Territoriality and site tenacity of Temminck's Stint *Calidris temminckii*

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The size of a breeding population of Temminck's Stint, studied for 10 years on the west coast of Finland, was limited mainly by territorial behaviour. The males were strictly territorial until they started steady incubation. The territories were small, only 0.15 to 0.25 ha in the best, central parts, corresponding to a density of up to 40 males/10 ha. Young males settling in the area for the first time took over vacant territories in the central parts, but some were forced into the margins or remained without permanent territory. Central males usually reoccupied their territory in later years, while marginal males tried to establish new territories in, or closer to, the optimal area. Females were less attached to their previous nest sites, and roughly one third were vagrants shifting their breeding grounds from year to year. Young birds which returned to their native area to breed did not tend to settle near their hatching site. Territory size in *Calidris* species and the factors affecting it are reviewed. The significance of territorial behaviour in the regulation of bird numbers, and the different strategies for site tenacity in sandpipers are discussed.

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Introduction

There is much variation in the territorial systems of waders. Some species establish large territories, resulting in low densities and fairly even dispersion, whereas others show a clumped spacing with small territories and high densities in favourable areas. As to site tenacity, waders seem to have two main strategies: some species are strongly attached to their breeding places and return year after year to the same territories, whereas others are opportunistic, moving about over large areas and settling only when they find a favourable breeding ground (review by Pitelka et al. 1974).

This paper is the third part of a long-term population study on Temminck's Stint, carried out in 1963—72 on the west coast of Finland (see Hildén 1975, 1978). The territorial system, breeding density and site tenacity of the species are described in detail and compared with those of other *Calidris* species. Special attention is paid to differences in territorial behaviour and site tenacity between old and young males. An ethological description of the territorial behaviour will be published separately.

Study area and methods

The study area consists of two adjacent, almost treeless capes near the town of Kokkola (63°52'N, 23°05'E). The terrain is partly sand with a sparse vegetation of grass, herbs and moss, and partly meadow, beside a shore leading to extensive mudflats. Particularly favoured by Temminck's Stints are the yards of some summer cottages. The study area was divided into eight areas, from A to H. The population increased slowly from about 27 adults in 1963 to 33—36 in 1966—69, and then declined rather abruptly to only 15 in 1972. In addition, 1 or 2 pairs usually inhabited the nearby Morsiussaari, 2.5 km east of the main study area.

Field work lasted usually from the arrival of the birds to the fledging of the young. Adult birds were marked with both coloured and aluminium rings, and were numbered according to the trapping order (M = male, F = female). Chicks were marked with numbered rings only, but many were also individually recognizable without trapping in later years, as their ring numbers could usually be read with a telescope. Almost all nests were found and plotted on maps. The territorial boundaries of each male were determined from their song posts, observed territorial fights, and the location of nests.

The study area and the methods have been described in more detail earlier (Hildén 1975).

Territoriality and breeding density

1. Breeding system. In Temminck's Stint, every female pairs in rapid succession with two males on different territories and lays one clutch on each. Every male also pairs successively on the same territory with two females and fertilizes one clutch of each. The first clutch is subsequently incubated by the male, the second by the female. The male delays the onset of incubation for several days, during which he continues to display and is able to fertilize a second clutch (for more details see Hildén 1975).

2. Dispersion and density. Temminck's Stint has a strongly developed territorial system, resulting in a fairly

TABLE 1. Annual numbers of territorial Temminck's Stint males (M) and nests found (N) in the eight part areas A—H at Kokkola in 1963—72. Only males holding a territory for at least one week are considered. The years 1969 and 1970 are excluded, since the surveys were incomplete.

	A		B		C		D		E		F		G		H		Total	
	M	N	M	N	M	N	M	N	M	N	M	N	M	N	M	N	M	N
1963	1	2	3	5	3	6	2	4	2	2	2	3	1	1	0	0	14	23
1964	1	2	2	5	2	7	2	6	2	2	2	2	1	1	0	0	12	25
1965	2	3	4	4	3	4	2	3	2	2	1	2	0	0	2	3	16	21
1966	1	2	3	6	4	6	2	5	1	3	1	2	1	2	2	2	15	28
1967	1	1	2	5	3	8	3	7	1	3	3	3	1	2	2	2	16	31
1968	2	3	2	3	3	9	1	5	1	2	3	3	1	2	2	2	15	29
1971	1	2	1	2	2	2	1	2	1	1	1	1	1	0	3	3	11	13
1972	1	1	1	2	2	4	1	3	1	2	0	0	0	0	0	0	6	12
Total	11	16	18	32	22	46	14	35	11	17	13	16	6	8	11	12	105	182

regular dispersion of males throughout the whole area of suitable nesting habitat. In my study area, the dispersion remained similar from year to year (Table 1). For instance, density was always highest and territories smallest in area C and near its borders, in areas B and D, where yards around the houses offered especially suitable habitats. However, the total size of the inhabited area varied in parallel with the size of the population. Thus, with low numbers in 1963—64 no Temminck's Stints nested in area H, but with the high population from 1965 to 1971 2—3 males held territories there each year; in 1972 it was abandoned again.

The territories were small, ranging from 0.15 to 0.25 ha in the best parts. In the more peripheral areas F—H where good habitat occurs only as small patches surrounded by less suitable terrain and where competition with conspecific males is weaker, territories were larger, up to 1.5 ha. The average territory size increased considerably in the last years of the study in parallel with the decline of the population. Thus, in 1971—72 only 4 males shared the best areas B—D, as against 9 in 1965—66, and correspondingly the defended territories were twice as large.

The territorial boundaries are somewhat flexible and may change according to the pressure exerted by neighbouring males. For instance, as soon as M5 was killed accidentally on 30 May 1964, the neighbouring M9 expanded his territory to include this vacant area; subsequently M9 was often seen trilling on the same pole which M5 had used as his regular song post. In addition, the boundary between two adjacent territories is not a sharp line but rather a zone which both males frequent and where repeated territorial conflicts take place. In this boundary zone two males may alternate in using the same song post.

