Habitat Deterioration and Efficiency of Antipredator Strategy in a Meadow-Breeding Wader, Temminck's Stint (Calidris temminckii)

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Habitat deterioration and efficiency of antipredator strategy in a meadow-breeding wader, Temminck's stint (*Calidris temminckii*)

Abstract Many populations of waders breeding on open shores and shores with short vegetation especially on the Baltic coasts have recently become endangered. The declines have taken place simultaneously with human-induced loss and deterioration of habitats due to eutrophication and overgrowth. To investigate mechanisms by which habitat changes could affect breeding success and ultimately population dynamics, we studied an endangered coastal population of Temminck's stint. We hypothesized that the rate of nest predation has become higher because the nest defence strategy (early detection of predator and early departure from the nest), which originally evolved in open habitats, is less effective on shores with reduced visibility. As predicted, nests survived better on wide than on narrow shores. Predation made a major contribution to this trend, although successful and predated nests did not differ in concealment at a microhabitat scale. The better the visibility from the nest, the longer was the flushing distance, but only in response to alarm calls or behaviour of other species, not when they were absent. Temminck's stints seem to obtain information about an approaching predator visually from sentinels. Therefore, it is essential that there is at least moderate visibility around the nest. We conclude that habitat characteristics – visibility from the nest and sentinel birds – affect the effectiveness of the nest defence strategy of Temminck's stint. These should be taken into account when seeking causes and mechanisms for declines of Temminck's stint and other waders of open and shortly vegetated shores.

Introduction

Destruction and deterioration of breeding habitats have been considered as primary causes for the decline of the threatened waders of the Western Palearctic (Tucker and Heath 1994). On the Baltic coasts, waders of open and short-vegetated habitats have suffered the most severely in recent decades (Soikkeli and Salo 1979; Emanuelsson and Kjellén 1981; Helle et al. 1988; Rönkä 1996). One of these species is the Temminck's stint (*Calidris temminckii*). Its decline has usually been linked to the decrease in habitat quantity and quality, i.e. overgrowth and narrowing of the shores caused by increased eutrophication and termination of cattle grazing on shore meadows (e.g. Rönkä 1996). Other suspected reasons include e.g. human disturbance on breeding areas due to increased leisure activities and increased predation (for a review see Rönkä 1996); along the coasts of the Bothnian Bay some Temminck's stint populations have suffered from extremely high nest predation (Hildén 1978; A. Rönkä and K. Koivula; unpublished work). A hypothesis that could account for these observations states that the ultimate cause for the Temminck's stint's decline is lowered breeding success due to habitat changes, and increased nest predation rate is the link between habitat changes and breeding success.

One proximate pathway leading to increased nest predation rate could be an increased edge effect caused by a decrease in the open area, because a reduction in habitat patch size increases the relative amount of the edge habitat. Several studies have shown higher nest predation rates near the habitat edge and in small habitat fragments than in sites further from the edge and in large fragments (e.g. Gates and Gysel 1978; Boström and Nilsson 1983; Wilcove et al. 1986; Møller 1989;

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Johnson and Temple 1990; Burger et al. 1994). A higher predation rate near edges may result from several reasons, e.g. more intensive foraging or higher abundance of predators there (e.g. Marini et al. 1995). In addition to an edge effect, the probability of a predator finding a nest by random searching may be higher on a narrow shore than on a wide shore.

Earlier we found that the rate of nest predation on artificial nests is not higher on narrow shores than on wide ones on the coast of the Bothnian Bay (in the current study area), which could mean that the predators' probability to find the nest incidentally is not affected by the width of the shore (Rönkä and Koivula 1997). Logically, this means that if the predation pressure on natural nests is higher on narrow than on wide shores, this difference is linked with the parental behaviour at or near the nest.

