

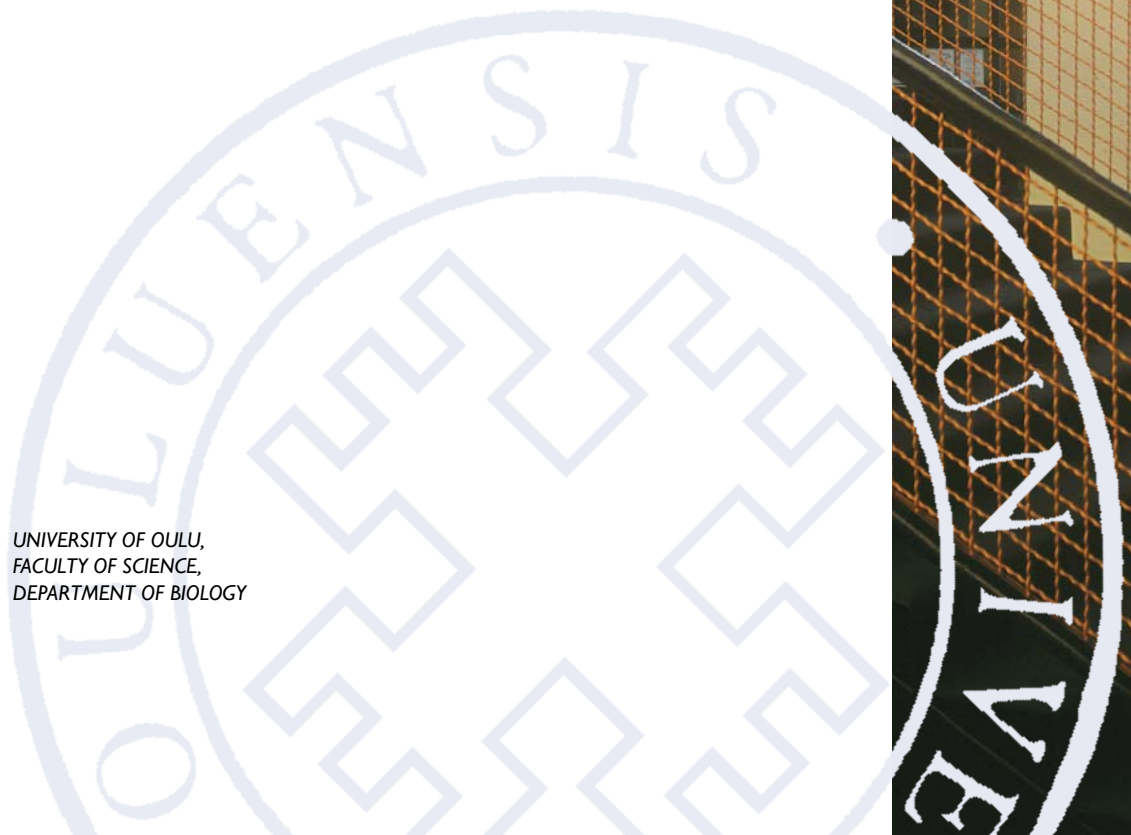
Veli-Matti Pakanen

LINKING DEMOGRAPHY
WITH DISPERSAL AND
HABITAT SELECTION FOR
SPECIES CONSERVATION

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FACULTY OF SCIENCE,
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VELI-MATTI PAKANEN

**LINKING DEMOGRAPHY WITH
DISPERSAL AND HABITAT
SELECTION FOR SPECIES
CONSERVATION**

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Abstract

In conservation biology, informed and sound management decisions depend on target specific information about the life history and demography of the endangered populations. I used long-term, individual-based life history data (breeding and capture-recapture data) to examine life-history and demography in order to assess population viability and management. My study systems consist of metapopulations of two endangered, long-distance migratory wader species breeding on Baltic coastal meadows, the Temminck's stint (*Calidris temminckii*) and the Southern Dunlin (*Calidris alpina schinzii*), whose breeding habitats are mainly managed by livestock grazing.

Demographic models indicated that both study populations were sinks, which persist through immigration due to low local recruitment insufficient to compensate for adult mortality or emigration. Philopatric Temminck's stints had higher nest and apparent adult survival compared to immigrants. Consideration of dispersal status in population models resulted in the most realistic estimates of population growth and revealed a low demographic impact of immigrants. Immigrants had low return rates after reproductive failure, suggesting that the difference in apparent survival was partly caused by different breeding dispersal strategies. Thus, management actions improving reproduction, and thus site fidelity, should also influence viability.

An artificial nest experiment indicated high trampling rates under recommended stocking rates on managed meadows. This was attributed to similar space use of nesting Dunlin and cattle. Cattle presence did not affect nest predation. Young Dunlin preferred intensively grazed low sward habitat over high sward habitat. Reproductive success was also higher in low sward habitat. However, nests in the preferred habitat had the highest risk of being trampled if not artificially protected. Thus, low sward habitat was found to work as an ecological trap if grazing was started too early in the breeding season. Due to the sink nature of the Dunlin population even small reductions in reproductive success caused by trampling were detrimental to long term viability. The results encourage continuation of the use of cattle grazing as a management tool, but also highlight the need for more detailed consideration of local grazing practices, especially when sketching management plans for endangered species.

Keywords: apparent survival, *Calidris alpina schinzii*, *Calidris temminckii*, demographic modeling, dispersal, ecological trap, endangered species, grazing management, population growth

Pakanen, Veli-Matti, Habitaatin valinnan ja levittäytymisen demografiset seuraukset ja niiden merkitys lajien suojelussa.

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Tiivistelmä

Uhanalaisten lajien suojelussa tehokkaiden suojelutoimien suunnittelu edellyttää tietoa hoito-kohteen elinkierron eri vaiheista ja niiden demografisesta merkityksestä. Käytän tutkimuksessani pitkäaikaisaineistoja (pesintä ja merkintä-takaisinpyynti) kuvatakseni tutkimuslajien demografiaa ja arvioidessani populaatioiden elinkykyä sekä hoitotoimia. Tutkimuskohteinani ovat lapinsirrin ja etelänsuosirrin, kahden uhanalaisen kahlaajan, Perämeren rantaniityillä pesivät metapopulaatiot. Näiden lajien elinympäristöjä hoidetaan pääosin laiduntamalla.