Display and chasing by males last until they start to incubate steadily. After this they do not defend their territories, allowing neighbouring males to expand theirs. Therefore, males which still display late in the season usually move around over wide areas covering many former territories. Such males include (1) birds which do not yet have a clutch or have not yet started to incubate, (2) unmated, usually one-year-old birds late to arrive, and (3) birds which have lost their clutches and begun to display again. As a result of the breakdown of territories, incubating males also frequent each other's territories to feed, sometimes far from their own nests, without provoking aggressive interactions.

Densities of Temminck's Stints in the most suitable parts of the area were high. During 1963 to 1968, before the population declined, the numbers of territorial males in areas A—D ranged from 7 to 12, corresponding to a density of 25 to 42 males/10 ha. In areas E—H, where a large proportion of the ground consists of luxuriant shore meadow, unsuitable to the species, densities were only 6 to 8 males/10 ha.

3. *Territories of young males.* New males settling in the area for the first time, usually at the age of 1 or 2 years, varied widely in their territorial behaviour. Some had permanent territories and others not.

Males with no permanent territories. Some of these males stayed only a few days in the area, displayed and then disappeared. Others stayed longer but moved within the area, trilling a couple of days in one place and then shifting to another. Regardless of how long they stayed, these birds kept to the less suitable, marginal parts of the area; only late in the season when most males were already incubating, did they also visit the optimal central parts. Those individuals which soon disappeared presumably moved to another area to prospect in the same way.

Only 7 males of this type were recorded, but their real number must have been much higher; such birds, not being colour-ringed and staying only a short time in the area or roving without a permanent territory, could seldom be recognized individually. A good example was provided by one male, later M51, which was recorded and recognized by the ring number only once (on 4 July 1965) in the first summer, without any sign of territorial behaviour. Not until two years later, at the age of three years, was he rerovered as a breeding bird in the same area.

Males with a permanent territory. As long as territorial defence is strong, most young males are forced to settle in the marginal parts of the breeding area where more space is available. In about half of the 15 cases recorded, such males succeeded in mating and thus obtained a clutch to incubate, whereas the remaining males stayed unpaired. Of the 7 males colour-ringed on the nest when breeding for the first time, all shifted in the following year (or in one case two years later) to another territory in or closer to the better parts of the area (see p. 60).

Young males can settle in the better parts either by taking over a vacant territory to which a former holder did not return (9 recorded cases), or occupying a territory late in the season when the holder is already incubating and no longer defends its territory (8 recorded cases). Males which take over a vacant territory in the central parts may at first settle in the marginal parts for some time, as observed once in 1965. This behaviour may be common but is difficult to observe as the young individuals were not colour-ringed. Of the 9 males which took over a vacant territory, 7 were known to be paired (the nest was found) but 2 probably remained unpaired. Both of these were found nesting in the same territory in the following year. All 8 late-arriving males remained unpaired, although they displayed and courted females vigorously, often up to the end of June or early July. One of them (M52) returned and nested on the same territory in the following year.

Site tenacity

1. Site tenacity of males. With respect to site-tenacity, males were separated into two main categories: (1) birds of unknown age when ringed (that is, birds ringed in 1963 when the study started), and (2) birds probably breeding for the first time when ringed (5 1-year-old, 4 2-year-olds, 2 3-year-olds, 4 unringed). The first-breeders were further divided into (a) males settled in optimal and (b) marginal parts of the area.

Figs. 1—2 show the successive nesting sites of males belonging to these three categories. The following conclusions can be drawn:

Category 1: Old males that had already nested in the area show a strong attachment to their territory thereafter (Fig. 1A). Only M2, which held a large territory in the marginal part (E—F) of the area moved his nest site three times from the previous site, 144, 152 and 115 m each time; for the other 8 males the average distance between nests in successive years was only 19.6 m (range 2 to 58 m, *N* 22).

Category 2a: Young males which succeeded in occupying a territory in the optimal parts of the breeding area usually reoccupied it in later years (Fig. 1B). There was only one exception: M35, which during the two first years nested in area B, switched in 1967 to area F (about 400 m) but returned to area B in 1968 and nested there also in 1969. With this bird excluded, the average distance between nests in successive years was only 25.5 m (range 6 to 70 m, *N* 16) or about the same as in category 1.

Category 2b: Those males which bred for the first time in the marginal parts of the area showed much weaker site tenacity (Fig. 2). Usually they tried in the following year to occupy a new territory in or closer to the optimal parts, and even in later years they were less attached to their territory than males in categories 1 and 2a. In category 2b, the average distance between nests in successive years was 179 m (range 0 to 1000 m, *N* 20). These figures exclude the longest move recorded, a switch of M34 for 2.5 km from Morsiussaari to Harrbåda in 1967, back to Morsiussaari in 1968 and back again to Harrbåda in 1969. Possibly other males nested temporarily in Morsiussaari; e.g. after three breeding seasons M42 was not seen at all in 1969 and 1970, but in 1971 he returned to his former territory.

2. *Territory change during the breeding season.* Normally, each male kept within its own territory until the territorial boundaries broke down (see p. 58). There were only a few exceptions where males abandoned their territories, either temporarily or finally, and moved to new territories where they continued to display. Some of these cases occurred after loss of the clutch, and others for unknown reasons.

The following three males reacted to nest robbing by moving to a new territory:

M8/1965: The nest, in the southern part of area D, was robbed on 16 June. Next day the male was trilling in the central part of area C; there he defended a territory for about one week and chased the original territory-holders, which were incubating at the time.

M15/1965: The nest of this male, in area E, was also robbed on 16 June. On 18 June he was trilling in area B, on 19 and 20 June in area C; on 23 June he had returned to his original territory.

M32: In 1969, the nest was in the southern part of area E and was destroyed on 18 June. Next day the male was seen in a territorial fight on the line between areas C and D, but later he settled in area B. Each year in 1970—72, the male at first held his old territory in area E—F (cf. Fig. 2) but later in June moved over to area B. Although the nest was not found in these years, probably it had been robbed and this caused the change of territory.

These cases can best be explained on the basis of the seasonal decline in territorial behaviour (see p. 58). At the time of nest failures, the strict territorial system was already breaking down, and hence the males were able to push themselves into areas already occupied. In all cases, the new territories were located in the optimal part (B—C) of the area.