In addition to nest concealment and cryptic coloration of eggs and young, the adaptations of birds to avoid nest predation include a multitude of antipredator behaviour (for waders, reviewed in Gochfeld 1984). Many shorebirds breed at open nest sites, where habitat provides little or no concealment, and a common nest defence strategy is early, surreptitious departure from the nest (Gochfeld 1984; Byrkjedal 1987; Colwell and Oring 1990). The stimulus for early departure may be the sight of the intruder (Gochfeld 1984), but the bird may also leave its nest before detecting the predator, responding to alarm calls of other birds or visual cues from e.g. mobbing birds (Nuechterlein 1981; Burger 1984; Gochfeld 1984). Early departure may decrease the risk of nest predation because the predators may use flushing or returning parents as cues when locating the nests (Skutch 1949; Erikstad et al. 1982; Westmoreland and Best 1985) and the detectability of the parents decreases with increasing distance (Carlson 1985; Byrkjedal 1987). Waders may select open nest sites with good visibility from the nest, because openness of the habitat and good visibility may be associated with the early detection of predators (e.g. Dyrcz et al. 1981; Burger 1987; Prindiville Gaines and Ryan 1988; Pampush and Anthony 1993; Lauro and Nol 1995). The early leaving strategy may be less effective on narrow shores with longer and denser vegetation and increased concealment of nests, because poor visibility reduces the flushing distance and increases the detectability of the nest.

In short, we suggest that a decrease in the size of open areas, and an increase in nest concealment and consequent decrease in visibility from the nest, increase the nest predation rate of waders of open habitats by lowering the efficiency of the antipredatory strategy of these species. The general prediction of our hypothesis is that flushing distances should be greatest when the nests are poorly concealed and the visibility from the nest is good. We tested this prediction by an observational field study on Temminck's stint during five breeding seasons on the coast of the Bothnian Bay, Finland.

Materials and methods

Temminck's stint

The Temminck's stint's breeding range covers the Eurasian tundra and the northern parts of taiga (Hayman et al. 1986). In Fennoscandia the core breeding area is in Lapland and the Scandes (Fig. 1), which are inhabited by c. 14 000 pairs (SOF 1990; Koskimies 1992; Breiehagen 1994). A geographically separated smaller population inhabits the coast of the Bothnian Bay (170–200 pairs on the Finnish coast of the Bothnian Bay; Rönkä 1996). The majority of the coastal Temminck's stints are considered vulnerable or endangered (Rassi et al. 1992).

The Temminck's stint breeds near water on sandy and gravelly meadows with low and sparse vegetation, also including industrial workings and other man-made habitats (Rönkä 1996). Temminck's stint is successively bigamous; if there are two clutches, the primary male incubates the first one and the female the second one, which she lays in a territory of another male (Hildén 1975; Breiehagen 1989). The breeding biology and population dynamics of the Temminck's stint in the Finnish Bothnian bay is described in detail in Hildén (1975, 1978, 1979).

The nests of Temminck's stint are predated by several avian (e.g. the hooded crow *Corvus corone cornix*, the common gull *Larus canus* and the ruddy turnstone *Arenaria interpres*) and mammalian predators (e.g. small mustelids and the fox *Vulpes vulpes*) (Hildén 1978; Brearey and Hildén 1985; Helle et al. 1988). The antipredator behaviour of the Temminck's stint includes early departure from the nest after detecting the predator or when other birds give warning of approaching predator, various distraction displays (e.g. injury-feigning), at least around hatching, but no aggressiveness towards the predator (Glutz et al. 1975; Cramp 1985).

Study area

This study was conducted on the coast of the Finnish Bothnian Bay (Fig. 1) in nine typical Temminck's stint's breeding sites. Four sites were in man-made habitats (harbour yards and industrial landfills) with areas of bare sand, gravel and debris and dominant
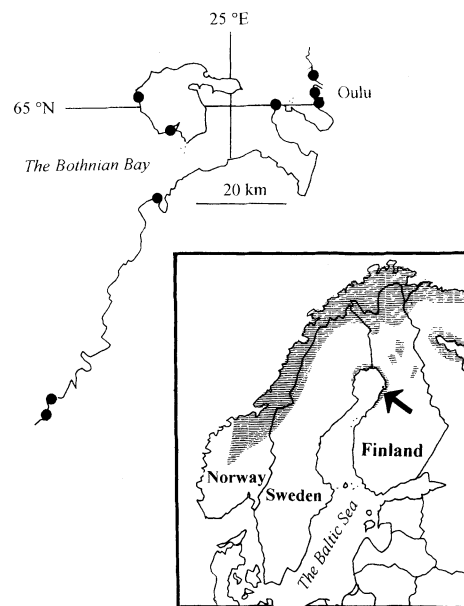

