

Increased nest predation in a declining and threatened Temminck's Stint *Calidris temminckii* population

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We measured nesting success of the Temminck's Stint *Calidris temminckii* along the Finnish Bothnian Bay coast during 19 breeding seasons (1983–2001) and conducted a population census (1999–2002). We found 105 pairs, showing a marked decline from the previous survey (170 pairs 1987–95). Of the 424 'known-fate' nests, 47% hatched. Depredation caused 79.9% of the nest losses. Nesting failures increased from 1983–91 to 1992–2001 owing to a rise in nest predation. The proportion of failed nests that failed because of predation rose from 48.9 to 87.7%. When only depredated nests were considered as losses, Mayfield nest survival probability over the incubation period dropped from 69 to 31% (461 nests). This pattern emerged both in man-made and in natural habitats. Survival probability was independent of habitat type (natural vs. man-made). In an experiment involving videotaping of dummy nests, Common Gull *Larus canus* and Ruddy Turnstone *Arenaria interpres* were found to be the most important egg predators.

The populations of many wader species (Charadrii) are declining in Europe for diverse reasons (Tucker & Heath 1994, Stroud *et al.* 2004). The decrease in abundance and the shrinkage in distribution of waders are especially troubling in northern Europe, because, unlike for most other taxa, the species-richness of waders increases from south to north (Järvinen & Väisänen 1978). On the Baltic Sea coast, several waders that use open and short-vegetated habitats have suffered the most severely in recent decades (Väisänen *et al.* 1998, Svensson *et al.* 1999). One of these species is the Temminck's Stint *Calidris temminckii*.

The breeding range of the Temminck's Stint extends from Scandinavia to the Bering Strait in the Eurasian tundra and northern parts of the taiga (Hayman *et al.* 1986). Russia holds the main world breeding population (Hagemeijer & Blair 1997). The core breeding area in Fennoscandia is in Lapland and the Scandes, and a smaller population inhabits the

coast of the Baltic Sea in the Bothnian Bay (Fig. 1; Breiehagen 1994, Väisänen *et al.* 1998, Svensson *et al.* 1999). Coastal Temminck's Stints have declined in number considerably during recent decades (Rönkä 1996, Strid 2003), and some populations in Lapland have also declined (Väisänen *et al.* 1998, Svensson *et al.* 1999). The Temminck's Stint is classified as vulnerable in Finland (Rassi *et al.* 2001, IUCN 1994) and near-threatened in Sweden (Gärdenfors 2000).

Locally, the decline of coastal Temminck's Stints has usually been attributed to habitat loss and deterioration caused by overgrowth and shrinkage of suitable open habitats because of the termination of hay-making and grazing on shore meadows prior to the 1950s (e.g. Hildén 1978, Rönkä 1996, Väisänen *et al.* 1998, Svensson *et al.* 1999). If the decline of the Temminck's Stint in the Bothnian Bay has been primarily caused by habitat loss, restoring shore meadows would be a sufficient measure to prevent a further decrease. However, Temminck's Stints have disappeared from many sites that have remained unchanged, and not all new, potential, breeding sites created by humans or as a result of land uplift have

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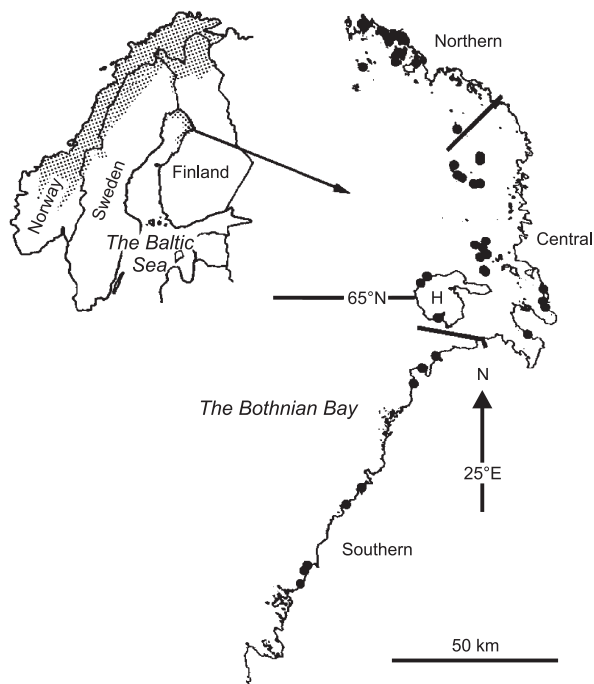


Figure 1. Breeding sites of Temminck's Stint in the Finnish Bothnian Bay 1999–2002 (filled circles). The thick lines separate the northern, central and southern subareas. H = Hailuoto Island. Shading in the index map indicates the distribution of Temminck's Stint in Finland, Sweden and Norway (Breihagen 1994, Väisänen *et al.* 1998, Svensson *et al.* 1999, Strid 2003, this study).

been occupied by Stints (Rönkä 1996). Thus, it is likely that processes other than habitat loss have contributed to the decline. These could include decreased immigration, deterioration of habitats and increased nest predation (Rönkä 1996).

Nest predation is the most important cause of reproductive failure in ground-breeding, open-nesting birds (Martin 1993a, 1993b). The correlation between increased rate of nest predation and population decline in waders is documented in a variety of species (e.g. Blomqvist & Johansson 1991, Parr 1993, Grant *et al.* 1999, Valkama & Currie 1999, Jackson & Green 2000). A rise in nest predation rates may be caused by increased predator populations, and/or by changes in habitat structure that benefit predators or increase nest vulnerability. For example, nest predation rates may be higher near habitat edges and in small habitat fragments than further from the edge or in large fragments (e.g. Gates & Gysel 1978, Wilcove *et al.* 1986, Möller 1989, Johnson & Temple 1990, Paton 1994). We have reported previously that the hatching success in Temminck's Stint nests was higher on wide shore meadows than it was on

narrow ones (Koivula & Rönkä 1998). Furthermore, the nest defence strategy of the Temminck's Stint seemed less effective on shores with reduced visibility around the nest (Koivula & Rönkä 1998), which is correlated with the width of open shore and the density and height of vegetation.

