

*Antti Rönkä*

DYNAMICS, GENETIC  
STRUCTURE AND VIABILITY  
OF A SMALL AND DECLINING  
TEMMINCK'S STINT (*CALIDRIS  
TEMMINCKII*) POPULATION

FACULTY OF SCIENCE,  
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*ANTTI RÖNKÄ*

**DYNAMICS, GENETIC STRUCTURE  
AND VIABILITY OF A SMALL AND  
DECLINING TEMMINCK'S STINT  
(*CALIDRIS TEMMINCKII*)  
POPULATION**

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## *Abstract*

Globally, populations of several wader species are in decline. However, for most populations, information on abundance, its changes and the causes of declines is insufficient for designing successful management strategies to recover threatened populations. In this thesis I studied the status and population trends, nesting success, genetic structure and viability of a small, declining and threatened Temminck's stint population in the Bothnian Bay in the northern Baltic Sea. Historical population data, recent population counts in the early 1990s and in 1999–2002 and the demographic data showed that the decline is continuing, paralleled by declines in nesting success, recruitment and adult survival.

Decline in nesting success was caused by a coincident increase in nest predation. Depredation was the main cause of nest losses. The common gull (*Larus canus*) and the ruddy turnstone (*Arenaria interpres*) were found to be the most important nest predators. I tested if an increase in nest concealment and consequent decrease in visibility lowers the efficiency of the early-departure antipredator behaviour of the species. An expected positive correlation emerged between visibility and flushing distance in the presence of alarm-giving birds, but not without them. This indicates that Temminck's stint exploits signals from other birds as early warning of an approaching predator. More nests were lost to predation on narrow than on wide shores. The nest predation rate was not related to habitat (natural vs. man-made) nor to differences in microhabitat characteristics associated with concealment.

Overall variability of the mitochondrial control region was low in the one northeast Siberian and the three Fennoscandian populations studied. The occurrence of two maternal lineages in all Fennoscandian populations points to mixing of two previously isolated populations. The overall microsatellite genetic structuring (6 loci) in Fennoscandia was low. The pairwise comparison revealed a low but significant degree of differentiation between the Bothnian Bay and the two other Fennoscandian populations. However, no clear indication of genetic effects of small population size in the Bothnian Bay was detected.

Matrix and Pradel- $\lambda$  projection models, based on a ten year (1994–2003) capture-recapture data set, predicted a steep future decrease and a high risk of extinction within 50 years. Without immigration the decline would lead to extinction within 20 years. Population growth was the most sensitive to changes in adult survival, the rate of which declined during the study. Factors affecting adult survival most likely operate primarily during the non-breeding season in locations specific to the study population that are virtually unknown. Management efforts in the Bothnian Bay should, in addition to improving hatching success, first of all guarantee availability of wide, low-sward coastal breeding habitats for potential immigrants and recruits.

*Keywords:* conservation, extinction, nest predation, wader



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Oulu, June 2006

Antti Rönkä



## List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Rönkä A (1996) Distribution, status and population trends in the Temminck's stint *Calidris temminckii* in the Finnish Bothnian Bay. *Ornis Fennica* 73: 1–11.
- II Rönkä A, Koivula K, Ojanen M, Pakanen VM, Pohjoismäki M, Rannikko K & Rauhala P (2006) Increased nest predation in a declining and threatened Temminck's stint *Calidris temminckii* population. *Ibis* 148: 55–66.
- III Rönkä A & Koivula K (1997) Effect of shore width on the predation rate of artificial wader nests. *Ibis* 139: 405–407.
- IV 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.
- V Rönkä A, Kvist L, Karvonen J, Koivula K, Pakanen VM, Schamel D & Tracy DM (2006) Geographical variation and population structure in the Temminck's stint *Calidris temminckii* as shown by mitochondrial DNA and microsatellites, with an emphasis on Fennoscandian populations. (Manuscript)
- VI Koivula K, Pakanen VM, Rönkä A & Belda E (2006) Dynamics and viability of a declining Temminck's stint (*Calidris temminckii*) population. (Manuscript)



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# 1 Introduction

## 1.1 General background

Anthropogenic habitat destruction and fragmentation, overexploitation of species, impact of invasive alien species and pollution have been the primary causes of population declines and extinction events during recent centuries (Baillie *et al.* 2004). In addition to these deterministic agents of decline, small populations are especially subject to intrinsic environmental, demographic, genetic and catastrophic stochasticity (Shaffer 1981). A positive feedback between population size, loss of genetic diversity and inbreeding, known as extinction vortex, may finally drive the population into extinction for other reasons than the ones that caused the original decline (Caughley 1994, Frankham *et al.* 2002). Therefore, considering both deterministic and stochastic factors is critical in diagnosing extinction processes. Decrease of a population is fundamentally a demographic process involving a decline in one or more vital rates. Analysing population dynamics may aid to track the critical vital rates and also the environmental mechanisms that could be targeted by conservation and management efforts (e.g., Hedrick *et al.* 1996).

Globally, almost half the wader populations of known trends are in decline and a fifth of wader species are threatened or near threatened (Delany & Scott 2002). The decrease in abundance and shrinkage of distribution in waders are especially troubling in the northern latitudes, because, unlike for most other taxa, the species-richness of waders increases from south to north (Järvinen & Väisänen 1978). However, for most wader populations, the basic information on abundance and its changes are inadequate and the causes of the declines are often poorly known (Stroud *et al.* 2004, Thorup 2006). This translates directly into incapability in designing successful management strategies to recover threatened populations. Especially long-distance migrant waders breeding at high latitudes form a problematic group from a conservation standpoint. Both breeding grounds and wintering areas may be inaccessible to monitoring programs, and therefore even dramatic population changes may happen without detection.

The causes of population declines of waders are manifold. Suggested causes include habitat loss and deterioration due to development of coastal wetlands (e.g., agricultural intensification), pollution, intensification of hunting and other forms of human

disturbance, increase in predation and parasite abundance and reduction in amount of prey (e.g., Tucker & Heath 1994, Zöckler *et al.* 2003, Stroud *et al.* 2004). Many of these causes may be associated with climate change (see reviews by Rehfisch & Crick 2003 and Smart & Gill 2003). Habitat loss can also be responsible for decreased connectivity between bird populations and consequent low immigration, leading to population declines, especially in peripheral populations (e.g., Ward 2005).