Demografinen mallinnus osoitti molempien populaatioiden olevan nielupopulaatioita, joiden säilyminen on tulomuuton varassa sillä poikastuotto ei kompensoi aikuisten kuolleisuutta ja poismuuttoa. Tutkimusalueella syntyneiden ja sinne rekrytoituneiden lapinsirrien pesä- ja aikuissäilyvydet olivat paremmat kuin tulomuuttajilla. Tämän huomioiminen populaatiomalleissa tuotti realistisimman kasvukertoimen arvion ja osoitti paikallisten rekryyttien olevan tulomuuttajia merkittävämpiä populaation kasvun kannalta. Pesinnässään onnistuneet tulomuuttajat palasivat seuraavina pesimäkausina epäonnistuneita todennäköisemmin. Paikallisilla rekryyteillä vastaavaa eroa ei havaittu. Ilmiö heijastellee tulomuuttajien muuttoalttiutta myöhemminkin ja voi kertoa erilaisista pesimädispersaalistrategioista. Lisääntymismenestyksen parantaminen voisi parantaa elinkykyä myös pienentämällä poismuuttoa.

Tekopesäkokeen perusteella pesien tallausriski oli laidunnetuissa ympäristöissä korkea vaikka laidunnuspaine noudatteli hoitosuosituksia. Tämä johtunee ainakin osin laskennallista korkeammasta todellisesta laidunpaineesta, mikä puolestaan johtui lintujen ja karjan yhtäläisestä tilankäytöstä. Rekrytoituvat suosirrit suosivat voimakkaasti laidunnettuja matalakasvuisia niittyjä, joissa poikastuotto oli parempi kuin, laiduntamattomilla niityillä. Toisaalta, tallausriski on voimakkaasti laidunnetuilla niityillä suuri ja jo pienetkin pesätappiot uhkaavat suosirripopulaation elinkykyä. Täten laitumet voivat toimia ns. ekologisin loukkuina, jos laidunnus aloitetaan liian aikaisin suhteessa pesintään. Laidunnus on kuitenkin suositeltava hoitomuoto, sillä se näyttää tuottavan parhaita pesimäympäristöjä etelänsuosirrille. Tulosten mukaan laidunnuksen ajoitusta, laajuutta ja laidunnuspainetta on muokattava kohdekohtaisesti, jotta saavutetaan paras tulos uhanalaisten lajien suojelun kannalta.

Asiasanat: aikuissäilyvyys, *Calidris alpina schinzii*, *Calidris temminckii*, demografinen mallinnus, ekologinen loukku, laidunnus, levittäytyminen, populaation kasvu, uhanalaiset lajit

To my family

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In Oulu, October 20th 2011,

Veli-Matti Pakanen

List of original articles

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

- I Koivula K, Pakanen V-M, Rönkä A & Belda E-J (2008) Steep past and future population decline in an arctic wader: dynamics and viability of Baltic Temminck's stints (*Calidris temminckii*). *Journal of Avian Biology* 39: 329–340.
- II Pakanen V-M, Rönkä A, Belda E-J, Luukkonen A, Kvist L & Koivula K (2010) Impact of dispersal status on estimates of local population growth rates in a Temminck's stint *Calidris temminckii* population. *Oikos* 119: 1493–1503.
- III Pakanen V-M, Hildén O, Rönkä A, Belda E-J, Luukkonen A, Kvist L & Koivula K (2011) Breeding dispersal strategies following reproductive failure explain low apparent survival of immigrant Temminck's stints. *Oikos* 120: 615–622.
- IV Pakanen V-M, Luukkonen A & Koivula K (2011) Nest predation and trampling as management risks in grazed coastal meadows. *Biodiversity and Conservation* 20: 2057–2073.
- V Pakanen V-M, Aikio S, Luukkonen A & Koivula K (2011) Modelling the impact of nest trampling on the viability of a meadow bird population. Manuscript.
- VI Pakanen V-M, Aikio S, Luukkonen A, Thomson RL & Koivula K (2011) Can grazing management create ecological traps for meadow breeding birds? Manuscript.

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1 Introduction

1.1 General background

The increased endangerment and extinctions following vast human development (Pimm *et al.* 2006) has created the need for conservation biology to seek ways of preserving biodiversity, one branch being species management (Akçakaya *et al.* 2004). One of the key issues in conservation biology was crystallised by Soulé (1986): “we cannot manage what we don’t understand”. However, practical conservation still often relies on the experience or common sense of the managers, which makes the work prone to error (*e.g.* Green 2002, Sutherland *et al.* 2004).

A scientific quest for understanding factors influencing the causes of endangerment and extinction has been approached by two traditions. “The declining population paradigm” concentrates on deterministic factors behind population declines by testing empirical data. “The small population paradigm” concentrates on stochastic factors that may drive small populations to extinction (Caughley 1994). However, for conservation planning, tools provided by both traditions are needed (Asquith 2001) and the dichotomy between the methods fades when population viability analyses (PVA) are applied (Boyce 2002). In their ideal form, PVAs incorporate both deterministic factors such as changes in breeding habitat and stochastic factors contributing to population persistence (Boyce 2002). Regardless of the approach used, population specific data on all demographic parameters (reproduction, local recruitment, survival, immigration, emigration), the ultimate drivers of population change, are needed for making informed and sound management decisions.

Despite the documented and hypothesized effects on population persistence, behavioural processes have been rarely considered in species conservation (Sutherland 1998, Reed 1999, Sutherland & Gosling 2000, Møller & Danchin 2008, but see Sutherland & Norris 2002, Ahlring *et al.* 2010). However, behavioural phenomena such as dispersal, that are closely linked to population dynamics and easily integrated to models (Hanski 2001), are more often considered in analyses relevant to conservation biology. Nevertheless, considering dispersal in specific cases is hindered by lack of empirical data (MacDonald & Johnson 2001). Less regard has been given to the factors influencing various stages of dispersal (Sutherland 1998) or the links between social behaviour and population parameters (Blumstein 2010). Habitat selection is of great interest in

conservation biology because it has consequences to populations by determining individuals' lifetime reproductive success and because the amount of suitable habitat is a key issue for many endangered species (Boulinier *et al.* 2008).

1.2 Population growth

Population growth rates less than unity indicate non-viable declining populations, but also those populations with average growth rates indicating an increase may be at risk if variation is large (*e.g.* Morris & Doak 2002). Population growth can be measured directly using census methods (*e.g.* Morris & Doak 2002), or indirectly using capture-recapture data (Pradel 1996, White *et al.* 2002) or demographic models (Beissinger & Westphal 1998, Caswell 2001). Reliable estimation that captures full variation requires long term data, usually 8 – 20 years (*e.g.* Beissinger 2002).

Demographic PVA models have an important role in conservation biology (Beissinger & McCullough 2002, Morris & Doak 2002). Because they describe population dynamics explicitly, they can be used to identify demographic rates that have the strongest influence on population growth. Demographic models can also identify those components that provide best solutions under feasible management and can be used to assess effects of management (Beissinger & Westphal 1998, Norris & McCullough 2003).