Birds may also select man-made habitats resembling natural ones as their breeding habitats. Currently, about one-fifth of the Temminck's Stints in the Bothnian Bay breed in man-made habitats (harbour yards, industrial landfills) usually close to human habitation (Rönkä 1996). In such sites, human disturbance may influence breeding success both directly and indirectly by increasing vulnerability of nests to predation (Prindiville Gaines & Ryan 1988, Colwell 1992, Gutzwiller *et al.* 2002). In addition, the influence of domestic predators (cats and dogs), as well as that of natural predators preferring urban environments (e.g. corvids), may be higher in man-made than in natural habitats. Thus, owing to proximate mechanisms involved in habitat selection, suboptimal breeding sites may be selected.

From a conservation and management standpoint, it is crucial to understand to which phases of the life cycle population growth is sensitive and which proximate mechanisms contribute to variation in critical vital rates. Such information is important when deciding upon conservation actions.

Here we report the results of a study of Temminck's Stint in the Finnish Bothnian Bay between 1983 and 2002. We focused on temporal changes in the rate of nest predation, causes of nest losses and population trends. We also designed a predation experiment with artificial nests to determine which types of predators were responsible for most of the nest losses. Finally, we compared the rate of nest predation between natural and man-made habitats.

MATERIALS AND METHODS

Study area and species

The study area lies between 63°–65°50'N and 21°–25°30'E in the Finnish Bothnian Bay, covering the present range of the Finnish coastal population (Fig. 1). There, Temminck's Stints occupy both dry sandy and gravel meadows with short and sparse vegetation near water, and industrial workings and other man-made habitats (for details see, for example, Rönkä 1996). The species is present in both coastal and insular habitats. For details of the succession of vegetation on the land uplift coast of the Bothnian

Bay in the northern Baltic Sea see Ericsson and Walentinus (1979) and Vartiainen (1980). The breeding biology and population dynamics of the Temminck's Stint in the Bothnian Bay are described by Hildén (1965, 1975, 1978, 1979).

Population survey

Population surveys of Temminck's Stint were conducted twice between 1985 and 2002. The first survey (spanning the years 1987–95 with the data mainly from 1992–95) covered almost the entire coastline and islands in the Finnish Bothnian Bay; virtually no potential Temminck's Stint habitat was overlooked (Rönkä 1996). In the current survey (1999–2002), most breeding sites found in the previous survey were included. The shores not covered in this study consisted mostly of habitats unsuitable for Temminck's Stint, and have held only a few pairs in recent decades (see Rönkä 1996 and references therein). However, Stints may desert old breeding sites and occupy new ones created, for example, by land uplift. To control for this, c. 170 km of shoreline outside known breeding sites were checked for Temminck's Stints on the mainland coast in southern and central subareas (Fig. 1) in 2001–02.

Surveying methods were the same in the two surveys (Rönkä 1996). As Temminck's Stints are polygamous ('successive bigamy') and the pair bond lasts for only about 1 week (Hildén 1975), a 'pair' in this study usually means a territory occupied by a male. Estimation of the number of pairs was based primarily on conspicuously displaying males. We augmented this with nests, broods and adult birds showing behaviour indicating an incubated nest or a brood nearby. The intensity of the survey varied between the sites from single counts to detailed territory mapping based on repeated visits. However, the within-site intensity (single vs. repeated visits) usually remained the same in the two surveys (see Appendix 1). At sites visited only once during the breeding season, we used the number of displaying males observed. At sites visited repeatedly, only stationary males (often identified individually by colour rings) were used. When a site was checked in more than one year during a survey the number of pairs from the last survey year was used (Appendix 1).

To detect changes in population distribution, we divided the study area into northern, central and southern subareas (Fig. 1). We also studied the population distribution between man-made vs. natural habitats and mainland vs. islands. When scoring

breeding sites as either 'insular' and 'mainland', we treated the large island of Hailuoto (200 km²) as mainland. We present habitat-specific data for between-survey comparisons from the southern and central subareas only, because these data were not collected in the northern subarea in the first survey. Comparison numbers (population changes, occurrence in different habitats) were calculated both including and excluding the sites in the southern ($n = 4$) and the central subarea ($n = 5$) that were not surveyed in the later survey.

The population estimate for the northernmost part of the Swedish Bothnian Bay (Norrbotten) was based on casual observations and shorebird censuses between 1990 and 2000 (A. Livbom pers. comm.).

Because of additional information that became available after the first survey, the estimated number of birds breeding in natural habitats in the central subarea islands was 33 rather than the 26 reported earlier (Rönkä 1996), and we use 170 pairs as the population estimate for the first survey (163 in Rönkä 1996).

Breeding data

Nests were searched for in 18 breeding sites on the mainland coast in the southern and central subareas during 19 breeding seasons from 1983 to 2001 (seven sites between 1983 and 1991, 17 sites between 1992 and 2001). Five sites were situated in man-made habitats and 13 in natural habitats. Site monitoring started in 1983 in man-made habitats and in 1988 in natural habitats.

The nest was usually found by flushing the adult and following the bird's return to the nest from a hide. The position of the nest relative to natural landmarks, or to inconspicuous plastic tags set at random distances and directions from the nests, was marked on a map to aid in nest re-location. The efficiency of nest searches and the interval between nest checks varied. At most nests, the adult bird and the young were captured and ringed with numbered metal rings; in addition, the adult usually received a unique combination of colour rings.

Determination of nest fate

Nests were considered as successful if (1) one or more chicks were seen in, or in the vicinity of, the nest, or (2) the nest was empty and the adult was performing conspicuous chick warning ('broody') behaviour near the nest. The presence of small eggshell

fragments in the nest was not used to classify nest fate, because they could indicate either hatching or predation (Mabee 1997, own observations).