Fig. 1 Study area (*dots* indicate the study sites) and its location (*arrow*) in Fennoscandia. *Shaded area* shows the present distribution of the Temminck's stint in Fennoscandia

plants including *Tanacetum vulgare, Artemisia vulgaris, Achillea millefolium, Equisetum arvense* and *Elymus repens.* Three sites were situated on natural dunes or sandy beaches with narrow meadows dominated by *Calamagrostis stricta, Agrostis stolonifera* and sparse *Phragmites communis.* The dominant plants on the foredunes are *Leymus arenarius, Hieracium umbellatum* and *Festuca ovina,* and the heath vegetation on the deflation behind the foredunes is dominated by *Empetrum nigrum* hummocks, *Festuca ovina* and mosses (*Ceratodon purpureus, Polytrichum piliferum*) with large spots of bare sand and gravel. One site was situated in a bird sanctuary with extensive, silty meadows dominated by *Agrostis stolonifera, Calamagrostis stricta, Juncus gerardii* and *Festuca ovina.*

At least some avian predators – mainly common gulls, ruddy turnstones and corvids – were present in all sites. Mammalian predators are common in all kinds of shore habitats.

Birds that could raise the alarm were present at all sites. The commonest were the Arctic tern *Sterna paradisaea,* the ringed plover *Charadrius hiaticula,* the redshank *Tringa totanus* and the common gull. Other such species were the common tern *Sterna hirundo,* the little tern *S. albifrons,* the ruddy turnstone, the oystercatcher *Haematopus ostralegus,* the lapwing *Vanellus vanellus,* the curlew *Numenius arquata,* the little ringed plover *Charadrius dubius,* the Temminck's stint, the little gull *Larus minutus,* the herring gull *Larus argentatus,* the yellow wagtail *Motacilla flava* and the wood sandpiper *Tringa glareola.*

Nests and breeding data

Nests were searched during the breeding season (late May – mid-June) during 1993–1997. The shores were searched systematically to flush the adults from nests and by following adults returning to nests from a hide. The nests were relocated according to their position in relation to stones, bushes and other natural landmarks, or they were marked with a 5-cm-long red stripe in a stick or reed about 10 m from the nest to varying directions. The marks nearer the nest were made inconspicuously of reeds or small stones to avoid the attention of predators.

The clutch size was checked each time the nests were visited. The clutch was considered complete when the number of eggs (which varied between two and four) remained unchanged between two visits separated at least *c.* 30 h (Breiehagen 1989). When the nest was found after the clutch was completed, the incubation stage was determined by checking the floating angle of the eggs in water. When analysing the data, the incubation period was divided into first and second halves. Incubation was expected to last 22 days (Cramp 1985). If the eggs disappeared before the expected hatching date the nest was considered predated even if there were no direct signs of predation (e.g. eggshells, tracks). Because the hatchlings stay, near the nest for several days and the parents behave conspicuously when they have young, it is unlikely that successful nests were missed and listed as predated. If flooding of the nests was expected (because of prevailing wind directions), the nests were checked at shorter intervals to confirm the cause of nest loss (flooding/predation). A nest was considered successful if at least one egg hatched.

To estimate nesting success we used a simple binomial successful/not successful scale, because we were not interested in absolute values, but rather the differences in relative success between habitat types. Therefore, and because we see no apparent reason why finding the nests should depend on habitat structure due to the searching methods, we did not employ methods based on nest-day data (e.g. Mayfield 1975).

Habitat structure

Shores were assigned to two categories. "Wide" includes shores where the width of the open area between the shoreline and edge of taller vegetation was at least 100 m and the view across the meadow was uninterrupted by e.g. high foredunes. Other shores were classified as "narrow".

In the first 3 study years microhabitats of the nest sites were described at the time around hatching or predation or other nest destruction. To measure the visibility of the nest, a silvery hemisphere with a diameter of 6 cm (originally a Christmas tree decoration) was placed in the nest. The longest distance from which the hemisphere could be seen was then measured from the cardinal points from heights of 160 cm (above ground visibility, AGV) and 10 cm (ground visibility, GV), to an accuracy of 1 m and 10 cm, respectively. The overhead-view coverage was also measured, on a scale from 0 to 4 (0/4 = no cover, 1/4 = cover ≤ 25%, 2/4 = 26–50%, 3/4 = 51–75% and 4/4 = >75%) by looking directly down from 150 cm.