Migratory waders are long-lived species with low reproductive rate and relatively high annual survival typically exceeding 50% (Evans & Pienkowski 1984, Piersma & Baker 2000). Adult survival seems to be the vital rate having the largest contribution to population growth in waders (Hitchcock & Gratto-Trevor 1997, Larson *et al.* 2002, Ottvall & Härdling 2005). Therefore, and because all arctic waders are long-distance migrants and spend most of their annual cycle away from breeding grounds, their breeding populations may be especially sensitive to environmental changes along migration routes and wintering areas (Myers *et al.* 1987). Nevertheless, changes in breeding wader populations may also be driven by breeding habitat changes or other factors operating in breeding grounds affecting breeding success. Long-term data on population size, productivity and survival and information about key factors in population regulation throughout the annual cycle are needed to identify the factors responsible for declines of populations and to assess the relative importance of different vital rates affecting them (e.g., Caughley 1994, Beissinger & Westphal 1998, Minton 2003, Stroud *et al.* 2004, Robinson *et al.* 2005).

## **1.2 Population declines and breeding habitat changes: the role of nest predation**

Nest predation is the most important cause of reproductive failure in ground-breeding, open-nesting birds (Suárez *et al.* 1993, Martin 1993a,b, Beauchamp *et al.* 1996). Consequently, nest predation can have a large effect on population dynamics of waders and other ground-nesting birds. Correlation between increased rate of nest predation and population decline has been documented in a variety of wader species, for example the Temminck's stint (*Calidris temminckii*, Hildén 1978), the dunlin (*Calidris alpina schinzii*, Blomqvist & Johansson 1991), the golden plover (*Pluvialis apricaria*, Parr 1993) and the curlew (*Numenius arquata*, Valkama & Currie 1999). Moreover, the significance of nest predators in limiting populations of waders and other ground-breeding birds has been demonstrated in studies where predator control (Anthony *et al.* 1991, Parr 1993, Donald *et al.* 2002, Nordström *et al.* 2003) or protection of nests with predator enclosures (Jönsson 1987, Rimmer & Deblinger 1990, Maxson & Haws 2000) was followed by improved breeding performance and/or a population increase (Tapper *et al.* 1996, Jackson & Green 2000; but see Côté & Sutherland 1997 and Mabee & Estelle 2000).

Various causal mechanisms have been suggested to explain how habitat changes may lead to a reduction in bird populations through triggering an increase in nest predation (reviewed by Evans 2004). These include, for example, an increase in predator densities and numbers, changes in food sources of generalist predators, increased nest or chick

detectability owing to habitat fragmentation and edge effect, declines in populations of species providing a “protective umbrella”, and reduced nest defence (see Smart & Gill 2003 and Evans 2004 for references).

At sparsely vegetated nest sites, good visibility from the nest may be associated with early visual detection of predators (e.g., Dyrce *et al.* 1981, Burger 1987, Lauro & Nol 1995) and consequent early, surreptitious departure from the nest, a common antipredator strategy in many waders of open meadows (Gochfeld 1984). Birds may also exploit alarm calls or visual observations of mobbing birds as early warning of an approaching predator (“information parasitism”; Nuechterlein 1981, Burger 1984, Pöysä 1988). Thus, increased vegetation height and density may decrease the efficiency of the early leaving strategy, i.e. flushing distances may be shorter on shores with longer and denser vegetation and poor visibility, because the predator or the mobbing birds are detected later. Overgrowth of vegetation can also contribute to the decline of populations of the “umbrella species”.

### **1.3 Genetic variation and population structuring in northern waders**

Genetic distinctiveness of populations within a species have been used in classifying populations into units deserving separate management (e.g., Gorman 2000, Ottvall *et al.* 2005), referred to as evolutionary significant units (ESU) or management units (MU) (Ryder 1986, Moritz 1994, Crandall *et al.* 2000). However, defining such units using solely genetic criteria may lead to incorrect management decisions. For instance, estimates of population structure and gene flow depend on the markers used (Bossart & Prowell 1998). Moreover, degree of diversity in neutral markers may be a poor predictor of genetic variation in quantitative traits (Reed & Frankham 2001; but see Merilä & Crnokrak 2001). Thus, also other sources of information have been recommended to be used together with genetic data (e.g., data on phylogeny, distribution, morphology, ecology, mortality, population connectivity and abundance) considering both recent and historical time frames (Paetkau 1999, Taylor & Dizon 1999, Crandall *et al.* 2000, Bruford 2002).

The distribution of genetic variation within and among populations of a species is shaped by historical and current population sizes, population bottlenecks, breeding systems, natural selection, different mutation rates, degree of current gene flow among populations and interactions among these factors (Frankham *et al.* 2002). Species such as arctic waders have repeatedly experienced major changes in range and availability of suitable habitats caused by climatic oscillations (Dynesius & Jansson 2000). Isolated refugial populations formed during the Pleistocene glacial cycles have played a profound part in within-species population differentiation and speciation (Avice & Walker 1998, Hewitt 2000 and 2004). An example is the dunlin, a wader inhabiting predominantly the low arctic zone, with several subspecies and a pronounced geographic population structure (Wenink *et al.* 1994, Kraaijeveld & Nieboer 2000, Wennerberg & Bensch 2001). However, most waders with a breeding range entirely or in part within the arctic zone show low degree of variation and low level of population differentiation in mitochondrial DNA (mtDNA). These include the white-rumped sandpiper (*Calidris fuscicollis*, Wennerberg *et al.* 2002), the knot (*Calidris canutus*) and the curlew sandpiper (*Calidris*

*ferruginea*, Wennerberg & Burke 2001). In addition, low level of variation and population differentiation in mtDNA is found also in populations of species with a range within or extending further south to the temperate zone, such as the ruddy turnstone (*Arenaria interpres*, Wenink *et al.* 1994) and the redshank (*Tringa totanus*, Ottvall *et al.* 2005).

Subspecies have been distinguished by biometrics in the above wader species except the white-rumped and the curlew sandpiper (Cramp 1985). Thus, lack of mtDNA sequence diversion need not indicate morphological monotypicity or vice versa. Nevertheless, no subspecies have been described for most low arctic waders and most arctic calidrid waders on morphological basis (Cramp 1985).

