males were observed, and mortality rates for males were no different than for females (Table 4), it is likely that alpha males retained their territories until death from causes other than fighting.

Eighteen males attained alpha status (i.e. gained a territory at the start of the breeding season) during this study: 12 by replacement and six by intercalation (Table 5). Twelve of the males that claimed new territories, including all six that obtained territories by intercalation, previously had home ranges that overlapped with their new territory (Table 5). To obtain a territory by intercalation required significantly longer prior residency than to acquire a territory by replacement (Mann-Whitney Rank Sum T = 81, P = 0.027). In every case (n = 6) where beta males had home ranges that overlapped with a territory that became vacant, one of them took control of the territory. If there was no 'resident' beta male the territory was absorbed by surrounding alpha males (n = 4) or taken over by a male not previously resident there (n = 6).

All males attempting to obtain a new territory were constrained by alpha male mortality, as the number of territories in the study area was relatively constant at all male densities (Fig. 1). Even males obtaining territories by intercalation could do so only if an alpha male had disappeared from a nearby territory, allowing adjacent alpha males to adjust their territory boundaries. As alpha male 'mortality' was about 18% per annum, only 0 - 7 territories were available to the 3 - 18 beta and gamma males each year (Table 6). The relatively constant ratio between alpha male mortality and number of nonterritorial males (Table 6) suggests that mortality of snipe may have been density-dependent. A similar relationship was not apparent for alpha and beta females, possibly because of the low density of beta females (Table 1). Most new alpha females were 1-year-olds or of unknown history.

TABLE 6 - Number of alpha males that disappeared between breeding seasons in relation to the number of beta and gamma males vying for territory ownership.

Year	Number of beta and gamma males present in the previous breeding season	Number of alpha males that disappeared	Proportion of beta and gamma males able to obtain a territory
1983	8	3	0.38
1984	3	0	0
1985	6	2	0.33
1986	18	7	0.39
1987	8	3	0.38

Density-dependent mortality

The effect of density of conspecifics on overall mortality rates of New Zealand Snipe during the non-breeding season is shown in Fig. 2.

Mortality rates were, apparently, density-dependent; the one outlier was the high mortality in the winter following the severe 1982-83 El Niño event (Miskelly 1990c). For the remaining four years, snipe density explained about 97% of mortality during the following winter (r_2 = 0.98, P = 0.011); this implies that there was intense intraspecific competition for a limiting resource, presumably food (see Miskelly 1989b, 1990a & c).

DISCUSSION

Territory defence

New Zealand Snipe on the Snares Islands had many life history features characteristic of insular vertebrates (Stamps & Buechner 1985): they occurred at high densities, adult and juvenile survival was high, clutch size was small and there was high parental investment per offspring (Miskelly 1990a), onset of breeding was delayed (at least for males) and alpha males accepted subordinate (beta and gamma) males on their territories.

The presence of beta and gamma males within alpha males' territories appears inconsistent with evidence that New Zealand Snipe were food limited during the breeding season (Miskelly 1990a). If food within a territory is a limiting resource, why share it with unrelated conspecifics? Alpha males maintained contiguous territories that included all suitable habitat within the study area; there were no interstices between territories, and no dispersal sinks (*sensu* Emlen 1979) for nonterritorial birds to occupy. Given that nonterritorial birds had no choice but to intrude into established territories, they could do so by being inconspicuous (e.g. Dhondt & Schillemans 1983) or by being blatant (Myers *et al.* 1979, Davies & Houston 1981). On the Snares Islands, snipe were difficult to detect at distances over 10 m from my eye level; from the ground, detection distances often would be