In the following four males the inclination to hold two territories was not a result of nest destruction:

M24: In 1964, the male held a regular territory in area G. The clutch was completed on 3 June, but he continued to display and moved on 8 June to a new territory in area E where he trilled lively up to 14 June and was seen courting F25. Then he returned to his original territory and started to incubate. — In 1965, the territory of M24 was in area H where he was seen regularly, except on two occasions: on 4 June he was trapped together

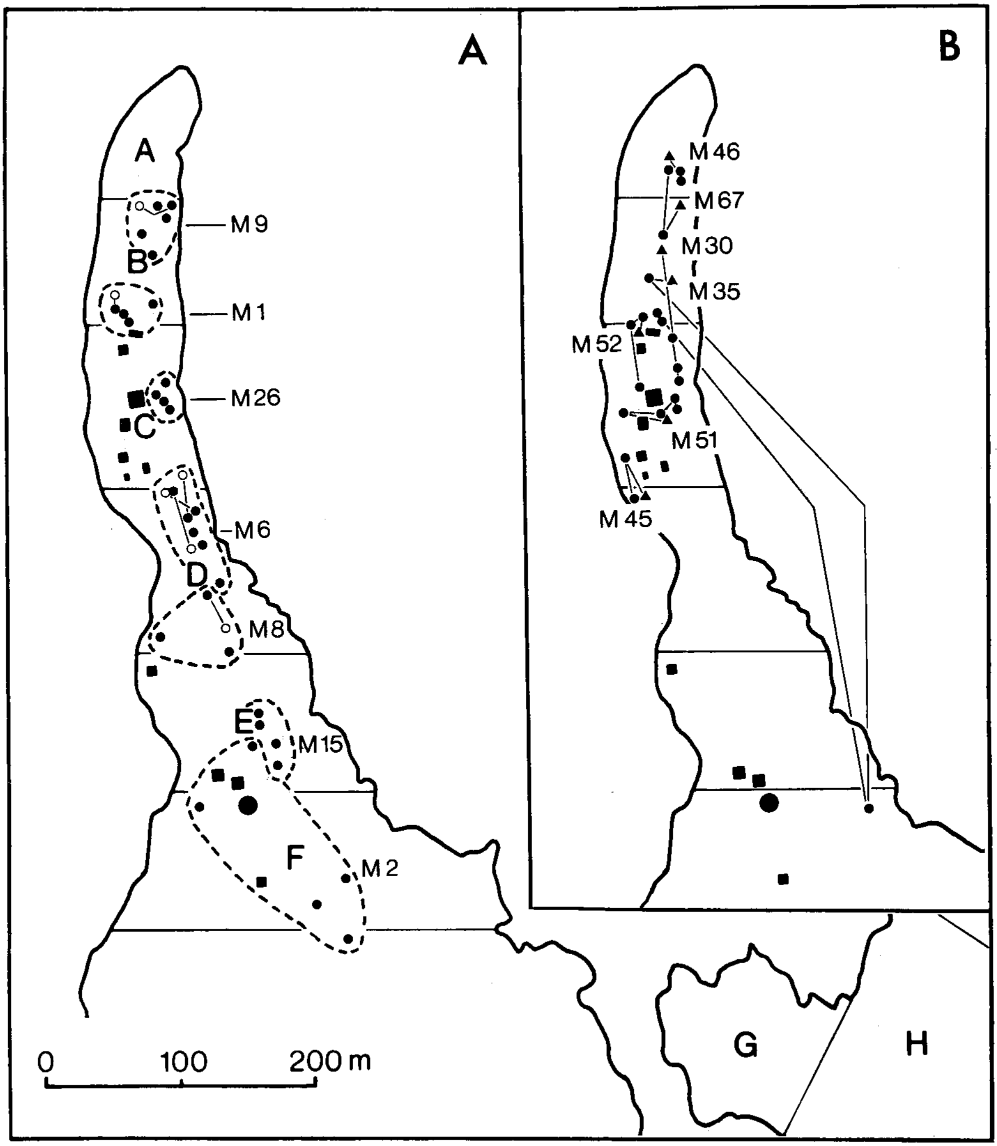

FIG. 1. Successive nest sites of males (=M) that nested in the study area during at least 3 years. Only the nests incubated by the males are included; if a male had two clutches to care for in a certain year, one is marked with an open circle. The rectangles are buildings and the large dot a lighthouse. — A. Males ringed in 1963 (age unknown) when the study was started. The areas used for nesting by each male are marked with broken lines. The symbols A—H refer to the eight subareas. — B. Males that settled in the optimal parts of the area (A—D) after 1963. The nest site of the first breeding year is marked with a triangle, and connected to the subsequent sites with lines. The years of settlement in the area were: M 30 and M 35 1965, M 45 and M 46 1966, M 51 and M 52 1967, M 67 1968.