The practical value of PVAs in guiding management has been questioned. PVAs may lack population specific data, have uncertainty among parameter estimation and poor model validation or consideration of alternative model structures (Beissinger 2002, Ellner *et al.* 2002, Reed *et al.* 2002). Furthermore, uncertainty about the future, especially environmental responses to management and concurrent changes in demographic parameters, further affect the reliability of PVAs (Coulson *et al.* 2001, Norris 2004). This relates to the lack of consideration about evolutionary processes working at the individual level (*e.g.* in behaviour), which affect the outcome of management decisions (Norris 2004).

With population specific data, demographic models provide useful information on the nature of the local population, whether it is a viable source population or a sink persisting only by rescue immigration (Pulliam 1988). However, the use of demographic rates (reproduction and survival) can lead to wrong conclusions on the source-sink nature of populations without considering movement among metapopulations, because survival is most often expressed as apparent survival that includes permanent emigration (Runge *et al.* 2006). High

observed immigration rates in local populations suggest a strong influence of movement (*e.g.* Orell *et al.* 1999). This problem relates also to the estimation of population growth with demographic models which usually ignore immigration and assume it to be counter-balanced by emigration of the same magnitude (but see *e.g.* Cooch *et al.* 2001, Sandercock & Beissinger 2002, Schaub *et al.* 2006). Biased survival estimates in the presence of emigration lead to false conclusions about the fate of populations (*e.g.* Nichols & Hines 2002).

Demographic models usually describe female life histories with age or stage structure (Caswell 2001). Consideration of males is rare despite contributions from both sexes (Rankin & Kokko 2007, Becker *et al.* 2008). Moreover, other sources of individual heterogeneity such as dispersal status or territory quality are rarely considered despite a marked potential influence on population growth or any other deductions from population models (Vindenes *et al.* 2008).

1.3 Habitat selection and ecological traps

In spatially heterogeneous environments, habitat patches differ in their abiotic, biotic and social environmental factors. Therefore, habitat selection decisions are tightly linked to lifetime reproductive success (Boulinier *et al.* 2008). Habitat selection is based on information about the quality of available patches that is acquired by using direct or indirect cues of the physical environment or personal information gained during natal or adult phases (Boulinier *et al.* 2008). In addition, individuals use social information where the presence of con- and heterospecific individuals and their reproductive performance are used as indicators of quality (Clobert *et al.* 2001). Such information can be gathered by prospecting potential patches (Clobert *et al.* 2001).

Sometimes the environmental cues that have indicated good quality habitat in the past become misleading, for example because of rapid environmental changes. In such situations, animals are unable to evaluate habitats. This leads to so called “ecological traps”, low quality habitats that cannot sustain viable populations, but are still preferred by animals over other available (better quality) habitats (Schlaepfer *et al.* 2002). In addition to natural processes, these changes are often anthropogenic and their prevalence may increase with human development (*e.g.* Best 1986, Battin 2004, Shochat *et al.* 2005, Gilroy & Sutherland 2007, Gilroy *et al.* 2011). At worst, ecological traps may increase extinction risks (Delibes *et al.* 2001, Kokko & Sutherland 2001). Therefore, understanding and recognising non-ideal habitat selection is vital for planning and executing sound conservation

measures, for example in habitat restoration projects in which environmental cues are altered (Pärt *et al.* 2007, Gilroy & Sutherland 2007).

1.4 Dispersal versus philopatry

Dispersal is essentially a habitat selection decision: dispersing individuals choose to leave and choose to settle at some destination habitat as opposed to being philopatric to their natal or former breeding habitats (Clobert *et al.* 2001, Boulinier *et al.* 2008, Clobert *et al.* 2008). Individuals may gain from dispersal by reducing competition and avoiding inbreeding, and also by escaping low quality environments (*e.g.* Clobert *et al.* 2001). On the other hand, dispersal can be costly due to stress experienced during the transient phase, disadvantages during the settling period in the new habitat and settlement to poor environments. Philopatric individuals may also benefit from genetic or phenotypic local adaptations such as site familiarity and even from kin cooperation (*e.g.* Pärt 1994, Clobert *et al.* 2001, Marr *et al.* 2002, Postma & van Noordwijk 2005). As a consequence of different costs and benefits, lifetime reproductive success of dispersing and philopatric individuals may differ (Belichón *et al.* 1996, Doligez & Pärt 2008). The net benefits from either strategy are likely to exhibit temporal variation, for example, due to frequency dependence or environmental variation causing variation in associated costs and benefits (*e.g.* Clobert *et al.* 1988).

Thus, dispersal behaviour is expected to be a plastic trait with low heritability, induced by internal or environmental conditions (Clobert *et al.* 2001, Pasinelli *et al.* 2004, Bowler & Benton 2005, Clobert *et al.* 2008). However, recent studies also suggest a genetic component behind variation in natal dispersal (Hansson *et al.* 2003, Pasinelli *et al.* 2004, Doligez *et al.* 2009). Genes are likely to be involved in determining response thresholds to environmental conditions (Clobert *et al.* 2008). Natal dispersal decisions are more likely to be influenced by genetic and maternal effects than on breeding dispersal decisions later in life, when accumulating information about resources (*e.g.* foraging, roosting and nesting sites) and own reproductive success affect dispersal decisions (Clobert *et al.* 2001, Doligez *et al.* 2009).

So far, it is unclear to what extent individuals differ in reaction norms to cues from the environment based on their genetic or phenotypic background (Ronce 2007, Doligez *et al.* 2009, Clobert *et al.* 2009). For example, dispersers and philopatric individuals may react differently to proximate cues triggering breeding dispersal decisions. Breeding dispersal is often a response to low habitat

quality, high conspecific density, mate loss or divorce (*e.g.* Naves *et al.* 2006, Pasinelli *et al.* 2007, Clobert *et al.* 2008). In particular, animals cue on individual reproductive success as an indicator of habitat quality (*e.g.* Switzer 1997). In birds, higher dispersal propensity among individuals with low breeding success is well documented (*e.g.* Lima 2009, Schaub & Hirschheydt 2009). Information from patch-specific reproductive success and increasing site familiarity with age also affect decisions on whether or not to return the next breeding season (*e.g.* Doligez *et al.* 1999, Schjørring *et al.* 2000, Boulinier *et al.* 2008).

Dispersal studies face the problem of a restricted size of study sites compared to dispersal distributions (Koenig *et al.* 1996). Thus, any parent offspring resemblance or within individual consistency in dispersal behaviour will bias fitness estimates in favour of philopatric individuals (Doligez & Pärt 2008). Therefore, dispersal status (immigrant vs. philopatric individuals) differences in apparent adult survival may reflect sensitivity to leave an unfavourable site. And measured apparent adult survival differences between immigrants and philopatric individuals should reflect the environmental conditions affecting breeding dispersal decisions (*e.g.* nest predation).