Nests were considered failed if no chicks hatched. They were considered depredated when at least one of the following conditions was met: (1) the eggs disappeared from the nest before the expected hatching date (determined by completion date of the clutch, or by checking the floating angle or the degree of buoyancy of the eggs in water); (2) remains of partially consumed eggs were found in or near the nest; (3) feathers of the adult bird were found at an empty nest; or (4) the nest was found empty after the expected or possible hatching date with no signs of predation or other cause of nest loss, and no chicks or broody parent bird were seen at the breeding site, despite a careful check. The last category may actually include some initially successful cases in which the chicks were consumed by a predator soon after hatching. However, we have no reason to suspect any systematic bias of '4' with respect to habitat types, sites or periods of time, because the depredation criteria were always applied in the same way.

Nest failure caused by flooding or trampling could be identified readily by the condition of the nest. Nests in which incubation was interrupted, or which were not incubated, were considered deserted.

Nesting success

Mayfield survival estimates were calculated according to Mayfield (1975). The number of nest failures and the sum of nest-days in each subset of data were used to calculate the daily probability of nest survival. This was used to calculate the survival probability over the incubation period (hatching success or probability of a nest producing at least one chick); incubation was expected to last 22 days (Hildén 1965). The survival probabilities were first calculated taking into account nests lost due to any cause. However, because our main focus was on the role of nest predation, we also calculated survival probabilities considering only depredated nests as losses. Variances were calculated according to Hensler and Nichols (1981) and compared with the method described by Sauer and Williams (1989). Test statistics were calculated using the program CONTRAST (Hines & Sauer 1989). Tests concerning nest survival were based on daily survival probabilities, although the results were partly presented by using survival probabilities over the incubating period. Otherwise,

statistics follow Sokal and Rohlf (1995). Daily survival probabilities are expressed as the mean \pm 1 se.

For the nests that terminated between observations we usually used the midpoint between the last observed active and the first observed inactive dates ('last active B' method, Manolis *et al.* 2000). Occasionally ($n = 19$) the hatching date was determined by the age of hatchlings, approximated by the size and degree of plumage development. The Mayfield method assumes constancy in daily survival probability throughout the study period (see Johnson & Shaffer 1990). We checked the daily survival probability for egg-laying and incubating periods separately. Finding no significant differences, we combined data from both periods to calculate the survival probabilities. When calculating the daily survival probability for the egg-laying period we assumed the egg-laying interval to be 32 h (Breiehagen 1989).

To analyse temporal changes in nesting success, we divided the time span into early and late periods (1983–91 and 1992–2001, respectively).

Identity of predators

The identity of predators was studied with dummy nests containing Japanese Quail *Coturnix japonica* eggs from a laboratory colony. During the late breeding season (7 to 23 July 2002), six sets of 18 dummy nests, with two eggs in each, were put out in four breeding sites of Temminck's Stints (two sites contained two sets), openly to attract visual predators. Each set consisted of nine pairs of dummy nests in a row. In each pair, one nest was unprotected and the other one was protected with a 60 \times 60-cm wire net (18-mm mesh) standing horizontally 10 cm above the ground and supported by a leg at each corner. Thus, the net would protect the nests against larger predators such as gulls, but not against smaller mammalian (e.g. American Mink *Mustela vison*) or avian (e.g. Ruddy Turnstone *Arenaria interpres*) predators going under the net. The distance between the nests within a pair was 10–15 m and between pairs was 10–20 m. Nests were videotaped with two cameras between 10:20 and 15:15 h for a total of 7 h 35 min.

The duration that each set of dummy nests was exposed varied between 15 and 48 h, after which the nests were checked for possible incidences of nest predation and traces of predators. The eggs in a dummy nest were considered depredated if at least one egg: (1) disappeared, (2) changed position or (3) was crushed. Depredated Temminck's Stint nests and egg remains were inspected for tracks left by predators.

Table 1. Number of Temminck's Stint pairs in the Finnish Bothnian Bay by subarea 1987–95 and 1999–2002 and the change as percentage. Percentages of the population are shown in parentheses.

Subarea	1987–1995	1999–2002	Percentage change
Southern	53 (31)	23 (22)	–57
Central	67 (39)	51 (49)	–24
Northern	50 (29)	31 (30)	–38
Total	170	105	–38

RESULTS

Population survey

In total, we found 105 pairs of breeding Temminck's Stints in the Finnish Bothnian Bay in 1999–2002. The population had decreased by almost 40% from the 170 pairs found in 1987–95 (Table 1; Rönkä 1996). When the nine sites in the southern and central subarea checked in the first but not in the second survey were excluded, the decline was 35%. On the coast of Sweden, regular breeding is restricted to Norrbotten in the northernmost part of the Bothnian Bay (Strid 2003); a population estimate for this area for 1990–2000 was 20–30 pairs (A. Livbom pers. comm.). Therefore, the minimum estimate for the whole Baltic population inhabiting the Finnish and Swedish coasts was 125 pairs.

We checked 28 of the 32 breeding sites situated on the mainland coast (including Hailuoto Island) in the southern and central subareas in the first survey (Rönkä 1996). Fifteen of these sites were deserted and 13 remained; in addition, two new breeding sites emerged between the surveys.

The population had decreased throughout the mainland coast. However, at the regional level the decline was most severe (57%) in the southernmost part of the range (Table 1). The smallest decline, by about 25%, took place in the central part of the range, which is now occupied by about half the population (Table 1). A decline was also clear in the northern part of the range. Despite regional differences, the current distribution pattern in the three subareas did not differ significantly from the 1987–95 distribution (χ^2 analysis: $\chi^2 = 5.35$, $df = 2$, $P = 0.07$). When the sites not checked in the second survey were excluded, the same trend remained: the decline was most severe (53%) in the southern subarea, the smallest decline (18%) took place in the

central subarea, and no difference in the distribution pattern between the surveys emerged (χ^2 analysis: $\chi^2 = 5.13$, $df = 2$, $P = 0.08$).