Recolonization of the current range from small, bottlenecked refugial populations has been suggested to explain the low mtDNA variability observed in many northern species (Baker *et al.* 1994, Zink 1996, Fedorov 1999, Ottvall *et al.* 2005). For waders, it has been suggested that the knot and the ruddy turnstone experienced a population bottleneck during the warm early Holocene around 8000–6000 years ago, when boreal forests and shrub tundra extended much further north than today, decimating cold tundra habitat in Eurasia and North America and restricting arctic breeding waders to extreme high arctic Canada, Greenland and small arctic tundra areas and mountains of Siberia (Kraaijeveld & Nieboer 2000 and references therein).

In the field of conservation biology, degree of genetic variation and population structuring are important issues especially concerning small populations (Frankham *et al.* 2002, Gaggiotti 2003, Frankham 2003). Such populations often suffer from deleterious consequences of genetic stochasticity, e.g., inbreeding depression and loss of genetic diversity due to genetic drift and lack of gene flow (e.g., Crnokrak & Roff 1999, Hedrick & Kalinowski 2000, Brook *et al.* 2002, Frankham *et al.* 2002). Moreover, most taxa are not driven to extinction before genetic factors affect them adversely (Spielman *et al.* 2004).

## 1.4 Projecting population future: population viability analysis

Population viability analysis (PVA) is a set of analytical and modelling approaches for assessing the risk of population or species extinction (e.g., Possingham *et al.* 2001, Beissinger & McCullough 2002). PVAs use actual life-history information to project population trends, estimate extinction risk and minimum viable population size, predict timing of decline and time of population persistence under different conditions, assess chances of recovery and rank management options (e.g., Hill & Carter 1990, Boyce 1992, Reed *et al.* 1998, Akçakaya & Sjögren-Gulve 2000, Beissinger 2002, Larson *et al.* 2002).

Because the predictions of the PVA models depend on the input parameter values, the accuracy of the predictions is affected by uncertainty about parameter estimates and variances therein. Data to obtain accurate estimates of variance in vital rates may require at least 1–2 generations of study, perhaps exceeding 10–20 years for long-lived vertebrates (Beissinger & Westphal 1998). Sufficient long-term data may be especially difficult to obtain from threatened species because they are often characterized by small population sizes. The effect of inaccuracies in estimation of vital rates from field studies should be assessed by sensitivity analyses (e.g., Reed *et al.* 1998).



Sensitivity analyses are used to estimate how important a given parameter is to population growth rate (Caswell 2001, Mills & Lindberg 2002). They constitute an important part of PVAs in the field of conservation biology because they may provide information of the demographic processes that should be chosen for the primary targets of conservation and management measures (Mills & Lindberg 2002). In sensitivity analysis, a parameter value is varied within biologically reasonable range to determine how much change in absolute parameter value is required to cause a significant change in population dynamics. Because survival, reproduction and other parameters examined in sensitivity analyses are measured on different scales, weighting their relative impact on population trends can be difficult. This problem is overcome by performing an elasticity analysis, which gives the sensitivity of population growth rate to proportional changes in the parameters (e.g., Caswell 2001).

## 1.5 Aim of the study

This thesis investigates dynamics, genetic structure and viability of a Temminck's stint population inhabiting the Bothnian Bay in the northern Baltic Sea. First, I summarise the population changes during the 20th century and establish the population level and range in 1987–1995 (I). I also indicate important breeding sites and discuss the causes of the decline (I). In paper II, I present the results of a population count carried out in 1999–2002 and focus on temporal changes in rate of nest predation and causes of nest losses in 1983–2001. In the next two papers, factors affecting the rate of nest predation are studied. I compare the level of nest predation on wide and on narrow shores, using dummy nests (III) and monitoring real Temminck's stint nests (IV). Effect of microhabitat structure (vegetation-related nest concealment) on nesting (hatching) success is studied in paper IV. I also test the hypothesis that an increase in nest concealment and consequent decrease in visibility lowers the efficiency of antipredator behaviour (IV), predicting that flushing distances should be greatest when the nests are poorly concealed and the visibility from the nest is good. The effect of “sentinel” birds on flushing distance is explored in paper IV. In paper V, I describe the levels and patterns of population differentiation in mitochondrial control region and microsatellite loci in the Temminck's stint populations in Fennoscandia and northeastern Siberia. In paper VI, ten year capture-recapture data are used to describe dynamics of the Temminck's stint population inhabiting the coasts of the Bothnian Bay. I present estimates of rates of nesting success, recruitment and adult survival and the realized finite rate of population growth ( $\lambda$ ). Finally, the risk of extinction of the coastal Temminck's stint population is assessed by projections based on  $\lambda$  and its variation (VI) and the sensitivity of population viability to changes in different vital rates is examined.

Because detailed descriptions of methods and results are presented in the original papers, the following comprises only brief summaries.

## 2 Methods

### 2.1 Species and the study population

The Temminck's stint is a monotypic Palaearctic wader (Cramp 1985, Hayman *et al.* 1986). Its breeding range extends from Scandinavia to the Bering Strait in the Eurasian tundra and northern parts of taiga (Hayman *et al.* 1986). The size estimates of the population vary considerably (e.g., 1–10 million pairs in Eurasia, Hagemeyer & Blair 1997; 85000–420000 pairs in Europe, BirdLife International 2004a). Russia holds the main world breeding population (Hagemeyer & Blair 1997). The conservation status of the Temminck's stint is favourable on a European scale (BirdLife International 2004a) and the species is evaluated globally as Least Concern in the 2004 IUCN Red List Category (BirdLife International 2004b). The core breeding area in Fennoscandia is in Lapland and the Scandinavian mountains, and a smaller population inhabits the coast of the Baltic Sea in the Bothnian Bay (I, II, Breiehagen 1994, Väisänen *et al.* 1998, Svensson *et al.* 1999). Fennoscandian Temminck's stints migrate across continental Europe to directions between southeast and southwest (I, Hedenström 2004). Wintering areas are located in sub-Saharan Africa, the Mediterranean region and southern and southeastern Asia (Cramp 1985, Hedenström 2004).

The coastal Temminck's stints in the Bothnian Bay in the northern Baltic Sea as well as some populations in Lapland have declined considerably during recent decades (I, II, Väisänen *et al.* 1998, Svensson *et al.* 1999, Strid 2003). The species is classified as vulnerable in Finland (Rassi *et al.* 2001, IUCN 1994) and near-threatened in Sweden (Gärdenfors 2000). The decline of the coastal population has usually been attributed to habitat loss and deterioration caused by overgrowth and shrinkage of suitable open habitats due to the termination of hay-making and grazing on shore meadows prior to the 1950s (e.g., Hildén 1978, Väisänen *et al.* 1998, Svensson *et al.* 1999).