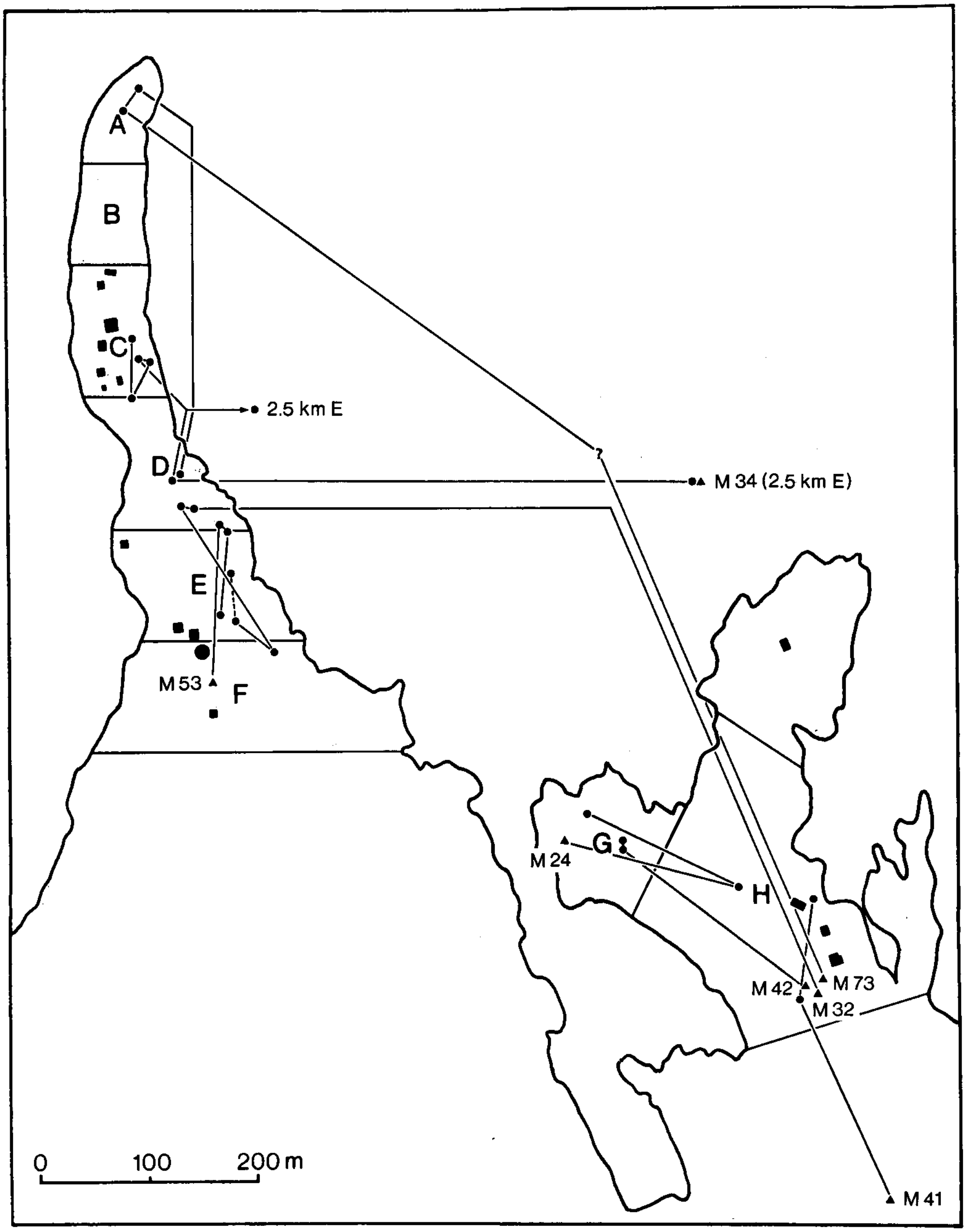

FIG. 2. Successive nest sites of males that settled in the marginal parts of the area (F—H) after 1963 (cf. Fig. 1). The years of settlement in the area were: M 24 1964, M 32 and M 34 1965, M 41 and M 42 1966, M 53 1967 and M 73 1969. The last two nest sites of M 32, united with a broken line, were occupied in 1969 and 1973; in the intervening years its nest was not found (see the text). In 3 years M 34 nested in Morsiussaari, 2.5 km E of the main study area. The nest of M 73 was not found in 1970.

with an egg-laying female on the nest in area F, and on 11—12 June he trilled in area D using the regular song post of M8, which was already incubating. On 13 June he began to incubate on his original territory.

M41: In 1968, the male was usually seen on his own territory in area H, but on 8 June he trilled all day in area E. Next day he had returned and started to incubate. The nest was destroyed on 11 June, after which the male switched to another territory in area F and stayed there until 17 June. This was the same territory that he had occupied in his first breeding year (1966), before he had settled in area H. — In 1971, the main territory was in area G, but he was seen trilling both east of it in area H and west of it in area F, i.e. on both those territories that he had used in earlier years.

M42/1966: The male trilled regularly on his territory in area H until on 9 June he started to incubate. But on 13 and 14 June he suddenly appeared in area C, displaying here excitedly, although he was still incubating in area H in the meantime. After 16 June he moved definitely to area C and deserted his nest.

M82/1971: The male was once seen outside his territory, situated in area F: on 4 June he was trilling and engaged in territorial encourters with other males in area H.

All these males belonged to category 2b (p. 60), i.e. males showing least site tenacity. Their weak attachment to territory presumably allowed changes to occur during the nesting season. The most probable cause leading to desertion of the original territory was the males' attempt to mate with a new female. In all cases except one (M42), the males left their territories before they had started to incubate, when they still showed strong sexual activity. If a male fails in his attempts to attract a new female, as easily happens in the less favoured marginal parts of the area, he may leave his territory and try to mate with a female farther away. Such pair association comes about easily, as male Temminck's Stints fly after every female which passes by, resulting in long erratic chases over the breeding area. If the female is not willing to accept the male's territory, he may follow her and so occupy a new, vacant territory. In early June, defence of territories is still strong, and probably for this reason the new territories were situated in the marginal parts, the only exception being M42 who occupied a new territory in area C as late as mid-June.

3. *Site tenacity of females.* Theoretically, site tenacity of females may appear in three different ways:

(1) They may be attached to the first of their two successive nest sites and hence return each year to the same area in which their first clutch was laid.

(2) They may be attached to their second nest site and thus lay their sec-

TABLE 2. Nesting site tenacity of female Temminck's Stints within the study area of Kokkola. The distances are in metres.

		0—100	101—200	201—300	301—500	500<	Mean	Range
Distances between the first nests in successive years	N	11	3	2	2	3	207	0—920
	%	52	14	10	10	14		
Distances between the second nests in successive years	N	17	9	7	1	1	133	6—800
	%	49	26	20	3	3		
Distances of the first nests from the second nests of the preceding year	N	7	10	3	4	3	236	22—870
	%	26	37	11	15	11		

TABLE 3. Distances (in metres) from hatching site to the first nesting site (for females: the second nest in the first breeding year) in the Temminck's Stint population at Kokkola.

		0—100	101—200	201—300	301—500	500<	Mean	Range
Males	*N*	3	1	1	4	3	359	135—930
	%	—	38	15	23	23		
Females	*N*	—	5	2	3	3	297	40—560
	%	25	8	8	33	25		
Total	*N*	3	6	3	7	6	329	40—930
	%	12	24	12	28	24		

ond clutch in the same area from year to year.

(3) They may tend to return in spring to the area where they incubated their second clutch in the year before, in which case they lay the first clutch near the second nest site of the preceding year. This possibility naturally excludes the other two, but (1) and (2) are not mutually exclusive.