In the early 1990s, 29.2% of the population in the southern and central subareas inhabited insular sites. In contrast to the overall picture, the numbers of insular breeders have not declined (the sites not checked in the later survey were excluded from the comparison). Consequently, the frequency of the insular breeders in these subareas is now higher (40.5%; $\chi^2 = 4.60$ $df = 1$, $P < 0.05$).

The greater part of the entire Finnish Bothnian Bay population currently occupies insular breeding sites (64.8%) and natural habitats (81.9%).

Nesting success and causes of nesting failures

We monitored 464 nests in total. Data from three nests in man-made habitat located in the southern subarea were excluded when calculating nesting success. The daily survival probability of the nests was 0.948 ± 0.0108 when all causes of nest losses were considered and 0.958 ± 0.0031 when only depredated nests were considered as losses. The survival probabilities over the incubation period were 31% when all causes of nest losses were considered and 39% when only depredated nests were considered as losses. About half (52.8%) of the 424 known-fate nesting attempts failed. Depredation was the main cause (79.9%) of nest losses. Desertion caused 10.3% of the failures (Table 2).

Changes in nesting success and in causes of nesting failures

The daily survival probability of the nests was significantly higher in the early than in the late period (0.965 ± 0.0052 in 1983–91, 0.941 ± 0.0043 in 1992–2001, $\chi^2 = 10.03$, $df = 1$, $P < 0.01$), and hatching success

Table 2. Causes of nest losses as percentages of all losses in Temminck's Stint nests in the Finnish Bothnian Bay 1983–91, 1992–2001 and 1983–2001. n = number of monitored nests. Number of nests is given in parentheses.

Cause of nest loss	1983–1991 $n = 115$	1992–2001 $n = 309$	1983–2001 $n = 424$
Predation	48.9 (22)	87.7 (157)	79.9 (179)
Flooding	4.4 (2)	2.8 (5)	3.1 (7)
Trampling	26.7 (12)	1.7 (3)	6.7 (15)
Desertion	20.0 (9)	7.8 (14)	10.3 (23)

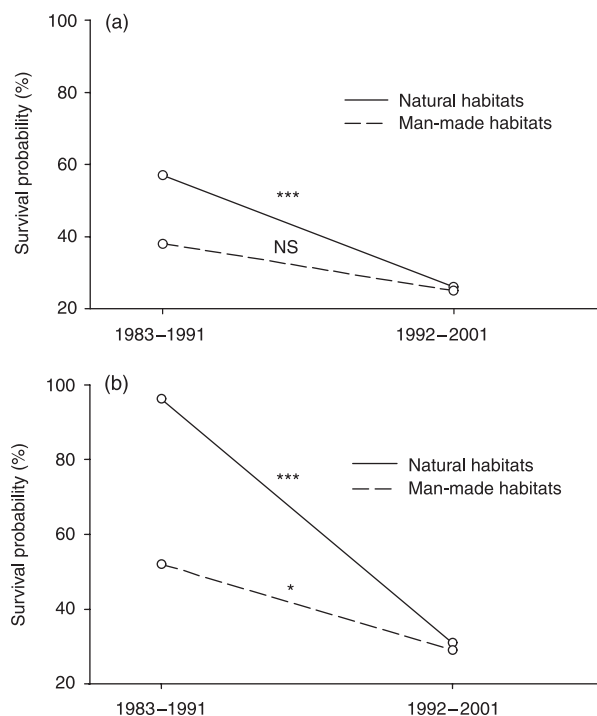


Figure 2. The change in Mayfield survival probability of Temminck's Stint nests over the incubation period from 1983–91 to 1992–2001. χ^2 tests refer to CONTRAST analyses and are based on daily survival probability. (a) Survival calculated considering all failed nests as losses; change in natural habitats from 0.974 ± 0.0065 to 0.941 ± 0.0052 , $\chi^2 = 11.06$, $df = 1$, $P < 0.001$ and in man-made habitats from 0.957 ± 0.0078 to 0.939 ± 0.0077 , $\chi^2 = 2.94$, $df = 1$, $P = 0.087$. (b) Survival calculated considering only depredated nests as losses; change in natural habitats from 0.998 ± 0.0017 to 0.949 ± 0.0049 , $\chi^2 = 65.65$, $df = 1$, $P < 0.001$, and in man-made habitats from 0.970 ± 0.0065 to 0.946 ± 0.0073 , $\chi^2 = 6.21$, $df = 1$, $P < 0.05$.

decreased from 46 to 26%. When only depredated nests were considered as losses, the same trend remained (0.983 ± 0.0036 in 1983–91, 0.948 ± 0.0040 in 1992–2001, $\chi^2 = 36.7$, $df = 1$, $P < 0.001$). Nest survival decreased from 69 to 31%, indicating a marked increase in nest predation. This pattern emerged both in natural and in man-made habitats (Fig. 2). Although

nesting success decreased, the number of failures due to causes other than predation did not; the proportion of the latter actually decreased from 20.0 to 7.1% between the two periods. By contrast, the proportion of depredated nests increased from 19.1 to 50.8%. Consequently, the proportion of depredated nests of the failed nests increased from 48.9 to 87.7% ($\chi^2 = 33.76$, $df = 2$, $P < 0.001$, Table 2).