Flushing distance

As microhabitat description, flushing distance data was collected during the years 1993–1995. To measure the flushing distances (hereafter FD) of the parents we approached the nests directly. When we saw the parent leave the nest, we measured the FD to the nearest meter. However, in many cases (see Results) we did not see the bird leave the nest, although warm eggs or a parent near the nest showed that the parent had flushed. We assumed that the absence of the parent signifies long flushing distances. Therefore, we also measured FD on an ordinal scale by recording presence or absence of the parent bird (hereafter, absence percentage, AP). Of course, in some "absent" cases the actual cause of nest departure may not have been us, and the bird may have been e.g. foraging instead. Therefore, we omitted "absent" cases with cool eggs.

The first visits (nest finding) to the nests were omitted, because nearly all the nests were found by observing the flushing parents. Thus, pooling the first visits with rest of the data would have caused sampling error, especially in the data where the absence of a parent was considered to imply long flushing distance. To avoid additional unexplained variation we also omitted the first visits when analysing the exact distances, although the difference between mean FDs of the first and later visits was not significant (2-tailed *t*-test: $t = 0.84$, $df = 80$, $P = 0.40$).

During the visits, we also recorded other antipredator behaviour of the adult, e.g. alarm calls and distraction displays. The visits were also scored in two categories according to the presence or absence of birds of other species raising the alarm.

Nests were visited throughout the breeding season (1–12 times each) and at all times of the day. These factors may generate additional variation in the data and may in some instances operate as potential sources of systematic error. Therefore, in addition to habitat characteristics, we also checked the existence of seasonal and daily effects on nest defence behaviour.

Statistical analyses

To ensure statistical independence, a nest was treated as an statistical unit in most analyses. Therefore, we used mean values of repeatedly visited nests in flushing distance analyses if not otherwise stated. Because of skewed frequency distributions, all distance variables were $\log(x + 1)$ transformed and parametric tests were employed whenever possible. In absence percentage data we use proportions, and non-parametric tests were employed, because despite transformation the distributions of absence percentages remained skewed. If not otherwise stated, the tests are two-tailed. We used one-tailed tests in cases where the structure of logical hypotheses was clearly one-tailed. In general, statistics follow Sokal and Rohlf (1995).

Results

Habitat and survival

We found 117 nests during the study period (Table 1). More than half of the nests were destroyed before hatching (Table 1). Predation was the commonest cause of nest destruction (Table 1). Other causes (flooding and desertion) accounted for only *c*. 8% of the losses.

Losses depended on shore type. On narrow shores over 70% of the nests were unsuccessful while on wide shores more than half of the nests hatched (χ^2-test for independence: $\chi^2 = 4.03$, $df = 1$, $P < 0.05$), and the relationship was still significant when the nests lost for other reasons than predation were excluded ($\chi^2 = 4.12$, $df = 1$, $P < 0.05$, Fig. 2). There were no great differences in microhabitat characteristics of successful and predated nests (Table 2). Ground visibility or above ground visibility did not differ between successful and predated nests (two-sample *t*-tests: GV: $t = 0.4$, $df = 45$, $P = 0.77$; AGV: $t = 0.95$, $df = 45$, $P = 0.35$). Similarly there were no significant differences in cover between successful and predated nests (Mann-Whitney *U*-test: $U_{17,17} = 129$, $P = 0.61$).

Table 1 Number of Temminck's stint's nests (*n*) and number and percentages of nest losses and nests predated during 1993–1997

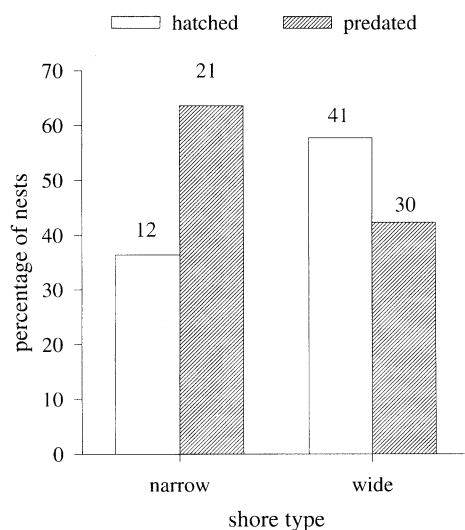| Year	*n*	Nest losses	Nests predated
1993	13	7 (53.8%)	5 (38.5%)
1994	24	10 (41.7%)	10 (41.7%)
1995	24	16 (66.7%)	13 (54.2%)
1996	18	9 (50.0%)	5 (27.8%)
1997	38	22 (57.9%)	18 (47.4%)
Total	117	64 (54.7%)	51 (43.6%)