Table 2 shows the distances between the nests of the same females in successive years, grouped into these three categories. Females showed a clear but not very strong attachment to both the first and the second nest site. In successive years they tended to lay their first clutches in one area, and the second clutches in another. Although longer movements up to 900 m were found, about half the females laid successive first clutches less than 100 m apart, and the same was true for successive second clutches. The third alternative, the female's tendency to lay her first clutch near the place where she incubated her second clutch in the preceding year, was not so apparent. This is surprising since females spend about one month on the second nest site (laying period + incubation + beginning of the brood period), but scarcely one week on the first one.

Individual females differed considerably in their attachment to their former nest sites. For example, F57 showed very strong tenacity: each year from 1967 to 1973 she returned to area C, and all but one of the 12 clutches laid by her were found within the same 50 m radius, 9 of them within a radius of only 15 m. Others moved long distances, either between the first or between the second clutches in successive years, or both.

In part, the females' weaker site tenacity, compared with the males, results from the mating system. Females seek males intent on pairing, and males display at any female that enters their territories (Hildén 1975). Consequently, the male holding the territory in which the female had laid her clutch the year before, is often paired on the female's arrival, so she is forced to move to another territory. This probably explains cases where a female returned in one year to her former nest site but moved the next year several hundred metres to a new territory.

Besides females which are faithful to the area, there are also vagrant females which are thought to shift their breeding grounds between years and also between successive nests within the same season (Hildén 1975). They make up about one third of the female population. Nothing is known about the distances they may cover, but considering the fast speed of flying waders even some hundred kilometres might be possible.

4. Tenacity to the place of birth. Of the young ringed in 1963 to 1971, altogether 26 were recovered later as breeding adults in the study area. Table 3 shows how far these birds had moved from their hatching sites to their first nesting sites; for females only the second nests of the year are used (that is, those incubated by themselves). They did not show any tendency to settle near the place of birth. Outside the study area, two breeding males were recovered in Morsiussaari and Kalajoki, at distances of 2.5 and 50 km, and a third bird of unknown sex on the Swedish side of the Gulf of Bothnia, about 170 km from Kokkola (Hildén 1978).

Discussion

1. Territory size. The density of Temminck's Stints in my study area was high, up to 25—42 males/10 ha in the most suitable parts. Elsewhere, the species is also known to breed at high densities. In the archipelago of the northern parts of the Gulf of Bothnia it has been reported to breed abundantly, being in places the dominant wader (e.g. Sandman 1892, Olofsson 1927, Grenquist 1947, Delje 1948, Merikallio 1950, Rautkari 1952, Salkio 1952). On small islets less than one hectare in area, densities may reach 60 pairs/10 ha, and on larger islands covering several hectares 10—20 pairs/10 ha (Table 4). High densities have also been reported inland. Southern & Lewis (1938) found 4 males occupying a 0.2 ha island in a river delta in Swedish Lapland. Rosenberg (1960) reports from Vittangi, Sweden, that Temminck's Stints preferred to nest on small, better drained "islands" within extensive wet marshes; such an island, covering not more than some hundred square metres, could hold 3 to 4 breeding pairs.

Table 5 reviews the available information on territory size in *Calidris* species. It gives only a rough picture, because the density values reported depend greatly upon the size of the census area and the uniformity of the habitat. Of the 15 species sufficiently studied so far in this respect, only *C. minuta* and *C. mauri* show densities as high as those recorded in Temminck's Stint. Most others breed much more widely dispersed, the density of *C. canutus* being less than one hundredth of that of Temminck's Stint. What may be the reasons for these wide variations between species?

I will not try to analyse this quest-

TABLE 4. Pair numbers and densities of Temminck's Stints on some suitable islands in the northern part of the Gulf of Bothnia.

	Pairs	Pairs/10 ha	Reference
Archipelago off Haparanda			
Ylikari (2.0 ha)	5	25	Delje 1948
Äijänpojanletto (8.0 ha)	10	13	—"—
Island group of Krunnit			
Luusiletto (0.6 ha)	4	63	Merikallio 1950
Törö (0.7 ha)	4	57	—"—
Kraasukka (4.5 ha)	8	18	—"—
Isonkivenletto (8.5 ha)	10	12	—"—

TABLE 5. Maximal breeding densities reported for different *Calidris* species.

Species	Locality	Breeding density	Reference
High densities (10—50 pairs/10 ha)			
C. temminckii	Finland	In 5 yrs, 7—12 ♂♂ in a 2.8 ha census area (= 25—42 ♂♂/10 ha)	This study
	Finland	On small islets up to 60 ♂♀/10 ha	Merikallio 1950
C. minuta	Siberia	In the best habitat 50 ♂♀/10 ha	Uspenski 1969
	Norway	8 nests within a c. 4 ha land area	Hildén, unpubl.
C. mauri	Alaska	In 4 yrs, 24—35 ♂♀ in a 10 ha study area, 7.2 ha of which was suitable as breeding habitat (= 34—49 ♂♀/10 ha)	Holmes 1971
C. pusilla	Alaska	In suitable habitat 15 ♂♀ in a 13 ha census area (= 12 ♂♀/10 ha), densest concentration = 4 nests/ha	Soikkeli, pers. comm.
C. minutilla	Nova Scotia	In 2 yrs, 30 nests in a c. 80 ha study area, c. 35 ha[1] of which was suitable as breeding habitat (= 8.5 ♂♀/10 ha, but not all nests were found); densest concentration = 6 nests/3 ha.	Miller 1979
C. ferruginea[2]	Siberia	Several pairs on a study plot of c. 450 m^2	Grote 1937
	Siberia	In places 2 pairs/ha	Uspenski 1969
Moderate densities (1—10 pairs/10 ha)			
C. alpina pacifica	Alaska	In 3 yrs, 13—14 ♂♀ on a 15 ha census plot (= 9 ♂♀/10 ha)	Holmes 1970
C. alpina schinzii	Finland	In 5 yrs, 24—27 ♂♀ in a 60 ha study area (= 4—4.5 ♂♀/10 ha)[3]	Soikkeli 1967
	Iceland	In the best habitat 10 ♂♀/8 ha	Wink 1973
C. himantopus	Canada	Mean territory size 6—8 ha, but on a 20 ha study plot 5 ♂♀ in 2 yrs	Jehl 1973
C. bairdii	Canada	In suitable habitat 20—25 ♂♀/100 acre = 5—6 ♂♀/10 ha	Parmelee et al. 1967
C. fuscicollis[2]	Canada	At least 20 ♂♀ in the most densely populated area of 32 ha (= 6 ♂♀/10 ha)	Parmelee et al. 1968
	Alaska	Maximal density 20 ♂♀/100 acre = 5 ♂♀/10 ha	Holmes 1971
C. melanotos[4]	Alaska	Maximal density 30 ♂♂/100 acre = 7—8 ♂♂/10 ha	Holmes 1966
	Siberia	In favourable habitats 10—25 ♂♂/100 ha	Kistchinski 1973
C. acuminata	Siberia	Clumped distribution, on two study plots 10—15 ♂♂/100 ha	Kistchinski, sec. Glutz et al. 1975
Low densities (<1 pair/10 ha)			
C. maritima[5]	Norway	On five study plots at most 2—5 ♂♀/100 ha	Lien et al. 1970, 1974
	Svalbard	Within a plot of 3.1 km^2 2.6—3.6 broods/100 ha in 2 yrs	Bengtson 1975