Survival in different habitats

In general, survival probability was independent of habitat type. Neither overall survival probability nor survival probability for predation significantly differed between natural and man-made habitats (Table 3). However, dividing the study period into early (1983–91) and late (1992–2001) periods revealed that habitat played some role. For total losses, no habitat-related differences (man-made vs. natural) in daily survival probability were observed (early: $\chi^2 = 2.95$, $df = 1$, $P = 0.09$; late: $\chi^2 = 0.54$, $df = 1$, $P = 0.46$; Fig. 2a). However, in the early period predation seemed to be more intense in man-made habitats than in natural habitats ($\chi^2 = 17.13$, $df = 1$, $P < 0.001$). This trend did not emerge in the late period ($\chi^2 = 0.37$, $df = 1$, $P = 0.54$, Fig. 2b).

Identity of nest predators

In two sets of dummy nests, all nests ($n = 36$) survived. In the remaining four sets, survival of dummy nests was dependent on protection: only seven (19.4%) of the 36 unprotected nests survived, whereas 32 (88.9%) of the 36 protected nests survived (2×2 contingency table analysis, $\chi^2 = 34.97$, $df = 1$, $P < 0.001$). By videotaping, Common Gulls *Larus canus* were witnessed taking eggs from 12 unprotected dummy nests. The fact that the nets clearly prevented depredation by Common Gulls indicates that the most serious threat to dummy nests were medium and/or large avian predators. Neither predation by

Table 3. Daily Mayfield nest survival estimates (± 1 se) of the Temminck's Stint nests in man-made and natural habitats in the Finnish Bothnian Bay for all nest losses and when only depredated nests were considered as losses in 1983–2001. Number of nests is given in parentheses. χ^2 statistics refer to CONTRAST analyses.

	Man-made habitats	Natural habitats	Test
All losses	0.946 ± 0.0056 (88)	0.949 ± 0.0043 (135)	$\chi^2_{(1)} = 0.18$ ns
Predation	0.956 ± 0.0051 (72)	0.960 ± 0.0038 (106)	$\chi^2_{(1)} = 0.39$ ns
Nest days	1638	2636	
No. of nests	170	291	

any other species nor predation of the protected nests was videotaped. There were usually no signs left by predators, but in three of the depredated protected nests, holes in the eggshells were typical for the Ruddy Turnstone.

The only predator at the natural nests that we could identify from the egg remains was the Ruddy Turnstone.

DISCUSSION

The Temminck's Stint population in the Bothnian Bay has declined by nearly 40% in less than 10 years. This decline has taken place throughout the range, but the trend in the distribution pattern in the subareas implies that the centre of abundance has moved northwards. This may reflect an ongoing contraction in breeding range, although such a process was not clear over the time-scale of this study. Nevertheless, the regular breeding range is now smaller than it was in the mid-20th century, when it extended hundreds of kilometres southwards from the current southern limit (von Haartman *et al.* 1963–1972, Hildén 1978, Rönkä 1996). Similarly, on the Swedish coast, the Temminck's Stint disappeared from the southernmost parts of its breeding range in the mid-1990s (Strid 2003), where it had been common in the 1940s (SOF 2002).

Only two new breeding sites emerged, whereas 15 of the known breeding sites on the mainland coast in the southern and central subareas were deserted. This supports the conclusion that the decline is real and not caused by birds emigrating to new sites within the study area.

The conclusion that the population is declining in the Bothnian Bay is based on only two surveys and therefore the result may be unrepresentative. However, a qualitative interpretation of the repeated population counts presented in Rönkä (1996) implies that the numbers of Temminck's Stints at different breeding sites in the Bothnian Bay area show no synchronous, high-amplitude fluctuations. Moreover, demographic data from the central and southern subarea based on capture–recapture methods show a relatively steep decline. From 1994 to 2003 the finite rate of population increase (λ) was 0.895 (our unpubl. data). This growth rate is a mean of 7 years and applies to c. 30% of the entire Bothnian Bay population.

Insular breeding sites persisted well in the central subarea between our surveys. This probably partly explains why the magnitude of the decline has been lower in the central than in the southern subarea,

where the frequency of insular breeding sites is much lower. In fact, the decline in the central subarea, when the insular sites were excluded, was much higher (36%) than when they were included (18%). In the southern subarea, the decline was of the same magnitude with (53%) and without the insular sites (52%).

Nesting success of Temminck's Stint in the Bothnian Bay has reached levels among the lowest reported for this species (see Hildén 1978, Breiehagen 1989) and is lower than usually published for shorebirds (e.g. Liker *et al.* 2001 and references therein; but see, for example, Grant *et al.* 1999, Ottvall 2004). Accurate data on adult survival, local recruitment and especially on migration rates are not currently available, but even without detailed demographic analysis one can suspect that too few surviving young are currently produced to compensate for annual adult disappearance. Hildén (1978, data from the southern subarea) reported adult and juvenile survival (from hatching to recruitment) of 76 and 15%, respectively, as estimated by return rates. Assuming also that on average 3.3 chicks hatch per successful clutch (Hildén 1978), that emigration and immigration are equal, and that recruitment rate compensates for adult mortality, nest survival rate would have to exceed 49% to maintain the population. This value is considerably higher than the nesting success rate of 26% observed in this study in 1992–2001. From Hildén's (1978) data, 58% of the nests survived until hatching in a stable population, but only 33% did so during a period of population decline.

Poor breeding success was mainly caused by nest predation, the increase in which coincided with a marked population decline. This suggests that an increase in nest predation and a consequent decrease in production of young could well have contributed significantly to the decline, as has frequently been reported for birds breeding in open habitats (e.g. Hildén 1978, Berg 1992, Suárez *et al.* 1993, Beauchamp *et al.* 1996, Grant *et al.* 1999, Valkama & Currie 1999, Jackson & Green 2000). Many Baltic waders favouring low-sward shore meadows – e.g. the Dunlin *Calidris alpina schinzii* (Soikkeli & Salo 1979, Blomqvist & Johansson 1991) and the Kentish Plover *Charadrius alexandrinus* (Tucker & Heath 1994) – have shown population trends parallel to those of the Temminck's Stint, coincident with high rates of nest predation and habitat deterioration. Thus, increased predation pressure on Temminck's Stint is not necessarily a species-specific problem but may well be a more general phenomenon among birds breeding on coastal meadows.