Fig. 2 Proportion of hatched and predated nests. *Numbers* above the *bars* indicate the absolute number of the nests

Antipredator behaviour

On 66% of the visits ($n = 160$) we did not observe the parents leave the nest. In the remaining 34% of the cases we recorded the exact flushing distance. It varied between 0.5 m and 86 m (mean = 25.0 m, SE = 2.5, $n = 83$). When a bird left the nest it usually flew or walked inconspicuously away. In only six cases (13.9%, $n = 43$) the parents either gave alarm calls (4.6%) or performed some antipredatory displays with or without alarm calls (9.3%). Alarm and distraction displays were associated with short flushing distance (display: mean FD = 10.0 m, SE = 3.8, $n = 6$; no display: mean FD = 22.2 m, SE = 3.3, $n = 37$), but the relationship was not significant, most probably because of the low-power test (two-sample *t*-test: $t = 1.4$, $df = 40$, $P = 0.17$).

Flushing distance increased over the course of incubation. During the second half of the incubation period flushing distance was about twice as long as it was in first half (Table 3). However, despite a similar trend, the proportion of the nests where parents were mostly absent (had long FDs), did not increase towards the end of incubation (Table 4). The increase in absolute flushing distance was probably caused by an increase in the number of cases where birds gave the alarm. When an alarm was given flushing distance was longer than when no birds were present to raise an alarm (Fig. 3, Table 5) and during the first half of incubation alarmers were present in 61% ($n = 33$) of the visits while in the second half the percentage rised to 87%, ($n = 119$, χ^2-test for independence: $\chi^2 = 12.3$, $df = 1$, $P < 0.001$). This was probably due to an increase in overall aggressiveness of other species in the course of breeding season. When controlling for the presence of "alarmers" and incuba-

Table 2 Ground and above ground level visibility (mean ± SE) of hatched and predated Temminck's stints' nests. Tested with two-sample *t*-test

	Hatched ($n = 27$)	Predated ($n = 21$)	*P*
Ground level visibility (m)	1.53 ± 0.13	1.47 ± 0.12	0.77
Above ground visibility (m)	13.11 ± 1.18	14.58 ± 1.30	0.35

Table 3 Flushing distance (nest mean ± SE) in relation to time of day (day/night) and incubation phase (1st/2nd half). First visits are excluded, *n* = number of nests. Tested with *t*-test

	Flushing distance (m)	*n*	*P*
Time of the day			
Day	30.84 ± 5.12	15	0.59
Night	26.50 ± 4.70	15	
Incubation phase			
1st half	15.98 ± 3.27	11	0.01
2nd half	31.43 ± 4.02	17	

tion stage simultaneously, the effect of incubation stage disappeared and only the alarmer effect remained significant (Table 5). Similarly, absence of parents was associated with the presence of alarmers during the second half of the incubation (Fig. 4), but not during the first half (Fig. 4). Because of this effect, the presence of birds that could raise the alarm is controlled for below in the analysis of the relationship between habitat structure and antipredator behaviour.

Flushing distance was not influenced by the number of previous visits (one-tailed Spearman rank correlation: $r_s = -0.02$, $n = 82$, $P > 0.1$) contrary to what could be expected due to e.g. habituation, changes in strategic decisions caused by increase in brood value, or so-called positive reinforcement of aggressive behaviour and subsequent loss of fear in parent birds

(e.g. Knight and Temple 1986). Therefore all except the first visits (see Methods) were taken into account when calculating the mean values for each nest. The nests were visited both day and night. Even though summer nights are not dark in the latitude of our study area, we suspected that dimness could cause some additional variation in flushing distances. However, time of day had no significant effect on flushing distances (Table 3) or absence percentages (Table 4). Therefore, in further analyses we do not consider day and night visits separately.

Flushing distance and habitat

When there were no birds present to give the alarm the variation in above ground visibility or ground visibility explained only less than 3% of the variation in flushing distance (Fig. 5). When there were alarmers present the situation was quite different: variation in AGV explained 25% and in GV 37% of flushing distance variation (Fig. 5). The existence of cover above the nests had no effect on mean flushing distance (Table 6). Unfortunately, because of the low number of cover measurements, we could not separate the nests with alarmers and those without.