The demographic differences between immigrant and philopatric individuals lead to different demographic and genetic impacts on populations. This, in turn, will have consequences to the conservation of populations, whether or not the differences are caused by different breeding dispersal behaviour. In the case of different breeding dispersal, the value of immigrants can be low for local populations. However, at larger spatial and temporal scales, the value of the strategies is likely to vary depending on environmental conditions.

1.5 Life history characteristics of waders

Waders are long lived species with low and variable productivity, thereby residing at the slow end of species life histories (Piersma & Baker 2000, Saether & Bakke 2000). In waders, adult survival is the most important component of population growth. As long distance migrants, arctic and temperate breeding waders spend most of their life cycle at the non-breeding grounds. Short visits of only two months at their breeding grounds suggest that most mortality occurs in the non-breeding areas (Evans 1991). There seems to be a strong advantage in departing early from the breeding areas and gaining access to high quality non-breeding habitats that ensure high survival (Piersma & Baker 2000). Waders are faithful and thus highly dependent on their stop-over and wintering sites. Habitat loss or

reduction in quality at wintering sites decrease body condition and increase mortality (Burton *et al.* 2006). Stop-over sites are particularly important for refuelling (Baker *et al.* 2004). Poor refuelling can have long lasting consequences to both survival and reproduction emphasising the role of non-breeding areas in the events occurring also at the breeding season (Piersma & Baker 2000, Baker *et al.* 2004). Wetlands are globally threatened because of human activity. Thus, the identification of key wintering and stop-over areas and an understanding of the causes of variation in mortality are of primary interest in the conservation of long distance migrants (Piersma & Baker 2000).

Despite having less impact on annual population growth, changes in the breeding areas and reproductive output have been linked to declines of shorebirds. Grassland breeding waders, in particular, have undergone severe population declines during the last decades in Europe (Thorup 2006). Their declines have been attributed to the destruction of breeding habitat mainly due to agricultural intensification (Donald *et al.* 2001, Vickery *et al.* 2001) and overgrowth following the cessation of traditional agricultural practices (hay making and grazing) on natural meadows (*e.g.* Soikkeli & Salo 1979, Ottvall & Smith 2006). In addition, nest predation rates have increased throughout Europe (MacDonald & Bolton 2008) partly caused by changes in the predator fauna, *e.g.* invasion of alien predators (*e.g.* Nordström *et al.* 2003, Jackson *et al.* 2004). Another reason for lowered reproductive success may be increased susceptibility to nest predation due to human-induced or natural changes in the quality of breeding habitat (*e.g.* Koivula & Rönkä 1998, Evans 2004, van der Wal & Palmer 2008). Because waders are site faithful to their natal and especially to their former breeding territories (Oring & Lank 1984), the conservation of existing breeding sites should prove to be advantageous. Moreover, reproduction is often the only demographic rate that can be managed feasibly.

1.6 Habitat restoration with livestock grazing

Livestock grazing is commonly used to restore low sward habitat suitable for waders. Nowadays it is an important and intensively funded part in agri-environment schemes (AES) of European Union (*e.g.* Wilson *et al.* 2007). Census data show that local wader populations breeding on coastal meadows respond positively to grazing (Norris *et al.* 1997, Olsen & Schmidt 2004, Ottvall & Smith 2006), but the relationship may also turn negative when grazing intensity is too high (Norris *et al.* 1998). Livestock are known to depress nesting bird

reproductive output by trampling nests (Beintema & Müskens 1987, Green 1988), consuming eggs and chicks (Nack & Biric 2005), increasing nest predation (Baines 1990, Hart *et al.* 2002), causing nest desertions (Shrubb 1990) and causing changes in food availability by affecting invertebrate fauna (Vickery *et al.* 2001, Evans *et al.* 2005). Thus, grazing may threaten the viability of endangered populations (Watson *et al.* 2006).

The potential negative effects of grazing highlight the importance of evaluating the impact of grazing management on population viability. However, this is often done with insufficient measures and relying on proxies such as territory counts. Waders prefer pastures that provide suitable shorter sward structure over ungrazed meadows (Durant *et al.* 2008). Thus, the observed response in density may partly reflect an influx of individuals attracted to the grazed pastures. Simultaneously, local reproductive output may be lowered by the negative side effects of management. Successful impact assessment should distinguish whether increased density in response to grazing reflects improved reproduction or immigration. Also, examining solely reproductive success and ignoring other demographic parameters does not give tools to evaluate the consequences on population viability. A preference for pastures and the negative effects on reproduction may create potential for management-induced ecological traps for ground nesting birds, a process that may increase population declines (Delibes *et al.* 2001, Kokko & Sutherland 2001, Schlaepfer *et al.* 2002, Battin 2004, Figure 1).

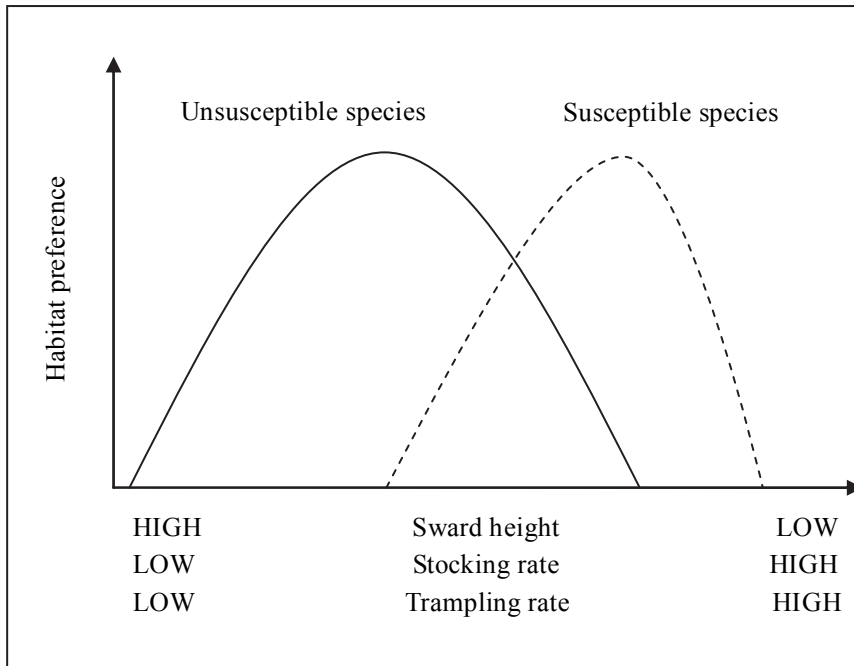


Fig. 1. The interaction between species preference for sward height and susceptibility to trampling. Preference for low sward habitat, nowadays created predominantly by grazing, makes those species particularly susceptible to high stocking rates. This may lead to a trap situation, where the most preferred habitats have the highest trampling mortalities, and thus lowest reproductive success.