Cont. from p. 66

C. canutus	Greenland	About 3 ♂♀/100 ha	Pedersen 1934
	Canada	3—5 ♂♀ in a 240 ha census area, i.e. at most 2 ♂♀/100 ha	Nettleship 1974
C. alba	Greenland	At least 10 ♂♀/100 ha	Pedersen 1934
	Canada	Up to 7 ♂♀/100 ha	Manning & MacPherson 1961
	Canada	Greatest concentrations: 6—8 pairs per square mile = 2.3—3.1 ♂♀/100 ha	Parmelee 1970
	Greenland	Within a census area of 4.5 km^2 13—15 ♂♀ (= 2.9—3.3 ♂♀/100 ha)	Meltofte 1979

[1] Calculated by me.

[2] Clumped distribution, densities varying both in time and space (Pitelka et al. 1974).

[3] In the most suitable parts of the meadow the density was 10—15 ♂♀/10 ha (Soikkeli, pers. comm.).

[4] Wide annual variations (Holmes 1966, Pitelka et al. 1974).

[5] Glutz et al. (1975) report at most 1 pair/10 ha, but according to Uspenski (1969) densities up to 1 pair/ha may be possible.

ion thoroughly, as it would involve reconsideration of the functions of territory — a much-debated problem in ornithology. In the following section, I list only those factors which may influence territory size in sandpipers, with short comments on each.

(1) Size of the bird. Large species tend to have larger territories than smaller ones (e.g. Schoener 1968). This relationship also appears clearly among sandpipers: of the six species with the smallest territories, all but *C. ferruginea* are small-sized, weighing less than 30 g, while *C. canutus,* which shows the lowest breeding densities, is the largest species in the genus (weight about 135 g).

(2) Abundance and availability of food. In birds, territories tend to be smaller in rich than in poorer habitats, probably because of more plentiful food (e.g. Stenger 1958, Schoener 1968, v. Haartman 1971, Orians 1971). In *C. alpina,* for instance, Holmes (1970) has shown that the pairs settle more densely where more food is available.

(3) Feeding within *versus* outside the territory; in the first case larger territories are needed to ensure enough food. In *C. mauri,* one important factor allowing the high breeding densities is that birds feed outside their territories on communal feeding grounds. Similarly, Temminck's Stints in my study area feed mainly on the mudflats off the shores, and the same holds true for *C. minuta* (personal observations in Norway). Thus, all three species with the highest breeding densities recorded feed to a considerable extent away from their territories.

(4) Mating system. Species with monogamous pair bonds tend to have larger territories than species with non-monogamous mating systems (Holmes 1971, Pitelka et al. 1974). This is probably one reason for the relatively small territories of *C. ferruginea, C. fuscicollis* and *C. melanotos,* which are polygynous or promiscuous. Extreme examples are *Tryngites subruficollis* (Pitelka et al. 1974, Prevett & Barr 1976) and *Philomachus pugnax* (Hogan-Warburg 1966), where polygynous males defend only small display stations within a communal lek area.

(5) Habitat structure, particularly

the uniformity or patchiness of the terrain. If the birds use only certain suitable parts of the habitat, the total area occupied is naturally enlarged. In my study area, for example, Temminck's Stint territories were much larger in the marginal parts, where suitable terrain occurred only in patches.

(6) Status of the population. Birds tend to hold larger territories when intraspecific competition weakens and when some vacancies remain unfilled. This may happen in years when low numbers result from previous poor breeding success and/or high winter mortality, or when populations show a decreasing trend. Thus in my study area, Temminck's Stints had territories twice as large after the population decline as before it.

2. *Territorial behaviour and population regulation.* Temminck's Stint males settling in the area for the first time at the beginning of the breeding season can be divided into three categories: (1) males which took over vacant territories in the most suitable central parts and later usually bred; (2) males which settled in the less suitable marginal parts and often remained unpaired; (3) non-breeding males without any permanent territories. In addition, there were (4) late-arriving males which held large territories and always remained unpaired. To which category a male belonged seemed to depend on his date of arrival and social position.

It was found, firstly, that the settlement of newcomers in the area was determined by the territorial behaviour of the older, already established males. The intolerance of territory-holding males towards intruders permitted settlement only in vacancies left by the death of former owners or in the less crowded marginal parts of the area. The only exceptions occurred late in the season, after cessation of territorial defence, when newcomers could also settle within occupied domains. Secondly, the newcomers were physiologically fully capable of breeding; that they commonly failed to get a mate was presumably due to their poorer territories or lack of any territories at all. Thirdly, although the food supply and its consumption were not studied, it seemed clear that the breeding birds were not completely using up their food resources, and certainly not the space or nest sites available. Hence, the three main conditions necessary for showing that territorial behaviour limits breeding populations (Watson & Moss 1970) are fulfilled in this study, at any rate in males.

The significance of territorial behaviour in the population regulation of Temminck's Stint is further indicated by several facts. (1) Marginal parts of the area were occupied only in the years when the numbers of birds were highest (p. 58). (2) More potential first-breeders seemed to be excluded from breeding in the years of highest density (Hildén 1978). (3) The lowest return rates of juveniles that had been ringed as young in the study area were recorded in years with the highest survival of adults, presumably because only a few vacated territories were available (Hildén 1978). (4) New suitable breeding grounds, created for example by lake reclamations, can be colonized rapidly, probably by a "floating surplus" (Hildén 1978).