Breeding biology and population dynamics of the Temminck's stint have been studied by Hildén (1965, 1975, 1978, 1979, in the southern Bothnian Bay in 1963–1972) and Breiehagen (1989, in southern Norway). The Temminck's stint exhibits a multiclutch breeding system involving successive bigamy by both sexes. The female usually lays two 4-egg clutches, the first incubated by her first mate and the second by herself in a territory

of another male; females may move considerable distances between clutches (Hildén 1975, Breiehagen 1989). Males show higher site tenacity than females (Hildén 1979). In the Bothnian Bay egg-laying starts in late May or early June (Hildén 1975). Incubation lasts for 22 days and the chicks fly by the age of 15–18 days (Cramp 1985).

## 2.2 Study area

This study was conducted in the Finnish Bothnian Bay (63°–65°50'N, 21°–25°30'E), divided into northern, central and southern sub-areas (II). In addition, tissue samples for molecular analyses (V) were obtained from Sodankylä region (67°25'N, 26°35'E) and Enontekiö (68°38'N, 24°40'E) in Finnish Lapland, two locations in southern Norway in Hardangervidda (60°16'N, 7°34'E and 60°36'N, 7°30'E) and the Chukotskiy Peninsula, northeastern Siberia (64°42'–64°47'N, 172°30'–177°30'E). All studies except the population counts (I, II) and the genetic studies (V) were restricted to the southern and central sub-areas.

In the Bothnian Bay, Temminck's stints occupy dry sandy and gravel meadows with short and sparse vegetation near water, as well as industrial workings and other man-made habitats. Paper IV describes typical breeding sites in further detail. In the study area land uplift (c. 8mm per year, Mäkinen & Saaranen 1998) creates new potential breeding sites. Thus, natural habitats are constantly undergoing change due to primary succession of vegetation (Ericsson & Wallentinus 1979, Vartiainen 1980). Eventually, dense vegetation formed chiefly by *Phragmites australis*, *Alnus incana* and *Salix phylicifolia*, make habitats unsuitable for breeding. In man-made habitats, succession of vegetation is frequently disturbed by development activities and mowing.

## 2.3 Population counts

The data concerning population changes from the beginning of the 20th century to the late 1980s came from faunistical reports in local and national ornithological periodicals and from numerous published and unpublished bird censuses (I). Similar sources, augmented by surveys carried out between 1987 and 1995 (I) and between 1999 and 2002 (II), were utilized to study recent population changes. We also studied the population distribution in man-made vs. natural habitats and mainland vs. islands.

## 2.4 Nesting success and fecundity

Nests were searched and monitored between 1983 and 2003. Nesting (hatching) success was estimated by using a successful/not successful scale (II, IV). We also calculated the daily survival probability of a nest and the survival probability over incubation period by

the Mayfield (1975) method (II, IV). Nests were considered successful if at least one chick hatched. Failed nests were categorized as flooded, trampled, deserted or depredated. For detailed analysis of nest predation, nest survival was calculated considering only depredated nests as losses (II). To analyse temporal changes in nesting success and causes of nesting failures, the time span was divided into early and late periods (II, 1983–1991, 1992–2001).

In the capture-recapture study (VI) fecundity was expressed by number of chicks hatched per clutch. This was multiplied by the mean breeding probability, separately for males and females, for three age classes (1, 2 and more than 2 years old; Hildén 1978). Each individual was assumed to incubate one nest per season. In matrix models fecundity was expressed in terms of local recruitment, i.e. the fecundity measure above multiplied by juvenile survival (VI).

## **2.5 Habitat effects on nest predation rate**

We compared nesting success in natural and man-made habitats (II, in 1983–2001) and explored the effect of shore width on the predation rate of artificial nests (III; in 1992) and real Temminck's stint nests (IV, in 1993–1997). In addition, the overhead-view coverage of the nests and the horizontal visibility of the nest, habitat characteristic negatively correlated with vegetation height and density, were estimated to assess the effect of microhabitat structure on the nest predation rate in 1993–1995 (IV).

## **2.6 Antipredator behaviour**

Factors affecting antipredator behaviour of Temminck's stint were studied during 1993–1995 (IV). To measure the flushing distances of the parents we approached the nests directly. When we saw the parent leave the nest, we measured the flushing distance to the nearest meter. Because, in many cases, we did not see the bird leave the nest, we also measured flushing distance on a presence/absence scale, assuming that absence of the parent signifies long flushing distances. Also alarm calls and distraction displays presented by the parent bird were recorded. Antipredator behaviour was analysed in relation to breeding phase (first/second half of the incubation period), time of the day, presence of alarm-giving birds, overhead-view coverage and horizontal visibility of the nest.

## **2.7 Identity of nest predators**

Identity of nest predators was studied by observing egg remains and other tracks left by predators at real nests (II, IV) and artificial nests with a protecting wire net standing

horizontally 10 cm above ground (II), without a protective net (II, III) and by videotaping artificial nests (II).

## 2.8 Molecular methods

Mitochondrial DNA (mtDNA) and microsatellite variation was explored in paper V. A 390 base pairs long part of the central domain of the mitochondrial control region was sequenced by ABI 377 automatic sequencer ( $n = 127$ ). Nucleotide diversity ( $\pi$ ; Nei 1987 eq. 10.5) and haplotype diversity ( $\hat{h}$ ; Nei 1987, eq. 8.4 and 8.12),  $\theta = 2N_e\mu$  (Tajima 1996, eq. 10) were calculated with DnaSP v. 3.51 (Rozas & Rozas 1999) to obtain estimates of genetic variation. Tajima's D, mismatch distributions and raggedness index to look for indicators of past changes in population size (Harpending 1994) were also calculated with DnaSP. Analysis of molecular variance using Tamura-Nei distances and haplotype frequencies were calculated with Arlequin v. 2.0 (Excoffier *et al.* 1992).

Nuclear DNA was analysed by six microsatellite loci originally designed for the dunlin (*Calp2*, *Calp5* and *Calp6*, Wennerberg & Bensch 2001) or the ruff (*Philomachus pugnax*; *Ruff10*, *Ruff5* and *Ruff8* (Thuman *et al.* 2002). The microsatellite allele frequencies were tested for Hardy-Weinberg equilibrium and linkage disequilibrium for each population and locus separately with program Genepop v. 3.4 (Raymond & Rousset 1995). The same program was used also to calculate the observed and expected heterozygosities and the number of migrants between the populations using the private allele method of Slatkin (1985).