Why has nest predation increased? This could be related to habitat, to changes in predator fauna, predator behaviour or a combination of these factors. Some earlier findings in the same population – a higher nest predation rate on narrow shore meadows and a less effective nest defence strategy on shores with reduced visibility around the nest (Koivula & Rönkä 1998) – point to habitat structure playing an important part.

During 1983–91, the nests survived depredation better in natural than in man-made habitats, but this was not so during 1992–2001. This difference was caused by a steeper decline in nest survival rates in natural habitats than in man-made habitats, which could reflect the differences in the change in habitat structure between the two habitat types in recent decades. The man-made habitats comprise harbour yards and coastal landfills. In these habitats, the natural succession of vegetation is largely prevented, or it is frequently disturbed by, for example, construction activities, and low-sward breeding sites have constantly been available. Therefore, the increase in nest predation in man-made habitats may not be correlated with a natural overgrowth of vegetation as strongly as in natural habitats. Instead, it could reflect, for example, a general increase in predator populations. In fact, Raccoon Dogs *Nyctereutes procyonoides* were not present in the man-made habitats in the central subarea during the early years of the study, but appeared there in the 1990s.

The high overall predation rate in both man-made and natural habitats implies that the main predators should be common and abundant generalists such as corvids or gulls. Our experiments with dummy nests suggest that the main culprits include the Common Gull and Ruddy Turnstone. It is important to note that increases in Common Gull and Ruddy Turnstone populations have been associated with declines in many local Temminck's Stint populations (Rönkä 1996 and references therein, Väisänen *et al.* 1998). Turnstones can specialize in consuming eggs of shorebirds (Brearey & Hildén 1985). We previously found that the predation rate on artificial nests was higher on shores with Common Gull colonies than on shores with no or few pairs of breeding gulls (Rönkä & Koivula 1997).

However, it is wise to exercise caution when extrapolating from predation experiments to natural predation events (e.g. Larivière 1999, Zanette 2002). For example, predation on artificial nests may lead to overestimation of the significance of avian predators, and artificial wader nests can be predated by predator

species different from those destroying natural nests (e.g. Valkama *et al.* 1999). The latter could include the introduced Raccoon Dog (Kauhala 1998) and American Mink (Kauhala 1996, 1998). Indeed, we observed heavy predation by Raccoon Dogs on the nests of Temminck's Stint and other shorebirds in 2003 at two sites located in man-made habitats.

The significance of nest predators in limiting populations of waders and other ground-breeding birds has been demonstrated in studies in which predator control (e.g. Anthony *et al.* 1991, Parr 1993, Donald *et al.* 2002, Nordström *et al.* 2003) or protection of nests with predator exclosures (Jönsson 1987, Rimmer & Deblinger 1990, Maxson & Haws 2000) was followed by improved breeding performance and/or a population increase (Tapper *et al.* 1996; but see Côté & Sutherland 1997, Mabee & Estelle 2000). Our evidence linking poor breeding success with population decline is purely correlative.

However, we conclude by stating that although an improvement in nesting success may be necessary to facilitate recovery of the population, alone it may nonetheless be inadequate to achieve this.

Temminck's Stint is categorized as vulnerable in Finland (Rassi *et al.* 2001) and near-threatened in Sweden (Gärdenfors 2000). According to our study, the Baltic population is small, fragmented and declining, and thus fulfils the criteria of the category 'endangered' (IUCN 1994). Especially worrying is the trend in nest predation rate found in natural habitats, which hold most of the population. It seems that without identification of the agents of decline and consequent effective management the population in the Bothnian Bay may face extinction. In fact, it is possible that this population will soon cross the 'small population threshold', after which its fate will be determined primarily by stochastic processes (e.g. Caughley 1994) regardless of management effort.