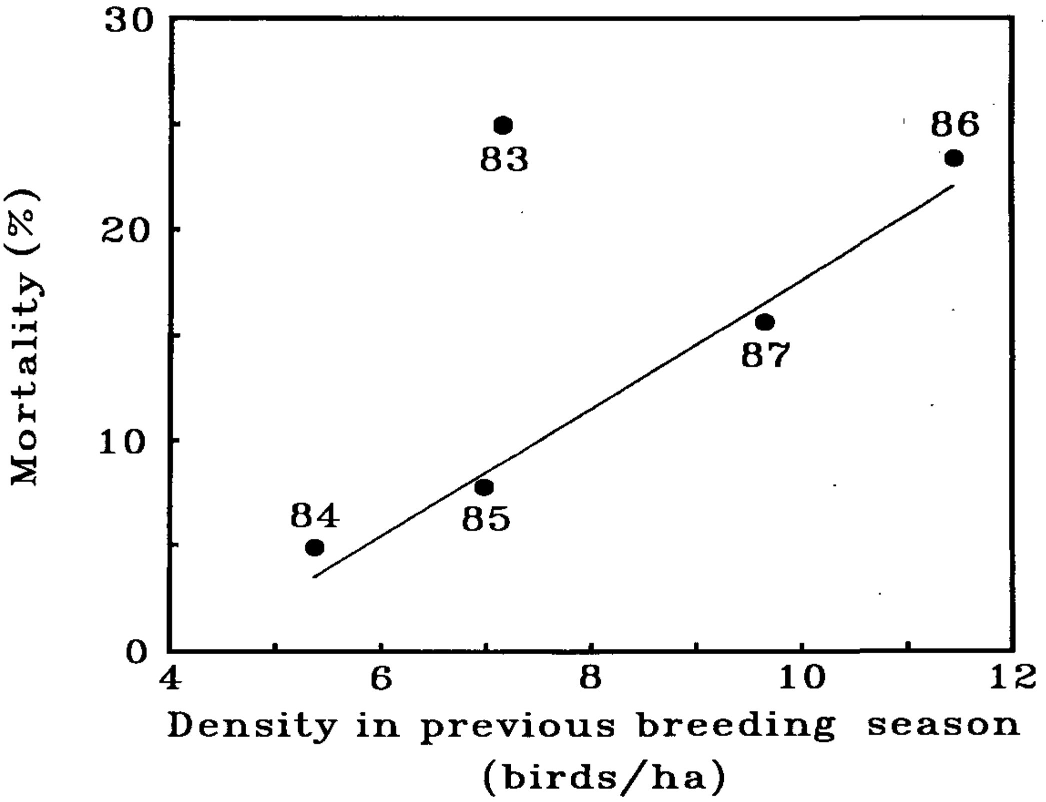

FIGURE 2 - Density-dependent mortality in New Zealand Snipe. The very high mortality during the 1983 winter followed the severe 1982-83 El Niño event (Miskelly 1990c). The regression line was fitted to the data for the remaining four years.

much shorter. An intruder that did not call could avoid detection by the alpha male much of the time. Beta males called rarely (and gamma males never did) and so were inconspicuous. However, intruding beta and gamma males made no attempt to avoid alpha males, and sometimes fed alongside them.

Assuming that expulsion of intruders is costly in terms of time or energy (Myers *et al.* 1979, 1981, Davies & Houston 1981), high rates of intrusion may lead to the cessation of territory defence (see also Gibb 1956, Davies 1976). Expulsion of intruding subordinates by alpha male snipe may be futile, as other subordinates could simultaneously be present, undetected, within the territory. While territory defence was a prerequisite for obtaining a mate, alpha males did not defend food resources within their territories. Alpha males guarded their mates during courtship and laying, and defended their territories against those intruders that attempted to claim territory ownership (i.e. by calling). Nonterritorial birds had no social constraints on where they established their home ranges, but could only breed when the resident alpha male stopped defending his territory - temporarily (while chick-rearing) or permanently (by disappearing, presumed dead).

Breeding site fidelity

Migration (or non-migration) is a factor that has received little attention in studies of breeding dispersal by waders, yet it undoubtedly affects return rates of adults and young. Oring & Lank (1984) explicitly ignored migratory dispersal in their review, as all the species that they discussed were migratory, breeding did not occur on the wintering grounds and "...the birds were capable of precise homing from wintering to breeding areas". Migratory birds are expected to have lower return rates due to a combination of: (1) migration-induced mortality, (2) increased opportunities to assess alternative breeding sites, (3) association with conspecifics from other populations while on the wintering grounds or on migration, leading to recruitment to a different breeding site, and (4) vagrancy due to navigational error (Baker 1978). All four factors are probably positively correlated with the distance travelled during migration, hence return rates should be negatively correlated with the distance between breeding and wintering areas. While there is no *a priori* reason to expect sexual differences in return rates to vary with migration distance (unless the sexes winter in different areas), interspecific comparisons of breeding site fidelity and natal philopatry could be affected greatly.

An appraisal of breeding site fidelity rates for sandpipers given by Oring & Lank (Table 1, 1984) supports the contention that migration distance affects return rates. Using mean breeding site fidelity rates for each species, short distance migrants (Redshank, Willet *Catoptrophorus semipalmatus*, Long-billed Curlew, and Black-tailed Godwit *Limosa limosa*) had the highest return rates (70 - 74%, mean 72%), while long distance migrants (Semipalmated Sandpiper, Stilt Sandpiper, Red-necked Phalarope *Phalaropus lobatus*, and Grey Phalarope *P. fulicarius*) had the lowest return rates (4 - 50%, mean 31%) regardless of their social systems. Medium distance migrants (Spotted Sandpiper *Actitis macularia*, Western Sandpiper, Least Sandpiper *Calidris minutilla*, Temminck's Stint *C. temminckii*, Dunlin, and Ruff *Philomachus pugnax*) had intermediate return rates (34 - 76%, mean 57%).