We sexed the samples using the conserved P2/P8 primers from avian CHD-W and CHD-Z gene and PCR conditions described in Griffiths *et al.* (1998). In addition to *Ruff5* and *Ruff8* (Thuman *et al.* 2002) we found that *Ruff10* is also likely to be located on the Z chromosome because all heterozygote individuals were males. The unequal migration rates between the populations and  $\theta$ -values for males from each population (Program Migrate v.1.7.3, with infinite allele model and default parameters, Beerli 1997–2003), and  $F_{IS}$  per population and locus, ignoring *Ruff5*, *Ruff8* and *Ruff10* for females (FSTAT v. 2.9.3.2, Goudet 1995), were estimated. Number of alleles and allelic richness were calculated with the same program coding females as homozygous for *Ruff5*, *Ruff8* and *Ruff10*. Pairwise and overall  $F_{ST}$  values (AMOVA) were estimated with Arlequin v 2.0 (Excoffier *et al.* 1992), coding *Ruff5*, *Ruff8* and *Ruff10* as the other allele missing in females. Significance was estimated with 100 permutations for pairwise  $F_{ST}$  values and with 1000 permutations for AMOVA.

## 2.9 Dynamics and viability of the population

### 2.9.1 Capture-recapture data

Population dynamics and viability were investigated during the years 1994–2003 (VI). Breeding adults were captured at nest with a mist net or a trap and newly hatched chicks were caught by hand. The birds were marked with a steel or aluminium ring provided by the Finnish Museum of Natural History. For the capture-recapture study, each ringed adult was also marked with a unique combination of 2–3 plastic colour rings for individual recognition from a distance. Chicks were marked with an aluminium ring only, and they received colour rings if they were captured as breeding adults in subsequent years. Resighting of a colour-ringed bird during the breeding season was considered a recapture. The data cover 177 adult and 385 chick capture histories.

We produced maximum likelihood estimates for adult and juvenile survival ( $\Phi$ ) and recapture probability ( $p$ ) using capture-recapture models for open populations based on the Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965). Analyses were conducted using program MARK (White & Burnham 1999). The realized finite rate of population increase ( $\lambda$ ) was estimated by the method of Pradel (1996). In addition, utilizing reversed capture histories, we estimated seniority parameter ( $\gamma$ ) that expresses the probability that an individual present in the population at some breeding season was there already in the previous season (Nichols *et al.* 2000). Similarly, we also estimated recruitment parameter ( $\rho$ ) expressing the probability of an individual entering the population in a specific season. Seniority parameter is analogous to the elasticity of adult survival, expressing the contribution of survival to  $\lambda$ . Similarly,  $1-\gamma$  represents the contribution of recruitment (including local recruitment and immigration) to  $\lambda$  (Nichols *et al.* 2000).

The modelling was started by building a global model after which a set of candidate models structured to include hypothetical *a priori* parameter patterns were fitted to the data. The parametric bootstrap approach in MARK was used to assess the goodness of fit of the global models to the data. An information theory approach based on AIC (Akaike's information criterion, Akaike 1973) was used to compare the relative fit of the models.

Parameter and variance estimates were acquired using the best fitting model. To cope with model selection uncertainty in cases with multiple models, model averaging was used and contribution of different models was controlled by Akaike-weights (Anderson & Burnham 1999, White & Burnham 1999).

In addition to apparent survival estimates, we also calculated return rates (proportion of resighted marked birds) to enable comparison with data from the southern Bothnian Bay, collected during 1963–1972 (Hildén 1978).

### 2.9.2 Viability analyses

The viability of the Temminck's stint population was examined by projections based on Pradel- $\lambda$  and matrix projections. Both approaches were used to predict the probability of

extinction within the next 20, 50 and 100 years. Manual sensitivities of extinction risk to parameter changes were examined by matrix projections to get insight into the importance of different vital rates and potential management targets.

Population growth was modeled as a ceiling type (see, e.g., Ginzburg *et al.* 1994), with carrying capacity set at 400 individuals. A quasi-extinction threshold was set at 20 individuals (see, e.g., Beissinger & Westphal 1998). Initial population size was set at 250 individuals (II).

Projections based on Pradel- $\lambda$  and matrix projections were made with program RAMAS metapop (Akçakaya *et al.* 1998). The stochastic model was used to assess the sensitivity of the population growth to changes in different parameters while other parameters were held constant. For comparison, stochastic models based on mean minimum and maximum estimates for both adult survival and reproduction presented by Hildén (1978) were built. Variance estimates used are the same that were used for projections based on present data.

## 3 Results and discussion

### 3.1 Past population trends

The Temminck's stint population has decreased in the Bothnian Bay virtually in all areas from which population counts are available during the 20<sup>th</sup> century (I). Both the count data (I, II) and the demographic data (VI) indicated that the decline is continuing. In 1987–1995 170 pairs were found (I), in 1999–2002 105 pairs (II). The capture-recapture data showed that in most years  $\lambda$  was below 1 and the mean for the seven estimated years between 1994–2003 was 0.892 (VI). Including the 20–30 pairs breeding on the Swedish coast (Andreas Livbom, pers. comm., Strid 2003) a minimum estimate for the whole Baltic population is 125 pairs (II).

The decline took place throughout the mainland coast between the two counts (II). The decline was the most severe (57%) in the southernmost part of the range and the smallest decline, by about one quarter, took place in the central part of the range, which is now occupied by about half the population (II). Despite regional differences, the distribution pattern in the three sub-areas in 1999–2002 did not differ significantly from the 1987–1995 distribution. However, the observed trend in the distribution pattern may reflect an ongoing contraction in breeding range and suggest that the centre of abundance has moved northwards (II). 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).

In contrast to the overall picture, the frequency of insular breeders in the southern and central sub-areas increased between our surveys (I, II). Insular breeding sites persisted well especially in the central sub-area (II). This probably partly explains why the magnitude of the decline has been lower in the central than in the southern sub-area, where the frequency of insular breeding sites is much lower.