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REFERENCES

- Anthony, R.M., Flint, P.L. & Sedinger, J.S. 1991. Arctic Fox removal improves nest success of Black Brant. *Wildl. Soc. Bull.* **19**: 176–184.
- Beauchamp, W.D., Koford, R.R., Nudds, T.D., Clarck, R.G. & Johnson, D.H. 1996. Long-term declines in nest success of prairie ducks. *J. Wildl. Manage.* **60**: 247–257.
- Berg, Å. 1992. Factors affecting nest-site choice and reproductive success of Curlews *Numenius arquata* on farmland. *Ibis* **13**: 44–51.
- Blomqvist, D. & Johansson, O.C. 1991. Distribution, reproductive success, and population trend in the Dunlin *Calidris alpina schinzii* on the Swedish west coast. *Ornis Svecica* **1**: 39–46.
- Brearey, D. & Hildén, O. 1985. Nesting and egg-predation by Turnstones *Arenaria interpres* in larid colonies. *Ornis Scand.* **16**: 283–292.
- Breiehagen, T. 1989. Nesting biology and mating system in an alpine population of Temminck's Stint *Calidris temminckii*. *Ibis* **131**: 389–402.
- Breiehagen, T. 1994. Temmincksnipe. In Gjershaug, J.O., Thingstad, P.G., Eldøy, S., & Byrkjeland, S. (eds) *Norsk fugleatlas*: 182–183. Klæbu: Norsk Ornitologisk Forening (in Norwegian).
- Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* **63**: 215–244.
- Colwell, M.A. 1992. Wilson's Phalarope nest success is not influenced by vegetation concealment. *Condor* **94**: 767–772.
- Côté, I.M. & Sutherland, W.J. 1997. The effectiveness of removing predators to protect bird populations. *Conserv. Biol.* **11**: 395–405.
- Donald, P.F., Evans, A.D., Muirhead, L.B., Buckingham, D.L., Kirby, W.B. & Schmitt, S.I.A. 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* **144**: 652–664.
- Ericsson, L. & Wallentinus, H.-G. 1979. Sea-shore vegetation around the Gulf of Bothnia. Guide for the international Society of Vegetation Science, July–August 1977. *Wahlenbergia* **7**.
- Gärdenfors, U. (ed.) 2000. *Rödlistade arter i Sverige 2000. The 2000 Red List of Swedish Species*. Uppsala: Artdatabanken, SLU (in Swedish).
- Gates, J.E. & Gysel, L.W. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**: 871–883.
- Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., Rodwell, S. & Moore, N. 1999. Breeding success and causes of breeding failure of curlew *Numenius arquata* in Northern Ireland. *J. Appl. Ecol.* **36**: 59–74.
- Gutzwiller, K.J., Riffell, S.K. & Anderson, S.H. 2002. Repeated human intrusion and the potential for nest predation by Gray Jays. *J. Wildl. Manage.* **66**: 372–380.
- von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. (eds) 1963–1972. *Pohjolan linnut värikuvina*: 392–396. Helsinki: Otava (in Finnish).
- Hagemeijer, E.J.M. & Blair, M.J. (eds) 1997. *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. London: Poyser.
- Hayman, P., Marchant, J. & Prater, T. 1986. *Shorebirds; an Identification Guide to the Waders of the World*. Bromley: Christopher Helm Ltd.
- Hensler, G.L. & Nichols, J.D. 1981. The Mayfield method of estimating nesting success: a model, estimation and simulation results. *Wilson Bull.* **93**: 42–53.
- Hildén, O. 1965. Zur Brutbiologie des Temminckstrandläufers, *Calidris temminckii* (Leisl.). *Ornis Fenn.* **42**: 1–5 (in German).
- Hildén, O. 1975. Breeding system of Temminck's Stint *Calidris temminckii*. *Ornis Fenn.* **52**: 117–146.
- Hildén, O. 1978. Population dynamics in Temminck's Stint *Calidris temminckii*. *Oikos* **30**: 17–28.
- Hildén, O. 1979. Territoriality and site tenacity of Temminck's Stint *Calidris temminckii*. *Ornis Fenn.* **56**: 56–74.
- Hines, J.E. & Sauer, F.R. 1989. *Program CONTRAST: a General Program for the Analysis of Several Survival or Recovery Rate Estimates*. US Fish and Wildlife Service Technical Report 24.
- IUCN. 1994. *IUCN Red List Categories*. Gland: IUCN.
- Jackson, D.B. & Green, R.E. 2000. The importance of the introduced Hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. *Biol. Conserv.* **93**: 333–348.
- Järvinen, O. & Väisänen, R. 1978. Ecological zoogeography of North European waders, or why do so many waders breed in the North? *Oikos* **30**: 496–507.
- Johnson, D.H. & Shaffer, T.L. 1990. Estimating nesting success: when Mayfield wins. *Auk* **107**: 595–600.
- Johnson, R.G. & Temple, S.A. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *J. Wildl. Manage.* **54**: 106–111.
- Jönsson, P.E. 1987. The Kentish Plover *Charadrius alexandrinus* in Scania, South Sweden, in 1987 – a report from a conservation project. *Anser* **26**: 259–264 (in Swedish with English summary).
- Kauhala, K. 1996. Distributional history of the American Mink (*Mustela vison*) in Finland with special reference to the trends in Otter (*Lutra lutra*) populations. *Ann. Zool. Fenn.* **33**: 283–291.
- Kauhala, K. 1998. The effects of introduced carnivores on native fauna in Finland: distribution history of the American Mink and Raccoon Dog. *Suomen Riista* **44**: 7–17 (in Finnish with English summary).
- Koivula, K. & Rönkä, A. 1998. Habitat deterioration and efficiency of antipredator strategy in a meadow-breeding wader, Temminck's Stint (*Calidris temminckii*). *Oecologia* **116**: 348–355.
- Larivière, S. 1999. Reasons why predators cannot be inferred from nest remains. *Condor* **101**: 718–721.
- Liker, A., Reynolds, J.D. & Székely, T. 2001. The evolution of egg size in socially polyandrous shorebirds. *Oikos* **95**: 3–14.
- Mabee, T.J. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bull.* **109**: 307–313.
- Mabee, T.J. & Estelle, V.B. 2000. Assessing the effectiveness of predator exclosures for plovers. *Wilson Bull.* **112**: 14–20.
- Manolis, J.C., Andersen, D.E. & Cuthbert, F.J. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* **117**: 615–626.
- Martin, T.E. 1993a. Nest predation and nest sites: new perspectives on old patterns. *Bioscience* **43**: 523–532.
- Martin, T.E. 1993b. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Natur.* **141**: 897–913.
- Maxson, S.J. & Haws, K.V. 2000. Population studies of Piping Plover at Lake of the Woods, Minnesota: 19 year history of a declining population. *Waterbirds* **23**: 475–481.