Table 4 Number of nests (percentages in parentheses) in which parent was mostly seen to leave the nest (modal flushing distance short) or parent mostly flushed out of sight (modal flushing distance long) in day and night visits and visits in the first and second half of incubation. Tested with χ^2-test for independence

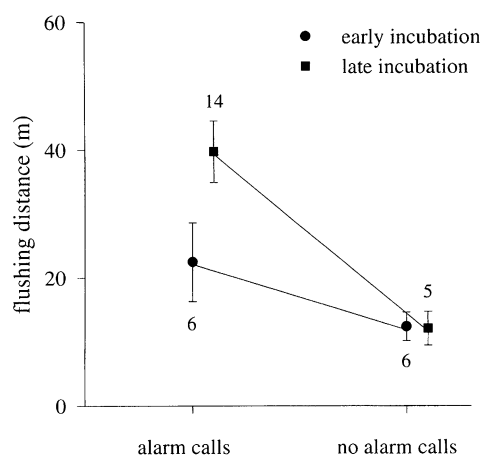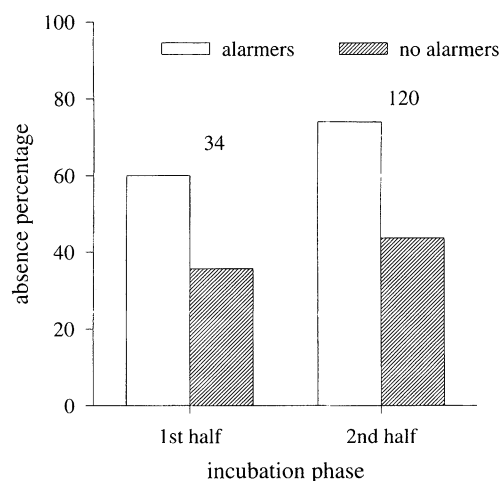|	Long distance	Short distance	P
Time of the day			
Day	23 (68%)	11 (32%)	0.42
Night	18 (58%)	13 (42%)	
Incubation phase			
1st half	10 (50%)	10 (50%)	0.19
2nd half	25 (68%)	12 (32%)	

Fig. 3 Mean flushing distance (mean values of nest means with SE, *bars*) in 1st half and 2nd half of incubation and in presence or absence of alarmers. *Numbers* below and above the *error bars* indicate the number of nests

Fig. 4 Absence percentage of parent bird (proportion of the visits when parent was not seen leave the nest) during 1st and 2nd half of incubation and in presence and absence of alarmers. *Numbers* above the *bars* indicate the number of the visits. Absence frequency of the parent bird was dependent on the presence of alarmers during the 2nd half (χ^2 analysis for independence: $\chi^2 = 6.06$, $df = 1$, $P = 0.013$), but not during 1st half of the incubation ($\chi^2 = 1.94$, $df = 1$, $P = 0.16$)
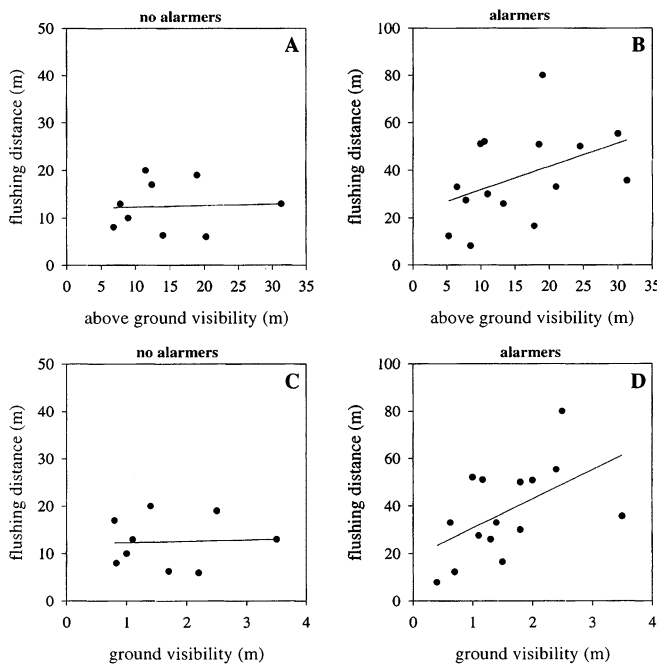
Table 5 ANOVA table for model explaining variation in flushing distance incubation phase (1st/2nd half) and presence of other species giving alarm calls (present/absent)