### 3.2 Nesting success and causes of nesting failures

We monitored 464 nests in total (II). Of the 424 nests with known fate, 47.2% produced at least one chick. The daily survival probability of the nests ( $n = 461$ ) when all causes of nest losses were considered was 0.948 and 0.958 when only depredated nests were considered as losses (II). 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 the nest losses. Other causes were desertion, trampling and flooding (10.3%, 6.7% and 3.1% of the losses, respectively).

The mean number of chicks produced per nest in 1994–2003 was 1.1 and varied from 0.7 to 1.9 chicks per nest between the years (VI,  $n = 255$ ). The number of chicks produced per nest seems to have declined from the 1.5–1.7 in 1963–1972 (Hildén 1978).

The daily survival probability of the nests was higher in the early than in the late period (0.965) in 1983–1991, 0.941 in 1992–2001), and hatching success dropped from 46% to 26% (II). When only depredated nests were considered as losses, the same trend remained (0.983 in 1983–1991, 0.948 in 1992–2001); nest survival dropped from 69% to 31%. Nesting failures increased from 39.1% in 1983–1991 to 57.9% in 1992–2001, the proportion of depredated nests increased from 19.1% to 50.8% and the proportion of depredated nests of the failed nests rose from 48.9% to 87.7%. Thus, the decrease in breeding performance was caused by a marked increase in nest predation.

We attribute most predation to the most abundant avian nest predators, the common gull *Larus canus* and the ruddy turnstone (I, II).

### 3.3 Habitat, antipredator behaviour and nesting success

Neither overall survival probability nor survival probability for predation significantly differed between natural and man-made habitats (II). A rise in the level of nest predation was evident in both habitat types (II). For total losses, no habitat-related differences (man-made vs. natural) in daily survival probability were observed neither in the early (1983–1991) nor in the late (1992–2001) period. However, predation was more intense in man-made than in natural habitats during the early period, but not in the late period, owing to a steeper decline in nest survival in natural habitats (II).

Due to alleged high level of human disturbance in man-made habitats and large numbers of predators associated with human habitation there (corvids, gulls, rats, cats, hedgehogs), more nest losses could have been expected to occur in man-made than in natural habitats. In contrast to this, our results point to that breeding in man-made habitats does not pose a risk in terms of decreased nest survival.

When a bird left the nest it usually flew or walked inconspicuously away and the parent bird only rarely either gave alarm calls or performed some antipredatory displays with or without alarm calls (IV). Flushing distances were longer in presence of alarm-giving birds than without them, indicating that Temminck's stint exploits signals from other birds as early warning of an approaching predator ("information parasitism"; Nuechterlein 1981, Burger 1984, Pöysä 1988). During the second half of the incubation

period flushing distance was about twice as long as it was in the first half. This was probably due to an increase in overall aggressiveness of the “sentinel species” in the course of the breeding season. Flushing distance was not influenced by the number of previous visits, existence of cover above the nest nor time of day.

In most nests the mean flushing distance was greater than visibility, maybe indicating that Temminck’s stints utilize other than visual information about approaching predators (IV). One alternative source of information is alarm calls of other birds. However, when there were alarm-giving birds present, positive correlation between visibility and flushing distance emerged, but not so in absence of alarm-giving birds. This implies that the early warning provided by the “sentinel species” is based on visual cues of, e.g., mobbing birds in addition to auditory signals. The alarm-giving birds may also detect the predator earlier in a habitat with good visibility and start giving the alarm earlier.

Predation rates on artificial nests did not differ between wide and narrow shores (III), but, in contrast, more real nests were lost to predation on narrow than on wide shores (IV). This could imply that the rate of nest predation is connected to factors associated with parent birds, such as flushing distance. Although the early-departure strategy appeared to be less effective in habitats with lower visibility, nest predation rate was unrelated to differences in microhabitat characteristics associated with concealment (visibility, vegetation cover) (IV). However, this discrepancy is not unexpected, if the early-departure strategy has originally evolved against other type of predators (e.g., mammalian predators) than the ones prevailing in our study area, the ruddy turnstone and the common gull. In fact, these avian predators do not usually trigger alarm-giving or mobbing behaviour of arctic terns (*Sterna paradisaea*) (Brearey & Hildén 1985, own observations), the most common alarm-raising species in our study area.

### 3.4 Population genetic structure

An overall low mitochondrial DNA (mtDNA) variability was found (V; nucleotide diversity 0.0018 and the overall  $\phi_{ST}$  -0.02616). There was evidence of two different maternal lineages (V) differing by four fixed substitutions (p-distance between the lineages = 0.0131). Lineage A occurred in 95% of the individuals and was the only one present in northeastern Siberia (n = 124). Lineage A and B coexisted and the three most common haplotypes were present in roughly similar frequencies in all Fennoscandian populations. The most common haplotype occurred in 81% of all individuals and in all birds in the Siberian sample. The occurrence of the two maternal mtDNA lineages in all Fennoscandian populations points to a mixing of two previously isolated populations during the post-glacial colonisation (e.g., Hewitt 2000) of the present range or earlier. However, we do not know if we failed to find haplotype B from Siberia just due to the small sample size (n = 6). Sampling more populations from northern Russia would increase resolution in this respect.

The virtual lack of genetic structuring in mtDNA suggests panmixis of the Eurasian Temminck’s Stint population. However, a recent recolonization of the current range from small populations, bottlenecked in refugia caused by postglacial climatic oscillations and consequent loss of suitable habitats (Dynesius & Jansson 2000, Kraaijeveld & Nieboer

2000 and references therein), could also account for the observed low mtDNA variability, as has been suggested for several northern species (Baker *et al.* 1994, Zink 1996, Fedorov 1999, Ottvall *et al.* 2005).

The overall microsatellite genetic structuring in Fennoscandia was low (V;  $F_{ST}$  0.03491). However, in contrast to mtDNA data, the pairwise comparison revealed a low but significant degree of differentiation between the Bothnian Bay and the two other Fennoscandian populations. In addition, the Bothnian Bay population was the only one with a positive overall  $F_{IS}$  value, which may indicate a higher degree of inbreeding than in the other populations, although the degree of inbreeding was still low. The linkage disequilibrium found only in the Bothnian Bay population possibly indicates effects of small population size.