Non-breeding females were not recorded. If all females did in fact nest, my observations would show nothing but a male surplus. However, female Temminck's Stints are much more difficult to find and observe than males, owing to their skulking, inconspicuous behaviour (Hildén 1978). Unlike unringed males, unringed females could therefore never be individually recognized, and only a few of the females carrying a metal ring were identified. Because it is unlikely that there would be a strong male preponderance among potential first-breeders, the non-breeding surplus in Temminck's Stint presumably also included females. This conclusion is further supported by facts (1), (2), (3) and (4) listed in the preceding paragraph, which concern females as well as males.

In recent years, evidence has accumulated that territorial behaviour limits breeding densities of birds (reviews by Wynne-Edwards 1962, Brown 1969, Watson & Moss 1970, v. Haartman 1971, 1972, Carrick 1972, Fjeldså 1973a). As in Temminck's Stint, this happens either because a fraction of the population is forced into marginal conditions where mortality is heavier and/or reproduction poorer, or because a fraction is prevented from breeding. The expelled fraction often consists mainly of young birds attempting to breed for the first time. Such results have been obtained in a number of bird species representing several groups, partly by direct observations, and partly by removal experiments in which the eliminated territory owners were quickly replaced by newcomers from the surplus population (e.g. Tompa 1962, 1964, Delius 1965, Watson & Jenkins 1968, Harris 1970, Holmes 1970, Southern 1970, Young 1970, Krebs 1971, Carrick 1972, Knapton & Krebs 1974).

What happens to birds that are repelled from the breeding grounds where they try to establish themselves? Four alternatives are:

(1) They breed in marginal, less attractive habitats, but rear fewer young and/or incur heavier adult mortality (e.g. Coulson 1968, Krebs 1971, Carrick 1972, Fjeldså 1973a).

(2) They occupy territories in the marginal habitats and remain unpaired or, if mated, fail to breed (e.g. Tompa 1962, 1964, Delius 1965, v. Haartman 1971, present study).

(3) They fail to claim permanent territories and form a "floating surplus" of non-territorial individuals, which live either solitarily, dispersed in the margins of or outside established territories (e.g. Kendeigh 1941, v. Haartman 1951, Delius 1965, Rowan 1966, this study), or gather in flocks outside the breeding grounds (e.g. Jenkins et al. 1963, Harris 1970, Young 1970, Carrick 1972, Fjeldså 1973b, Böhmer 1976). These flocks may suffer heavy, socially-induced mortality (Jenkins et al. 1963, Watson 1977).

(4) They soon die, or emigrate to seek vacant territories in other areas, where many probably also die (e.g. Southern 1970). In many population studies, including the present one, some marked individuals have suddenly disappeared at the time when territorial activity revives. The higher the population density, the heavier one would expect the exodus and the socially-induced mortality to be.

To conclude, the present evidence of population limitation by territorial behaviour in birds can be considered sufficient to prove the existence of this regulation mechanism and to disprove the opposite opinion, argued especially by Lack (1954, 1966, 1968). Of course, the importance of this mechanism varies greatly, not only between species but also within species, due to annual fluctuations in population level and varying densities in different habitats or different parts of the geographical distribution. Thus care is needed in generalizing from the results obtained so far.

3. Site tenacity. Two main strategies for site tenacity can be seen in sandpipers (see Pitelka et al. 1974). Some species, e.g. *C. alpina* (Soikkeli 1967, 1970) and *C. mauri* (Holmes 1971), show strong site attachment and return faithfully to their former breeding grounds. Presumably the advantage of such behaviour, widespread throughout the avian kingdom in temperature latitudes, lies in the birds' knowing the place very well and forming the same pair bonds each year, but a prerequisite is that conditions in the area remain sufficiently stable from year to year. In the opportunistic strategy, birds show no attachment to their previous breeding grounds but settle each year in new areas. If a species is adapted to food resources or habitats whose occurrence is highly unpredictable due to weather, time of snow melt etc., shifting of the breeding grounds might be more advantageous than returning annually to the same place. This strategy, comparable to the vagrant life of crossbills *(Loxia)*, which settle to breed only in areas with a high food supply, has been found in *C. ferruginea, C. fuscicollis* and *C. melanotos* (Pitelka et al. 1974), and more recently in *C. minuta* (Hildén, unpubl.).

As both strategies have their advantages, one may expect to find some species in which both site-tenacious and vagrant individuals occur in the same population, as discovered by v. Haartman (1949, 1960) in females of *Ficedula hypoleuca.* The same applies with Temminck's Stint: the males and most females are strongly site-tenacious, but about one third of the females shift their breeding grounds from year to year (Hildén 1975). In *F. hypoleuca,* v. Haartman showed that the proportion of vagrant females increases towards the north. The same trend might also be expected in Temminck's Stint, as arctic conditions are more changeable from year to year. Results supporting the existence of such a trend were obtained in northern Norway in 1977—78: only 6 of the 16 individuals colour-ringed in the previous year were recovered in the study area (Hildén, unpubl.). Such a low return-rate was never found in the more southerly population at Kokkola (Hildén 1978).

Within my study area, male Temminck's Stints are much more strongly attached to the territory than females. In *C. alpina* (Heldt 1966, Soikkeli 1967, 1970) and *C. mauri* (Holmes 1971), females also show weaker site tenacity than males; indeed, this seems to be true for most birds. The main reason for this difference between the sexes may lie in the different mechanisms of site selection. As the male occupies the territory and defends it, it is adaptive for him to return from year to year to the same site with which he is familiar. For the female, on the other hand, the presence of an unmated male is more decisive than the quality of the site itself.