Source of variation	SS	df	MS	F	P
Incubation phase	0.146	1	0.146	2.375	0.135
Presence of alarmers	0.692	1	0.692	11.229	0.002
Incubation × alarmers	0.188	1	0.188	3.050	0.092
Error	1.663	27	0.062		
Total	3.144	30	0.105		

Fig. 5 Relationship between visibility (ground visibility GV, aboveground visibility AGV) and mean flushing distance in **A, C** absence and **B, D** presence of alarmers. Each *dot* represents mean flushing distance of a single nest. For convenience, *regression lines* refer to original data although actual analyses were performed using transformed data. Variation in both GV and AGV explained a large portion of variation in flushing distance when there were alarmers present (regression analysis GV: $P = 0.02$, $r^2 = 0.37$, AGV: $P = 0.06$, $r^2 = 0.25$). No such relationship was found when there was no alarmers present (GV: $P = 0.97$, $r^2 = 0.0003$, AGV: $P = 0.88$, $r^2 = 0.004$)

Table 6 Mean ($\pm$ SE) flushing distances and mean absence percentage ($\pm$ SE) in nests with no overhead cover and nests with cover. Test for distances one-tailed *t*-test ($t = 0.21$, $df = 14$) and for percentages one-tailed Mann-Whitney *U*-test ($Z = 0.736$)

	Cover	No cover	P
Flushing distance (m)	25.3 $\pm$ 6.5	28.9 $\pm$ 5.9	0.42
	$n = 6$	$n = 10$	
Absence percentage	55.5 $\pm$ 14.2	69.6 $\pm$ 8.2	0.23
	$n = 9$	$n = 16$	

When flushing distance was measured using absence percentage AGV or GV did not correlate with absence percentage whether alarmers were present (AGV: $r_s = -0.01$, $n = 30$, $P > 0.01$, GV: $r_s = 0.08$, $n = 30$, $P > 0.01$) or absent (AGV: $r_s = 0.52$, $n = 11$, $0.05 < P < 0.1$, GV: $r_s = 0.43$, $n = 11$, $0.05 < P < 0.1$). The median absence percentage did not differ between nests with overhead cover and those without (Table 6).

Discussion

More Temminck's stints' nests survived on wide than on narrow shores. Among factors affecting nest survival and depending on the shore width, the probability of flooding might be higher on narrow than on wide shores. Birds breeding on narrow shores are forced to place their nests near the waterline where they are vulnerable to alterations in sea-level, as is the case in piping plover (*Charadrius melodus*), an open-nesting North American wader, which is suggested to prefer wide shores to avoid flooding of nests (Prindville Gaines and Ryan 1988). In the Bothnian Bay the tide is practically lacking but strong southern and western winds can rise the sea-level tens of centimeters in a short time. On low-level shores this means that shoreline can move hundreds of meters. However, flooding accounted for only a minor proportion of the total nest losses.

We attribute the difference in nest survival between shore types to differences in predation rate. Predation was the main cause of nest losses and the predation rate depended on the shore width. Since no relationship between nest predation and shore width was found in the same area in a study involving dummy nests (Rönkä and Koivula 1997), we conclude the rate of the nest predation is connected to factors associated with parent birds.

When we approached the nests the Temminck's stints tended to leave their nests silently and without displays. This strategy is probably especially effective against ground predators that use olfactory cues to find the nests, because nests without parents are not easily found (Österholm 1964; Byrkjedal 1987), but it is quite probable that visual predators can also be deterred by parents leaving the nest early (Carlson 1985; Byrkjedal 1987). Displays and alarm calls are rare during incubation, but after the chicks have hatched they are usual. We could not show clearly that displays were restricted to situations where predators had approached near to the nest, as is the case in golden plover (*Pluvialis apricaria*) and Eurasian dotterel (*Charadrius morinellus*) (Byrkjedal 1987), which are open-nesting waders with antipredator behaviour resembling that of Temminck's stint.