Sex-specific dispersal patterns could account for the difference between population differentiation indicated by the microsatellite and the mtDNA data (V). If the dispersal pattern of the species is female-biased, a lower degree of mtDNA than microsatellite genetic structuring can be expected. As mtDNA is maternally inherited, female-biased dispersal homogenizes both mtDNA and nuclear variation, while male-biased dispersal tends to homogenize only nuclear variation (Piertney *et al.* 1998, 2000). Male Temminck's stints' site fidelity is higher than that of females' and males stay at their territories throughout the breeding season, but females change mates and many females leave the nesting area between successive clutches (Hildén 1975, Breiehagen 1989). Hildén (1975) suspected that movements of up to some hundred kilometres between successive clutches might be possible.

The methods to estimate migration rates, based on geographical patterns of microsatellite variation, point to gene flow among all the studied populations (V), but these methods are not able to distinguish between current patterns of gene flow and historical population events. In addition, direct observations, i.e. resightings of ringed birds indicating breeding or natal dispersal between the Bothnian Bay and any other populations are lacking. However, the results of the population viability analysis (VI) indicate that the Bothnian Bay population receives c. 40 individuals yearly. One potential source of the immigrants is northern Finnish Lapland; resightings of stints colour-ringed there show that the Bothnian Bay is on their migration route both in spring and autumn.

## **3.5 Population dynamics and viability**

### ***3.5.1 Survival and migration***

Apparent adult survival declined in the Bothnian Bay during the study (VI). This may reflect a true temporal trend in survival, but because the apparent survival estimate is a product of emigration and true survival probability, it may also result from a shift in migration balance. The survival probability estimates ranged from 0.74 the first year to 0.63 the last year. The overall mean apparent adult survival probability was 0.70. The mean annual return rate was 0.63. Apparent juvenile survival (local recruitment) tended

to be higher during the early (0.072) than the later (0.052) study years. The mean apparent juvenile survival was 0.061.

Apparent adult survival was within the range measured in other wader populations and near the median value observed in arctic calidrid sandpipers (Warnock *et al.* 1997, Sandercock & Gratto-Trevor 1997, Sandercock *et al.* 2000, Summers *et al.* 2001, Brochard *et al.* 2002, Fernandez *et al.* 2003, Dinsmore *et al.* 2003). In contrast, apparent juvenile survival was quite low compared to other calidrid species and waders in general (e.g., Dinsmore *et al.* 2003, Sandercock 2003 and references therein).

A marked drop in local recruitment and adult survival seems to have happened in c. 30 years. In a study in the southern Bothnian Bay (Hildén 1978) the return rate for juvenile Temminck's Stints was 15% and adult survival was estimated to be 76%–81% (6% and 70% in this study, respectively). In fact, the decline in survival may be even more pronounced because Hildén's (1978) estimates were based on return rates and thus likely underestimate apparent survival. Moreover, our study area is larger than in Hildén's (1978) study; permanent emigration may strongly bias survival estimates if the study area is small (Koenig *et al.* 1996). This may especially concern juvenile survival because natal philopatry is usually weaker than adult breeding site fidelity (Greenwood & Harvey 1982, Paradis *et al.* 1998). We observed only weak breeding and natal dispersal between our study sites despite the relatively large study area. In several wader species most juveniles seem to settle within 10 km from their natal site (Jackson 1994, Thompson *et al.* 1994), a distance well covered by our study area. Therefore, a reasonable conclusion is that Temminck's stint dispersal is minimal at a regional scale within the Bothnian Bay and apparent survival estimates represent true survival fairly well. However, some migration from outside the Bothnian Bay is a necessity, since the local recruitment cannot account for all the observed recruitment (VI).

In our study area, the intensity of nest predation has increased in the late 1900s (II). Poor breeding success may trigger dispersal in calidrid sandpipers and other birds (Hildén 1979, Gratto *et al.* 1985, Hitchcock & Gratto-Trevor 1997). Therefore, although we had no evidence for marked breeding dispersal, emigration forms a hypothetical link between parallel decreases in nesting success and in apparent survival.

### ***3.5.2 Seniority and recruitment***

The estimates of the seniority parameter ( $\gamma$ ) model varied between 0.549 and 0.869 (VI). The mean  $\gamma$  for seven years was 0.746. The estimates of recruitment ( $\rho$ ) based on the time dependent model varied between 0.099 and 0.490. The mean for seven years was 0.213. As implied by the high value of  $\gamma$ , adult survival seems to have a high contribution to the growth rate. The remaining 25% contribution of the recruitment consists mainly of immigration. High elasticity of adult survival implies that the Temminck's stint resides at the slow end of the "slow-fast continuum" of animal life histories (Sæther *et al.* 1996, Heppel *et al.* 2000, Sæther & Bakke 2000). Adult survival has appeared to be the most important component of population growth also in other wader species (e.g., Hitchcock & Gratto-Trevor 1997, Wemmer *et al.* 2001, Larson *et al.* 2002, Ottvall & Hårdling 2005).

The mean recruitment parameter (0.213) times the population size was used to give an indication of the magnitude of immigration. Applied to the latest population census (II, 125 pairs/territories or 250 individuals) the product yields 53 individuals per year. Taking the local recruitment rate (0.061) out leaves an immigration rate of 0.151, equalling to 38 immigrants. It seems clear that juvenile recruitment is insufficient to maintain the Temminck's stint population in the Bothnian Bay. It can be treated as a sink population (Pulliam 1988) and a target of rescue migration that at least recently has decelerated the population decline.

### 3.6 Sensitivity analyses

The impacts of the vital rates were examined with manual perturbations based on a model including immigration in the fecundity term. The hatching of all the four eggs in all nests was required for the population to stop declining. Population growth was quite sensitive to changes in juvenile survival; however, local recruitment rate around 0.2 was required to stop the decline. Current immigration rate is not sufficient to stabilize the population; increasing immigration to 0.3 was needed to stabilize the decline. The smallest proportional change that was needed to stop the decline was in the adult survival. However, survival of over 0.8 would be needed. To sum up, only major changes near the limits of a biologically realistic range in any single trait would turn the population to increase.

A large part of juvenile mortality arises likely between hatching and fledging. Still, part of it takes place on migration routes and wintering areas. First year birds migrate about a month later than adults and at the start of migration they have less fat reserves than adults, suggesting potential age-related differences in stopover strategies (Hedenström 2004). However, juvenile and adult survival may be coupled to some degree because they both may be affected by the same processes during the non-breeding phase of the annual cycle. Therefore, any improvement in adult survival may also reflect to juvenile survival, i.e. local recruitment.