- Mayfield, H.F.** 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.
- Møller, A.P.** 1989. Nest-site selection across field–woodland ecotones: the effect of nest predation. *Oikos* **56**: 240–246.
- Nordström, M., Högmander, J., Laine, J., Nummelin, J., Laanetu, N. & Korpimäki, E.** 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biol. Conserv.* **109**: 359–368.
- Ottvall, R.** 2004. Breeding success and adult survival of Redshank (*Tringa totanus*) on coastal meadows in SE Sweden. In Ottvall, R. *Population Ecology and Management of Waders breeding on Coastal Meadows*. PhD thesis, University of Uppsala.
- Parr, R.** 1993. Nest predation and numbers of Golden Plovers *Pluvialis apricaria* and other moorland waders. *Bird Study* **40**: 223–231.
- Paton, P.W.C.** 1994. The effect of edge on avian nest success: how strong is the evidence? *Conserv. Biol.* **8**: 17–26.
- Prindiville Gaines, E. & Ryan, M.R.** 1988. Piping Plover habitat use and reproductive success in North Dakota. *J. Wildl. Manage.* **52**: 266–273.
- Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. (eds)** 2001. *Suomen Lajien Uhanalaisuus 2000*. Helsinki: Ministry of Environment and Finnish Environment Institute (in Finnish).
- Rimmer, D.W. & Deblinger, R.D.** 1990. Use of predator exclosures to protect Piping Plover nests. *J. Field Ornithol.* **61**: 217–223.
- Rönkä, A.** 1996. Distribution, status and population trends in the Temminck's Stint *Calidris temminckii* in the Finnish Bothnian Bay. *Ornis Fenn.* **73**: 1–11.
- Rönkä, A. & Koivula, K.** 1997. Effect of shore width on the predation rate of artificial wader nests. *Ibis* **139**: 405–407.
- Sauer, J.R. & Williams, B.K.** 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.* **53**: 137–142.
- SOF.** 2002. *Sveriges fåglar. Vår Fågelvärld Suppl.* **36**: 108–109 (in Swedish).
- Soikkeli, M. & Salo, J.** 1979. The bird fauna of abandoned shore pastures. *Ornis Fenn.* **56**: 124–132.
- Sokal, R.R. & Rohlf, F.J.** 1995. *Biometry*, 3rd edn. New York: Freeman.
- Strid, T.** 2003. Fågelrapport för 2002. In *Fågelåret 2002*: 85. Stockholm: SOF (in Swedish).
- Stroud, D.A., Davidson, N.C., West, R., Scott, D.A., Haanstra, L., Thorup, O., Ganter, B. & Delany, S. (eds)** 2004. Status of migratory wader populations in Africa and Western Eurasia in the 1990s. *International Wader Studies* **15**: <http://web.uct.ac.za/depts/stats/adu/wsg/home.html>.
- Suárez, F., Yanes, M., Herranz, J. & Manrique, J.** 1993. Nature reserves and the conservation of Iberian shrubsteppe passerines: the paradox of nest predation. *Biol. Conserv.* **64**: 77–81.
- Svensson, S., Svensson, M. & Tjernberg, M.** 1999. Svensk fågelatlas. *Vår Fågelvärld Suppl.* **31** (in Swedish).
- Tapper, S.C., Potts, G.R. & Brockless, M.H.** 1996. The effects of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix*. *J. Appl. Ecol.* **33**: 965–978.
- Tucker, G.M. & Heath, M.F. (eds)** 1994. *Birds in Europe: Their Conservation Status*. BirdLife Conservation Series no. 3. Cambridge: BirdLife International.
- Väisänen, R., Lammi, E. & Koskimies, P.** 1998. *Muuttuva Pesimälinnusto*. Helsinki: Otava (in Finnish).
- Valkama, J. & Currie, D.** 1999. Low productivity of Curlews *Numenius arquata* on farmland in southern Finland: causes and consequences. *Ornis Fenn.* **76**: 65–70.
- Valkama, J., Currie, D. & Korpimäki, E.** 1999. Differences in the intensity of nest predation in the Curlew *Numenius arquata*: a consequence of land use and predator densities? *Ecoscience* **6**: 497–504.
- Vartiainen, T.** 1980. Succession of island vegetation in the land uplift area of the northernmost Gulf of Bothnia, Finland. *Acta Bot. Fenn.* **115**: 1–104.
- Wilcove, D.S., McLellan, C.H. & Dobson, A.P.** 1986. Habitat fragmentation in the temperate zone. In Soulé, M.E. (ed.) *Conservation Biology: the Science of Scarcity and Diversity*: 237–256. Sunderland, MA: Sinauer.
- Zanette, L.** 2002. What do artificial nests tell us about nest predation? *Biol. Conserv.* **103**: 323–329.

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APPENDIX 1

Number of Temminck's Stint pairs per site by year in the 1999–2002 survey and the surveying method used in the 1987–95 and 1999–2002 surveys. The population estimate for 1999–2002 consists of the number of pairs given in bold type. The data from the northern subarea (sites 1–23) include only the sites having Stints in the later survey. For the central subarea (sites 24–52) and the southern subarea (sites 53–70) numbers of pairs are shown for breeding sites surveyed in both surveys. **Surveying method: 1a = single visit, species-specific; 1b = single visit, not species-specific; 2a = repeated visits, species-specific; 2b = repeated visits, not species-specific.**

Site(s)	Number of pairs				Surveying method	
	1999	2000	2001	2002	1987–1995	1999–2002
1–2	2				1b	1b
3–13		13			1b	1b
14–15			2		1b	1b
16–21				9	1b	1b
22				4	1b	1a
23				1	1b	2a
24			3		2b	1b
25			4		1b	1b
26			1		1b	1b
27			1		1b	1b
28			2		1b	1b
29				2	1b	1b
30				1	1b	1b
31				2	1b	1a
32				1	1b	1a
33				1	1b	1a
34				0	1b	1a
35				2	1b	1a
36				6	1b	1a
37				2	1b	1a
38				2	1b	1a
39				0	1b	1a
40				0	1b	1a
41	3	3	3	1	1a	1a
42	9	4	4	6	1a	1a
43	7	9	9	7	1a	1a
44	3	2	0	0	1a	1a
45		0	1		2b	2b
46				1	2a	1a
47		1		0	2a	1a
48	2	3	3	3	2a	2a
49				0	2a	2a
50	2	1		2	2a	2a
51				0	1b	1a
52				0	1b	1a
53				1	1a	1a
54		19	20	8	2a	2a
55				2	1b	2a
56				0	1b	1a
57				0	1b	1a
58				0	1b	1a
59				0	1b	1a
60				0	1b	1a
61				0	1b	1a
62				1	1b	2a
63				2	2a	2a
64				0	2a	2a
65	1	0	0	0	2a	1a
66	3	3	2	2	2a	2a
67	6	5	5	5	2a	2a
68				2	2a	1a
69				0	2a	1a
70				0	1b	1b