Why do young Temminck's Stints born in the study area not show any tendency to settle to breed near their hatching site? First, Temminck's Stint broods often move over long distances during their first days of life and may stay for long periods far from their birth-site. Second, first-breeders must make do with those territories which are vacated or situated in the margins, and thus they do not have free choice. Faithfulness to the birthplace in a wider sense, i.e. to the general area where born, is strongly affected by the availability of other suitable areas in the vicinity. At Kokkola, such areas were lacking except for the nearby Morsiussaari, and therefore I could not make any thorough analysis of the dispersal of young Temminck's Stints. However, the two birds that did settle far away, at distances of 50 and 170 km from Kokkola, suggest that some first-breeders do disperse relatively far from their birthplaces. On the whole, my results agree with those obtained by Soikkeli (1970) for *C. alpina.*

The tendency observed in Temminck's Stints to shift in later years from their first-occupied marginal territory to another in or closer to the more suitable central parts is probably common in birds, even though such movements have only seldom been demonstrated in known individuals (e.g. Carrick 1972). Such changes in territory between the first nesting attempt and later years would be of survival value if breeding in the central territories generally increased reproductive potential. However, some birds stay on the same territory once they have bred there (e.g. Hildén 1965), the main benefit presumably being their improved ability to exploit a well-known territory. It may be that such birds would do better if they could move, but that they are unable to do so because of poorer social position or other reasons.

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Selostus: **Lapinsirrin territoriaalisuus ja paikkauskollisuus**

1. Kirjoitus on kolmas osa populaatiotutkimuksesta, joka suoritettiin 1963—72 Kokkolan lähistöllä (ks. Hildén 1975, 1978). Kukin koiras puolustaa tiukasti omaa reviiriään, mikä aikaansaa kannan jakautumisen yli koko pesimiseen soveliaan alueen. Jakauma pysyi suunnilleen samanlaisena vuodesta toiseen, mutta asutun alueen laajuus vaihteli jonkin verran kannan suuruuden mukaan (taul. 1).

2. Reviirit olivat pieniä: alueen keskustan parhaissa osissa vain 0.15—0.25 ha, laitojen huonommissa biotoopeissa jopa 1.5 ha. Niiden suuruus kasvoi kannan pienetessä. Reviirien puolustus kestää siksi kunnes koiras aloittaa tiiviin haudonnan. Tästä syystä myöhään soidinvireessä olevat, parittomat tai pesyeensä menettäneet koiraat voivat liikkua laajalla, useita alkuperäisiä reviirejä käsittävällä alueella.

3. Nuoret, alueelle ensi kertaa asettuvat koiraat voidaan jakaa neljään ryhmään: (1) parhaisiin keskiosiin, kuolleiden koiraiden vapautuneisiin reviireihin asettuvat yksilöt, jotka yleensä pesivät; (2) vähemmän haluttuihin reunaosiin asettuvat yksilöt, jotka usein jäävät parittomiksi; (3) myöhään saapuvat, laajalla alueella hautovien koiraiden reviireissä livertävät yksilöt, jotka aina jäävät parittomiksi; (4) ilman pysyvää reviiriä kiertelevät pesimättömät yksilöt, jotka usein häviävät muutaman päivän kuluttua.

4. Parhaisiin keskiosiin asettuneet koiraat yleensä valtasivat saman reviirin uudestaan seuraavina vuosina ja pesivät näin samalla paikalla jopa vuosikausia (kuva 1). Alueen reunoille joutuneet koiraat sen sijaan pyrkivät seuraavina vuosina valtaamaan uuden reviirin lähempää keskustaa (kuva 2). Seitsemän koiraan todettiin vaihtaneen reviiriä kesken pesimäkauden, joko pesän tuhouduttua tai tuntemattomasta syystä; kaikki kuuluivat alueen laidoille asettuneiden, vähiten paikkauskollisten lintujen ryhmään.

5. Naaraat olivat paljon vähemmän uskollisia menneenkesäisille pesimäpaikoilleen kuin koiraat. Kuitenkin noin puolet niistä muni sekä ensimmäisen että toisen pesyeensä alle 100 m:n päähän edellisen vuoden vastaavista pesäpaikoista (taul. 2), mutta loput siirtyivät jopa 900 m:n matkoja. Yksilölliset erot olivat suuria. Noin kolmannes naaraista oli kierteleviä ja vaihtoi pesimäseutujaan vuodesta toiseen.

6. Alueella syntyneet ja sinne pesimään palanneet nuoret linnut eivät pyrkineet asettu-

maan synnyinpaikkansa läheisyyteen (taul. 3). Tämä johtunee osaksi poikueiden laajasta liikkumisesta, osaksi siitä ettei ensipesijöillä ole vapaan valinnan mahdollisuutta. Kolme nuorta lintua tavattiin pesimäaikana 2.5, 50 ja 170 km:n päästä synnyinalueelta.

7. Lapinsirrin on todettu pesivän muuallakin tiheinä keskittyminä (taul. 4). Nykyinen tietämys *Calidris*-lajien pesimätiheyksistä on koottu taulukkoon 5. Vain pikku- ja maurinsirri pesivät yhtä tiheässä kuin lapinsirri, kun taas isosirrin tiheys on yli sata kertaa pienempi. Lajien välisiin suuriin eroihin reviirin koossa vaikuttavat (1) linnun koko, (2) ravinnon runsaus, (3) ruokailu reviirissä tai sen ulkopuolella, (4) parinmuodostussysteemi, (5) elinympäristön rakenne ja (6) kannan runsaus.

8. Tutkitun lapinsirrikannan koko määräytyi pääasiassa reviirikäyttäytymisen perusteella. Sama säätelymekanismi on todettu lukuisilla muillakin, eri lintulahkoja edustavilla lajeilla. Kaikki tietylle alueelle pyrkivät yksilöt eivät nimittäin pääse asettumaan sinne, vaan (1) joutuvat pesimään epäedullisemmissa biotoopeissa, missä poikastuotto on pienempi ja/tai aikuiskuolleisuus suurempi; (2) joutuvat tyytymään huonompiin reviireihin ja jäävät parittomiksi; (3) eivät pysty valtaamaan reviiriä lainkaan ja muodostavat liikkuvan ylijäämän; (4) kuolevat nopeasti tai lähtevät etsimään vapaita reviirejä muualta.

9. Paikkauskollisuuden kannalta sirrit edustavat kahta päätyyppiä: toiset lajit palaavat vuodesta vuoteen samalle paikalle pesimään, toiset taas vaihtavat vuosittain asuinsijojaan asettuen sinne missä olosuhteet kulloinkin ovat parhaat. Lapinsirrikannassa on molempia tyyppejä; ei-paikkauskollisten osuus näyttää kasvavan pohjoiseen päin, luultavasti siksi että olot ovat epävakaimmat arktisessa pesimäympäristössä.

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