### 3.7 Viability analyses

The stochastic model based on Pradel- $\lambda$  predicted a rapid decline of the population (VI). The probability of decline to a quasi-extinction threshold of 20 individuals within the next 20 years was 50%. Extinction within the next 50 years appeared almost certain. Matrix projections gave fairly similar results. Quasi-extinction probability within 20 years was 39% and within 50 years 97%. After 100 years extinction is almost certain. Without immigration the decline was predicted to be fast with an extinction probability of  $\sim 1$  within the next 20 years. Stochasticity had no marked effect to the projections. Effect of environmental and demographic variation was masked by the steep decline due to deterministic growth. The same probably applies to genetic stochasticity, although it was not considered in projections.

Matrix models based on estimates of survival and fecundity presented by Hildén (1978) resulted to growth rates implying a rather stable population (VI). Additionally, the stochastic models based on the deterministic models predicted that the population would be relatively stable. Currently, adult survival, reproductive success and local recruitment are in lower level than in Hildén's (1978) study population (II, VI). Considering the fact that Hildén's (1978) survival estimates were return rates and therefore probably underestimated true survival, one can speculate that the drop in critical vital rates and the consequent negative population growth steepened in the last decades of the 20<sup>th</sup> century. In fact, Hildén's (1978) study population in the southern part of the Bothnian Bay has now gone extinct.

## 4 Conclusions

The Temminck's stint population in the Bothnian Bay is undergoing a continuous decline, paralleled by declines in adult survival, recruitment and nesting success during recent decades. In addition, the volume of immigration is not sufficient to compensate for the increased adult disappearance from the population. However, in part owing to immigration, the population is currently not suffering from a loss of genetic variation. Nevertheless, it is evident that it will face a very high risk of extinction in near future for other than genetic reasons.

The question of ecological and genetic distinctiveness of populations is important in determining the units of conservation (e.g., Crandall *et al.* 2000). For example, the Bothnian Bay population is unique with respect to breeding environment, shore meadows of a brackish, temperate zone sea. Considering the high level of immigration, it seems unlikely that the Bothnian Bay population could currently take an evolutionary trajectory different from the large source population of the immigrants (see e.g., Westemeier *et al.* 1998, Madsen *et al.* 1999, Keller *et al.* 2001, Ebert *et al.* 2002, Vilá *et al.* 2003), even though it shows significant, albeit low, differentiation from the other Fennoscandian populations in variation in microsatellite loci. Taking only the microsatellite allele frequency divergence into account, the Bothnian Bay population could be considered as a management unit *sensu* Moritz (1994) separate from the rest of Fennoscandia. However, applying the categories based on ecological and genetic distinctiveness suggested by Crandall *et al.* (2000) all Fennoscandian populations should be treated as one population.

Adult survival is now at a level considerably lower than c. 30 years ago when the population was stable or showing only a slight decline. The large contribution of adult survival to growth rate implies that the decrease in adult survival is the main cause of the population decline. Factors affecting adult survival in northern waders most likely operate largely during the non-breeding season during migration and wintering. However, the wintering sites of the study population are virtually unknown. Therefore, evaluating causes of declines is difficult and managing the wintering population next to impossible. Instead, management efforts should concentrate on the vital rates with smaller elasticity but higher potential for improvement. In our study population, these could include local recruitment, immigration (a vital rate with moderate elasticity) and hatching success.

Because of insufficient production of young and recruits for population persistence, immigration is vital to prevent the extinction of the study population. Actually, an immigration rate higher than that of today is essential for persistence of the current population. Therefore, management actions taken in the Bothnian Bay should first of all guarantee availability of suitable wide, low-sward coastal breeding habitats for potential immigrants and recruits.

Whatever the formal categorization of the Fennoscandian Temminck's stint populations into units of conservation is, the different demographic properties of the populations and factors affecting them must be taken into account when deciding conservation and management actions. For instance, actions aimed to improve hatching success may be required in the Bothnian Bay because of the high level of nest predation there but not in Fennoscandian inland populations, where the level of nest predation may be lower (Breiehagen 1989, own unpublished data). These actions, e.g., thinning alien predators and using predator exclosures against native, protected predators, could have at least local importance (see e.g., Rimmer & Reblinger 1990, Parr 1993, Nordström *et al.* 2003). However, these actions are difficult to apply coastwide.

The Bothnian Bay population forms only a fragment of the global population and thus its decrease could be considered to be only of local importance. However, if the decline is driven mainly by factors operating in sites along migration routes and in wintering areas, they should affect also birds from other populations sharing these sites during the non-breeding season. Therefore, the decline in the Bothnian Bay may be an indicator of a larger-scale population change, not independent from the parallel population development in Finnish Lapland. The Fennoscandian Temminck's stints migrate along continental-wide flyways to directions between SE and SW pointing to wintering sites scattered in the Mediterranean, subtropical and tropical Africa and coasts of the Indian Ocean (I, Cramp 1985, Hedenström 2004). Thus, candidate factors suppressing survival should have a large geographical range of occurrence. For example, widely used agricultural pesticides could be that kind of factor having serious effect on a large part of the world population.



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## Original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Rönkä A (1996) Distribution, status and population trends in the Temminck's stint *Calidris temminckii* in the Finnish Bothnian Bay. *Ornis Fennica* 73: 1–11.
- II Rönkä A, Koivula K, Ojanen M, Pakanen VM, Pohjoismäki M, Rannikko K & Rauhala P (2006) Increased nest predation in a declining and threatened Temminck's stint *Calidris temminckii* population. *Ibis* 148: 55–66.
- III Rönkä A & Koivula K (1997) Effect of shore width on the predation rate of artificial wader nests. *Ibis* 139: 405–407.
- IV 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.
- V Rönkä A, Kvist L, Karvonen J, Koivula K, Pakanen VM, Schamel D & Tracy DM (2006) Geographical variation and population structure in the Temminck's stint *Calidris temminckii* as shown by mitochondrial DNA and microsatellites, with an emphasis on Fennoscandian populations. (Manuscript)
- VI Koivula K, Pakanen VM, Rönkä A & Belda E (2006) Dynamics and viability of a declining Temminck's stint (*Calidris temminckii*) population. (Manuscript)

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I was the primary author of the papers I, II and V. I wrote papers III and IV and performed most analyses in papers I, II, III and IV jointly with Kari Koivula. In paper V, analyses were performed by Laura Kvist. Co-authors discussed ideas and commented on the text. My co-authorship of paper VI reflects this as well.

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