1.7 Aims of the study

This thesis describes demography and examines the effects of dispersal behaviour, habitat selection and livestock management. The study objects include metapopulations of two endangered long-distance migratory wader species breeding on Baltic coastal meadows, the Temminck's stint (*Calidris temminckii*) and the Southern Dunlin (*Calidris alpina schinzii*). Analyses use long term individual-based life history data (breeding and capture-recapture data) acquired from the breeding areas.

Firstly, I estimate local recruitment, apparent adult survival, immigration rates and analyse their relative contributions to population growth (I, V). I assess temporal changes in demography as possible causes of population declines. Further, I use population models to examine extinction risks within the near future

(I, V) and assess the feasibility of directing conservation actions to different life history parameters by examining the sensitivity of population growth and extinction risk to possible changes in life history parameters (I).

The remaining part is divided into two sections. The first concentrates on dispersal status associated heterogeneity in demographic rates. I analyse the correlates of dispersal by comparing demographic rates of immigrant and philopatric individuals (II, III). I also examine the potential effect of within individual consistency in dispersal behaviour on apparent survival (III). I examine the effect of dispersal status on population growth rates and the relative importance of immigrant vs. philopatric individuals to local dynamics. This is done by constructing a male-based population matrix model with separate stages for the groups (II).

The remaining part concentrates on examining the effect of livestock grazing on demography. I first experimentally quantify trampling rates of nests and assess whether livestock presence affects nest predation rates (IV). Then, I build a simulation model that quantifies local recruitment by considering re-nesting and temporal changes in reproductive parameters (V). Using the re-nesting model together with population models, I analyse the effect of different grazing practises (differing in stocking rates and the timing of grazing) to population viability (V). I evaluate whether intensively grazed pastures with low sward height can work as ecological traps for waders by estimating habitat preference and habitat specific demography (VI). Finally, I use a habitat specific model to evaluate the possible effect of such habitat preference on population persistence (VI).

2 Materials and methods

2.1 Study species and populations

Life history data of two small meadow breeding waders, the Temminck's stint and the Southern Dunlin (hereafter Dunlin), were collected from the northern Baltic Sea at the Finnish coast of the Bothnian Bay near Oulu (ca. 64 ° 50' N, 25° 00' E) (I-V) and Kokkola (63 ° 53' N, 23° 04 30' E) (III). The study sites near Oulu cover an area of 30 km in N - S direction and 50 km in W - E direction. The ten Temminck's stint and seven Dunlin local populations include nearly all of the species' breeding sites within the area (Figure 1). Breeding sites of Dunlin are located solely in "natural" coastal meadow habitats, but Temminck's stints breed also in man-made habitats (coastal landfills and harbour yards) (Figure 2).

Temminck's stint sites are separated by more than 20 kilometres of unoccupied areas along the coastline. The study population represents about 30% of the entire Bothnian Bay population (125 territories in the early 2000s, Rönkä *et al.* 2006). The Bothnian Bay population is separated by a minimum of 300 km from the core breeding range (Lapland), which extends through the arctic region up until the Bering Strait (Hayman *et al.* 1986, Rönkä *et al.* 2006). The whole Finnish population is currently categorised vulnerable according to IUCN criteria (Rassi *et al.* 2010, I). The Bothnian Bay population has been declining rapidly during the last hundred years (Rönkä 1996, Rönkä *et al.* 2006) and is categorised as endangered in a regional evaluation (Aleksi Lehikoinen pers comm.)

The Dunlin population studied holds ca. 45 pairs (80% of the Finnish Baltic Dunlin population, Thorup 2006). The rest of the breeding sites are situated in Kalajoki (100 km, 0–2 pairs), Pori (400 km, 4–5 pairs) and Jurmo (550 km, 4–5 pairs), all south of the study area. The Bothnian Bay population is a part of the critically endangered Baltic Dunlin meta-population (Thorup 2006), which has been declining rapidly and is now listed in Annex I of EU's bird directive. The Finnish population has declined from its peak of 200 pairs in the 1960s, but has currently stabilised at 50–60 pairs (Jorma Pessa, pers comm.). It is listed as critically endangered (Rassi *et al.* 2010).

Temminck's stints have continent-wide flyways and they winter in sub-Saharan Africa, the Mediterranean and S-SE parts of Asia (Cramp 1985, Hedenström 2004). Baltic Dunlin migrate through coastal areas along the Baltic and Wadden Sea and winter in estuaries of northern Africa (Thorup *et al.* 2009).

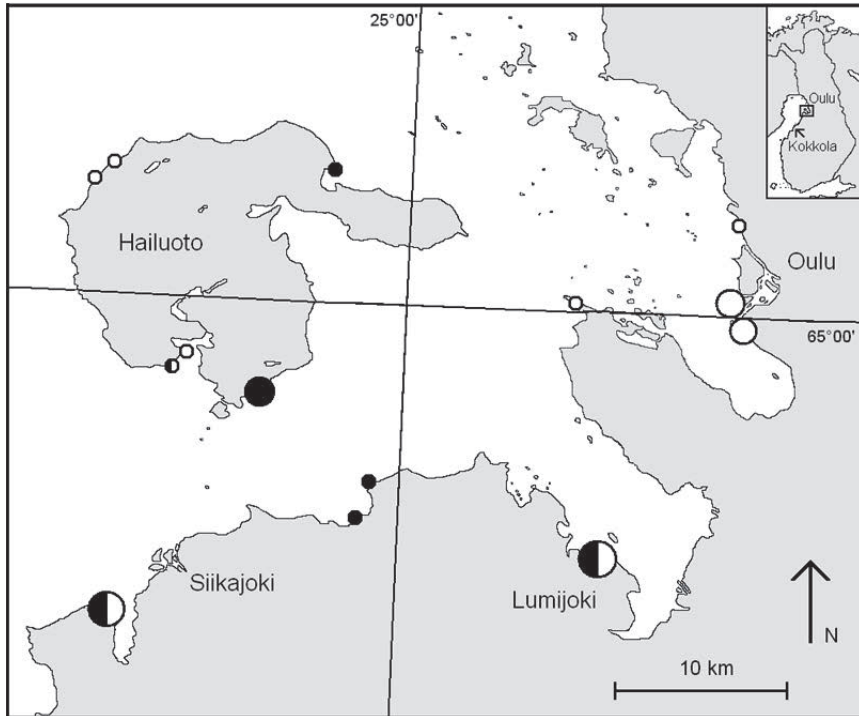


Fig. 2. Location of the study sites with breeding Temminck's stints (open symbols), Dunlins (filled symbols) or both (half-filled symbols). Size of the symbol indicates the number of pairs / territories (small < 5, medium 5 - 15, large over 15). The Dunlin population in Siikajoki Tauvo (SW corner) has declined from 7 to 3 pairs.