Visibility affected flushing distance. Interestingly, the positive correlation between visibility variables and flushing distance emerged only when there were birds present to raise an alarm. In most nests the average flushing distance was greater than the distance at which the predators became visible, indicating that Temminck's stints may get other than direct visual information about approaching predators and leave the nest before detecting the predator. One alternative source of information is other birds. This "information parasitism" has been verified for grebes nesting in gull or tern colonies (Nuechterlein 1981; Burger 1984). The connection between visibility and flushing distance of stints might mean that the early warning provided by the "sentinel species" is based on visual cues in addition to alarm calls and other auditory signals. The birds giving the alarm might also see the predator earlier in a habitat with good visibility, and start giving the alarm earlier. Against expectation, when flushing distance was measured by absence percentage, there was no correlation between visibility and absence percentage, whether alarmers were

present or not. This might be due to stochastic factors that strongly affect low-power tests. Alternatively, this might imply that for some unknown reason, the presence of alarmers is important only in conditions where flushing distances are usually short. AP data surely include longer overall flushing distances than FD data.

In our study sites the colonially breeding Arctic tern is the commonest species that raises the alarm. It protects its own nest aggressively, and thereby, indirectly, also nests of accompanying species. Shorebirds and waterfowl may prefer tern and gull colonies as breeding sites for protection, and there is empirical evidence that egg predation can actually be lower in colonies than outside them (e.g. Bengtson 1972; Dyrcz et al. 1981; Brearey and Hildén 1985; Götmark 1989; Alberico et al. 1991). The protective effect of breeding in a tern colony is not straightforward. Predation pressure can also be higher in colonies than outside them. For example, colonies may attract predators because they are easy to detect (e.g. Wittenberger and Hunt 1985). Moreover, predators may even prefer colonies as breeding sites for the same reason that their prey do, as does one of the most serious nest predators, the ruddy turnstone (Brearey and Hildén 1985; Alberico et al. 1991).

We obtained no strictly empirical evidence that habitat characteristics related to concealment contributed to predation rate. However, nest concealment was negatively associated with flushing distance – the early-departure strategy appeared to be less effective in habitats with higher nest concealment and lower visibility. Consequently, if habitat changes operate in the way that we hypothesized, decreased visibility could be sufficient to cause increased nest predation. Moreover, since flushing distances were longer when there were other birds present to raise an alarm, the risk of nest predation might also increase when habitats become unsuitable for these alarming and often aggressive species, e.g. Arctic tern.

It is possible that the relationship between concealment and nest survival is not a simple one. Instead, there may be a trade-off between the benefits of visibility and concealment (Götmark et al. 1995). For example, when concealment decreases the visibility increases but the nests become also more easily detectable for predators. In terms of net survival, the optimal solution could be moderate concealment (Götmark et al. 1995). Therefore, and also because there are earlier observations on waders (also Temminck's stint) suggesting that elevated intensity of nest predation is associated with narrowing and overgrowth of the shores (Soikkeli and Salo 1979; Hildén 1978; A. Rönkä and K. Koivula, unpublished work), we consider our hypothesis logically valid and its testing meaningful.

To sum up, habitat changes may have affected nest predation on Temminck's stint in several ways, as well as that of other ecologically similar species. Habitat changes (or other reasons) may have generated an increase in predator numbers. The common gull, herring gull and ruddy turnstone have increased in the Bothnian Bay since the 1950s (e.g. Helle et al. 1988; Hildén and Hario 1993). However, predation pressure may have increased even if there has not been a change in numbers of predators. This might be due to edge effects, habitat-generated changes in number of species that offer protection, or changes in effectiveness of antipredator strategies. These alternatives are not mutually exclusive, but may well reinforce each other. We cannot tell anything definite about predator numbers and landscape-level processes. Our results, however, show that the last two alternatives are possible and that it is highly probable that ineffectiveness of antipredator strategy in less open habitats may have a significant role in explaining the low nesting success. Further, we suggest that the same mechanism may apply to other endangered waders of shores with short vegetation (e.g. dunlin *Calidris alpina schinzii* and ringed plover *Charadrius hiaticula*; for references on population trends see Rönkä 1996) whose nest defence strategy resemble that of Temminck's stints. Finally, we want to stress that the decline of these species may well have multiple causes (including causes operating outside the breeding grounds) that can also act in concert. Among these, predation and the process suggested here are just one, although a promising, alternative.

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