A sedentary species, such as New Zealand Snipe, would not only avoid the detrimental effects of migration on return rates, but continuous residency at the breeding site would enhance familiarity with the territory and prevent take-over attempts in the territory-owner's absence. Breeding site fidelity rates for New Zealand Snipe (males 82%, females 88%) are considered equivalent to mean annual survival rates, as territory fidelity was so high (males 100% of birds that 'returned', females 89%; the six females that changed territories between seasons all moved to adjacent territories, i.e. about 58 m). The much lower breeding site fidelity rates for migratory scolopacids (see above) must be due to higher mortality rates, plus an unknown percentage of birds that change breeding sites between seasons.

In many birds, breeding site fidelity decreases following nesting failure (e.g. Richdale 1957, Darley *et al.* 1977, Harvey *et al.* 1979), including waders (Oring & Lank 1982, Redmond & Jenni 1982, Gratto *et al.* 1985, Thomson & Hale 1989). Only in the Dunlin, which has high breeding site fidelity, were return rates independent of breeding success in the previous year (Holmes 1966, Soikkeli 1967, 1970a & b).

Previous breeding success and experience did not affect breeding site fidelity, territory fidelity or mate fidelity in New Zealand Snipe. Failed breeders had very few opportunities to change mates or territories, as all available habitat was contained in contiguous territories and mortality rates of territory holders were low (about 17% per annum). A breeding bird that chose to abandon its territory or mate (and therefore move location) would have had difficulty replacing it due to competition from the pool of nonbreeding birds (Baker 1978, Greenwood 1980). Some beta males may have even held a competitive advantage over an hypothetical alpha male that had left his territory: a prior resident (if present) always obtained a territory that was vacated. The reluctance of failed breeders to undergo breeding dispersal even though their breeding site or mate was possibly inadequate was not surprising as the costs of dispersal were high. The best option for a breeder with a low quality mate or territory may have been to stay on the territory until death of the mate or a neighbour permitted access to a new mate or a change in the territory boundaries.

Nonbreeding birds benefitted from occupying the same potential breeding site each year because prior residency was an important factor in the acquisition of a territory (see Greenwood 1980). Even within a breeding season, a nonterritorial bird that maintained a topographically fixed home range occasionally bred (as a beta male or female) whereas a transient bird (gamma male) never did. The most profitable strategy for a male unable to obtain a territory was to maintain a home range overlapping 2 - 3 territories, thus permitting a low chance of breeding that season (with an alpha female that had lost her dependent chick) and a high chance of acquiring one of the territories over the next 1 - 2 years.

Natal philopatry

New Zealand Snipe breed close to their natal territories. The 'return' rate of snipe chicks (30% overall, and 46% of fledglings) was far higher than recorded for scolopacids elsewhere (1 - 11% for ten species; Oring & Lank 1984). In the only other study that has looked at the effect of pre-fledging mortality on the rates of return, Thompson & Hale (1989) recorded an overall return rate of 2.2% for Redshank chicks, but suggested that up to a third of fledglings return to breed near their birth site. Pre-fledging mortality for New Zealand Snipe (about 1.6% per day; Miskelly 1990a) was much lower than for Redshank (13.2% per day for the first 20 days; data from Thompson & Hale 1989), presumably due to the absence of predators on the Snares Islands (see Miskelly 1990a). The low levels of natal philopatry recorded for other waders are probably due mainly to higher mortality in their first year of life, although a proportion of birds would disperse to other breeding sites (e.g. Soikkeli 1967, 1970a & b, Hilden 1978).

As with most other monogamous scolopacids, New Zealand Snipe showed no sex bias among returning young (Soikkeli 1970a & b, Holmes 1971, Gratto *et al.* 1985, but see Redmond & Jenni 1982). However, there was a slight male bias in natal dispersal distances. Most young males established territories within two territory diameters of their natal territory after 1 - 2 years of maintaining a home range adjacent to their natal territory. Males chose where to live as beta males; there were no constraints on where a male established his home range. The location of a male's eventual territory was determined by the disappearance of alpha males within or adjacent to his home range during his first three years.

Most young female snipe were paired as 1-year-olds, 3 - 4 territory diameters from their natal territory. The location of a female's territory was determined largely by the disappearance of alpha females from the study area during her first two years. The sex bias in natal dispersal distances was due to young males choosing to live near their natal territories, while young females moved to wherever there was an unpaired alpha male. Sex biased natal dispersal in New Zealand Snipe was apparently driven by the presence of a pool of nonterritorial males and the relative absence of nonterritorial females. The underlying cause of the male-biased sex ratio within the study area (range 0.50 - 0.96 females per male) was not determined, but it was operating during the six years of this study.

The island environment

Stamps & Buechner (1985) concluded that as other ecological factors that might regulate density are relaxed or absent on islands, intraspecific regulative processes are probably more important than for mainland populations. Intraspecific competition (density) was positively correlated with mortality rates in New Zealand Snipe. Access to breeding opportunities for males and females was constrained by deaths of alpha males and females leaving vacancies to be filled. Thus, intraspecific competition in New Zealand Snipe not only determined what proportion of nonbreeders gained access to mates, but also the total number of nonbreeders able to enter the breeding population.

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