Both species are semicolonial, breeding in solitary territories or in larger aggregations of up to 30 pairs (Rönkä 1996, Rönkä *et al.* 2006; Soikkeli 1967, V). Temminck's stint and Dunlin show high site fidelity to their natal areas and breeding sites, with higher site fidelity for males than females (Soikkeli 1970a, Hildén 1979, II, V).

The breeding system of the Temminck's stint is a multi-clutch system ("successive bigamy"), where nests are cared for uniparentally (Hildén 1975, Breichagen 1989). Females change mates between successive clutches. The first clutch is incubated by their first mate, a territorial male. The second nest can be incubated by other males or by the females themselves within the first or other males' territory. Thus, females' breeding dispersal propensity and distribution are more extensive than those of males (Hildén 1979). Still, breeding dispersal from local populations to another is rare (Pakanen, unpublished data).

The Dunlin is a monogamous species with long-lasting pair bonds, 67 - 75% of pairs reunite (Soikkeli 1967, 1970a, Thorup 1999, own observations). Both sexes incubate and provide care for the chicks, but females tend to leave the responsibility to the males soon after chicks are hatched. Dunlins start laying in late April or early May. Temminck's stints start a month later in late May or early June (Soikkeli 1967, Hildén 1975). Nest period lasts ca. 26 days in both species, including an egg laying phase of 4.5 days (1–1.5 day laying interval) and a 21–22 day incubation period (Soikkeli 1967; Cramp 1985). Temminck's stints fledge at 15–18 days and Dunlins at 19–21 days of age (Cramp 1985).

2.2 Breeding habitat and management

The Bothnian Bay is characterised by a low coastline, where constant land uplift (c. 8 mm per year, Mäkinen and Saaranen 1998) creates new mudflats, wet and drier short-vegetated meadows, suitable nesting habitats for Temminck's stints and Dunlins (Hildén 1975, Koivula and Rönkä 1998). Currently, overgrowth of these habitats due to succession of vegetation has accelerated, thereby altering the habitats and making them unsuitable for breeding. Most known Dunlin breeding sites would not survive without management by grazing or mowing (Pessa *et al.* 2006).

Mowing, carried out after the breeding season, does not pose any risk to the birds. In contrast, the livestock brought to pastures in the early summer and kept there until the autumn, constitute a potential danger for the birds for example in terms of nest trampling and increased nest predation. In the pilot study year 2002, two out of three Dunlin nests were trampled within few days of livestock being released to the meadows. Since then, because of the apparently high trampling risk and the endangered status of the study species, Dunlin nests have been protected against trampling (IV). Recommended densities for suckler cows on coastal meadows is 0.5 – 1 livestock units/ ha (Decree 14.11.2000/106 of the Finnish Ministry of Agriculture and Forestry). Nowadays, grazing is the most popular management tool of coastal meadows and considered successful in management for the Dunlin (Rassi *et al.* 2010). Different management regimes (mowing or cattle grazing) result in varying sward heights. In the present work, meadows with no grazing or a low grazing intensity (LG) are categorised into high sward habitats and meadows with high grazing intensity (HG) into low sward habitats (VI).

2.3 Data collection

The Temminck's stint data were collected in 1963–1972 and in 1994–2009. Data from 1963 to 1972 were collected in Harrbåda, Kokkola by Olavi Hildén. Following Hildén (1978), the data is used only until 1970, after which the study site suffered from sudden habitat deterioration. The study population in Kokkola was geographically separated from other breeding sites in the Bothnian Bay (see Hildén 1975, 1978, 1979). The data from 1994 to 2009 were collected near Oulu and Siikajoki, ca. 150 km north from Kokkola (Figure 2).

The Dunlin data cover the period 2002–2010. Starting from the pilot year 2002, data were gathered from all but two small sites that were included from 2004 (in Siikajoki) and 2006 (in Hailuoto) onwards (Figure 2). The nest trampling experiment was conducted during the 2007 breeding season in Lumijoki (IV).

2.4 Life history data

Dunlin territories and nests were searched intensively throughout the breeding season from late April until early July. Temminck's stint nest searches started from late May and lasted until late July. Nests with at least one egg were considered active. Small inconspicuous markers and a GPS device were used to relocate the nests. Starting from 2003 a portion of Temminck's stint nests were protected from predation (Rönkä *et al.* 2006, II). Nests were checked every 1–7 days until hatching to determine nest fate and to mark the parents and hatching chicks. Causes of nest failure were recognised following the criteria in Rönkä *et al.* (2006). Nest initiation and hatching dates were determined by the number of eggs during laying, egg floatation during the incubation period or hatching date. If the chicks had left the nest, their size at ringing was used to approximate the hatching date. When the eggs had obviously hatched (based on marks left in the nest cup), but the chicks were not found, the hatching date estimate was based on egg floatation. If the exact date was not available, failure was approximated to have taken place in the mid-day between last two visits. Hatchlings were ringed with numbered metal rings.

Capture-recapture data were based on colour ringed adult birds, whose origin was known (either locally born or immigrant). The origins of the birds were ensured by nest searches and ringing of young. Adult birds were captured from nests when incubating or beside newly hatched young with mist-nets or traps. Adults were marked with numbered steel rings and individually identifiable

combinations of 3 UV-resistant darvic colour rings. Resighting or trapping of a colour-ringed bird during the breeding season was considered as a recapture. Sex was determined by behaviour, molecular techniques (CHD-gene, Griffiths *et al.* 1998) or sexual dimorphism.

2.4.1 Nest trampling experiment

Non-vegetated, round patches (15 cm in diameter) served as nest models when measuring trampling rates. Hoof prints in the patches were used to recognize a trampling event. The experimental nests were positioned close (5–10 m) to known Dunlin nests.

The experimental design should not affect trampling by changing cattle behaviour. The absence of eggs is not a problem because eggs hardly affect trampling. Because Dunlins do not actively defend their nests against the cattle (*e.g.* Thorup 1998) the results should not be affected by the absence of parents. Possible researcher influence on cattle behaviour was reduced by setting the experimental patches before the release of the cattle to the meadow. Landscape characteristics that may influence the cattle behaviour, such as elevation and distance to the shoreline, were measured from the experimental patches. Separate trampling probabilities were calculated for three consecutive weeks starting from the onset of grazing.

2.4.2 Habitat preference and life history

Habitat preference of the Dunlin between low and high sward habitats was estimated by examining both natal and breeding dispersal between habitats. Due to nest protection, the effects of trampling at the HG habitat could not be directly quantified. Therefore, reproductive success was estimated *post hoc*. A stochastic re-nesting model, considering estimated daily trampling and other causes affecting the nest survival rates, was used in estimating habitat-specific reproductive success (V, VI, Beintema & Müskens 1987).

2.5 Data analysis

Reproductive success was expressed as the number of hatchlings per laid clutch (I), daily nest survival (II, IV, V), mean number of hatchlings per breeding attempt (II) or the product of daily nest survival and number of hatchlings per

successful nest (V, VI). Fecundities include also local juvenile survival (I, II, V, VI). For the Temminck's stint, the number of incubating females per male territory (F_n) was estimated (II).

Capture-recapture data (Table 1) was used to estimate apparent survival (Φ). Analysis involved models developed for open populations, which provide survival rates corrected with recapture probability (p) (e.g. Lebreton *et al.* 1992) and movement rates between sites (Multi-state models; White *et al.* 2006). Additionally, reversed capture histories with temporal symmetry models were used to estimate retrospective population growth rates (λ), per capita recruitment rates (f) and the seniority parameter (γ) that is analogous to the elasticity of adult survival (Pradel 1996, Nichols *et al.* 2000). Analyses were done with program MARK (White and Burnham 1999). Parameter estimates are reported as mean \pm S.E.

All previously unmarked adults were classified as immigrants, because practically all locally born (philopatric) individuals were ringed at birth. In the dispersal status studies (II, III), the unmarked individuals caught in the first study years (1994 and 1995) were excluded from the analyses to reduce the probability of misclassifying philopatric individuals as immigrants. All individuals were included in the analysis of the 1960s data (low predation period, III), because chicks had been ringed at the study site for five years prior to the onset of ringing the adults and the chance of misclassification was negligible (see Vikström 1999).

Table 1. Summary of the data used in the analyses. Studies I-III were on Temminck's stints and studies IV-VI on Dunlin. In studies II and III the number of individuals do not include previously unringed individuals caught in the first two years.

Study, Data collection	Nests	Chicks	Adults					Encounters
			Total	Males	Females	Philo	Immigrant	
I, 1994–2003	255(373) ^a	385	177	-	-	-	-	389
II, 1994–2006	385(491) ^a	354	184	119	65	38	146	388
III, 1994–2009	-	-	197	128	69	44	153	469
III, 1963–1970	-	-	85	30	55	31	54	202
IV, 2002–2008	204	-	-	-	-	-	-	-
V,VI, 2002–2010	337	362	206	105	101	-	-	531

^a The number of breeding attempts

2.5.1 Model selection

Akaike's Information Criterion with a small sample correction (AICc) was used to assess the relative fit of the models (Burnham & Anderson 2002). The modelling was started by building a global model, after which a set of less constrained candidate models structured to include hypothetical a priori parameter associations were fitted to the data. Due to small sample sizes, the goodness of fit of global models, that included all potential variation, were mostly tested with the parametric bootstrap and median \hat{c} approaches in MARK, but also program U-Care was used (Choquet *et al.* 2005).

The corrected quasi-AIC (QAICc)-values were used, if the overdispersion quantified by \hat{c} was over 1 or less than 3. Models were compared based on the difference between their AICc values (Δ -AICc). Additionally, the Akaike weights (w) for different models were used to calculate an evidence ratio (w_1 / w_2), that quantifies the support for different effects. Parameter and variance estimates were acquired using the best fitting or multiple models. Model selection uncertainty was taken into account by calculating model averaged parameter estimates, in which the contribution of each model was controlled by their Akaike-weights (Burnham & Anderson 2002).

2.5.2 Fecundities

Daily nest survival (II, IV, V, VI)

Maximum likelihood estimates of daily nest survival (for natural nests and experimental nests) were calculated and the effects of independent variables were modelled with the nest survival approach in program MARK (White & Burnham 1999, Dinsmore *et al.* 2002).

When analysing the daily nest survival of Temminck's stints, the egg laying and incubation periods were pooled (average duration 26 days) (II) following Rönkä *et al.* (2006). In the Dunlin data (IV, V), suspected nest age specific variation was considered in the models. Nests with unknown fate were included until the last known active date. When modelling the impact of a given cause, *e.g.* predation, to the daily nest survival, nests destroyed by other causes were treated as successful until the estimated time of failure.

A set of a priori hypotheses were used to construct models explaining variation in nest survival. When modelling nest survival of Temminck's stints (II),

the explanatory variables included age (breeding experience, 2 classes), sex and dispersal status (immigrant vs. philopatric) of incubating birds and nest protection (protected or not). In the Dunlin studies (IV, V, VI), the models included breeding site, year (2002–2008), nest age, within season temporal changes, nest initiation date, habitat type (LG vs. HG) and the nesting attempt (first vs. re-nest). The effect of grazing on the predation rate was investigated by comparing the nest survival before and after the grazing season started (IV).

Re-nesting model (V, VI)

A simulation model accounting for re-nesting (Beintema & Müskens 1987, Green *et al.* 1997, Ratcliffe *et al.* 2005) was used to calculate reproductive success (the proportion of successful breeding females, number of hatchlings produced and local recruitment) per female Dunlin (V). The model followed the breeding cycle from the start of breeding to the recruitment of juveniles using estimated parameter distributions for nest initiation (timing of breeding), daily fate of the nests until hatching (no trampling effect), the nesting period (26 days), the re-nesting probability defined by calendar date, the re-laying interval between nest failure and re-laying, the number of possible nesting attempts (two), the number of chicks hatching and an estimate for hatching day specific juvenile survival.

The re-nesting model was used to calculate the reproductive performance for management scenarios differing in stocking rates (hence trampling rates) and the timing of grazing initiation. Trampling is most severe at the start of grazing and declines gradually at least until the third week of grazing (IV). This was considered by setting an increasing trend to the survival from trampling in all of the scenarios according to the slope described in IV. Trampling rates were assumed to stabilise in the third week. The results were compared to those modelled with constant trampling rates. All of the scenarios were examined for each day of grazing initiation from the 15th of May to the 30th of June. Simulations included 10000 replications for each day of grazing initiation. Modelling was done in program MATLAB.

2.5.3 Capture-recapture data

Return rates in relation to reproductive failure and dispersal status (III)

The dispersal response of immigrants and philopatric individuals to nest failure was first investigated by contrasting return rates of the successful and unsuccessful first time breeders. Individuals that managed to hatch at least one chick were classified as successful. By considering only the first breeding, pseudo-replication and potential effects from earlier breeding were avoided. Experienced second time breeders were used to examine age or prior breeding success effects on dispersal decisions in a separate analysis. Because there are no data on actual movements, the difference in return rates (proportion of marked individuals resighted in the year following capture) of successful and unsuccessful individuals was used as a proxy for difference in the dispersal behaviour (Porneluzi 2003). Return rate is the product of four different probabilities: true survival, site fidelity, site propensity (the probability that an individual is available for encounter in the sampling area) and detection (Sandercock 2006). The unsuccessful and successful individuals were assumed to have similar survival rates. Similarly, there was no evident reason to suspect that unsuccessful and successful individuals would have a different probability of detection in the following year if they are present. Therefore, a difference in return rates of unsuccessful and successful individuals should reflect differences in site fidelity to the breeding site and site propensity, and thus the breeding dispersal.

Apparent survival (I, II, III, V, VI)

Apparent adult survival, was considered a priori to be influenced by a time dependence with year effects (I, V) or temporal trends (I), sex (II, III, V, VI), dispersal status (II, III), habitat (HG vs. LG, VI) and the time since marking (I, II, III, V). The time since marking effects were used to control for possible age-specific survival, age-specific site fidelity or presence of transience. Recapture rates were constrained by time (I, II, III, V, VI), sex (II, III, V, VI), dispersal status (II, III), average yearly nest success (II, III) and habitat (HG/LG, VI).

Models for apparent juvenile survival from hatching to age one (I, II) included two age classes and those analysing juvenile survival to age two (V, VI) had three age classes. Juvenile survival parameters were constrained by time (I),

sex and dispersal status of the incubating bird (II), habitat (HG/LG, VI), hatching date (V, VI) and exposure time to cattle trampling (V). In both the adult and juvenile data, multi-state models were used to estimate habitat-specific survival and movement between habitats (HG/LG, VI).

Age at first breeding and breeding probabilities

The age at first breeding was estimated using ringed local recruits, whose exact age was known. The age-specific breeding probabilities were calculated assuming that all the individuals that bred at age i also bred at age $i + 1$, if they were alive, even when not seen. Breeders may remain undetected especially in years of high nest failure. These birds may have bred elsewhere, although no such events were observed. In any case, their contributions in those years to the local population were zero, which is included in the estimate of hatching success per breeding attempt (II). Breeding probabilities calculated only from the observed individuals would underestimate the breeding success. The immigrants have a breeding probability of one, because their initial capture is dependent on breeding.

Pradel and multi-state models (I, II, V, VI)

Pradel models were used to estimate population growth rates and recruitment parameters (I, II, V, VI). Goodness of fit was judged based on tests made for the CJS model (*e.g.* Sandercock and Beissinger 2002). Pradel models are sensitive to changes in field effort and difference in capture probabilities between marked and unmarked individuals (Pradel 1996). Additionally, immigration is most reliably estimated by excluding the first years, because locally born, but unmarked birds may recruit in the first years. Therefore, the first year (in papers I, II), the first four years (paper V) or the year 1999 (in papers I, II) were discarded. Analyses were done for both sexes (papers I, V, VI) or males only (paper II).

Immigration rate (I, II, V, VI)

The recruitment parameter (f) expresses the number of new individuals (local recruits or immigrants) that enter the population at time $i+1$ per adult individual already in the population at time i (Nichols *et al.* 2000). The immigration rate (IMM) was derived by extracting local recruitment (LR) from the recruitment parameter (*e.g.* Peery *et al.* 2006),

$$\text{IMM} = f - \text{Pb1} * \text{LR} + \text{Pb2} * \text{LR} * \text{S}_{\text{AD}} + \text{Pb3} * \text{LR} * \text{S}_{\text{AD}}^2 \quad (1)$$

where LR is the product of the number of produced juveniles per breeding attempt and juvenile survival (II) or local recruitment per female from the re-nesting model (V, VI), Pb_i is the proportion of birds breeding for the first time at the age i and S_{AD} is the mean adult survival. Because some individuals returned after their second (II) or third summer (V), for which the local recruitment was measured, local recruitment was divided into proportions based on age at first breeding. Then, the proportions reflecting age specific returns were multiplied by adult survival to consider that they do not return on their first year. When modelling the dynamics of Temminck's stints (II) the production of chicks in female nests was considered by adding a proportion of local recruitment defined by the number of female breeding attempts per male territory.

2.5.4 Population modelling

Matrix projection models (I, II, V, VI)

Matrix projection models were used to describe deterministic population growth with an estimate of a prospective λ (I, II, V, VI). The models were based on a pre-breeding census and included stages based on three (I, II) or four (V, VI) age classes starting from age one (Caswell 2001). The last stage was a composite group for older birds with similar life history. Models depict dynamics of either females (V, VI) or males only (II), or of both sexes (I).

Model structures differed in how immigration was included. Matrices generally describe dynamics in terms of survival and reproduction while emigration and immigration are assumed to cancel each other out (I, model A in II, V). This describes whether local recruitment is sufficient to compensate for mortality (and emigration), but it will bias the overall estimate of population growth, because estimates of apparent survival are confounded with permanent emigration (II). The importance of immigration to local dynamics was described by including the estimated immigration rate (number of immigrants recruiting at time $t+1$ per adult in the population at time t) into the fecundity transition (I, model B in II) or by making separate stages for immigrants (II). In the latter case, immigration had its own transition in the matrix and was included for all classes (model D II, V, VI). These were designed to check the effect of immigration and dispersal status specific demography (see also Vindenes *et al.* 2008, II).

The fecundities express per capita number of local recruits per breeding attempt,

$$F_i = \frac{1}{2}(P_i * LR) + F_n * \frac{1}{2} * LR, \quad (2)$$

where P_i is the breeding probability at age i and LR is local recruitment. LR is the number of chicks hatched per laid clutch (I), product of breeding success per breeding attempt and juvenile survival (II) or local recruitment estimated with the re-nesting model (V, VI). Hatching sex ratios were set even. In the Temminck's stint work describing a male matrix (II), the progeny produced in female incubated nests was added to the fecundities. Contribution of females was calculated by multiplying average local recruitment with the number of female breeding attempts per male territory (F_n). In the work including both sexes in the model (I), sex ratio of adults was assumed even and females were assumed to always lay two clutches (I). When calculating habitat specific local reproduction (V), the proportion of locally produced recruits that emigrate to other habitat was taken out.

Depending on the specific purpose, models were parameterised with average (I, II, V), dispersal status specific (II) or habitat specific (VI) life history parameters. Juvenile survival estimates for the Dunlin are from birth to two years of age. Thus, survival to age one was fixed to one and fecundity for the first year birds was fixed to zero (Becker *et al.* 2008).

Analytical elasticity values were calculated to investigate the sensitivity of λ to proportional changes in the matrix elements. In addition to elasticities, the relative contribution of the stages to population growth was compared by examining the stable stage distribution (SSD) and the stage specific reproductive values (RV), which are calculated as the associated right and left eigenvectors of the matrix, respectively (Caswell 2001). The delta method considering yearly matrix estimates was used for calculating variance and confidence intervals for the population growth rates (Alvarez-Buylla and Slatkin 1994). Analyses were performed with program MATLAB.

Population viability analyses (I, V, VI)

RAMASmetapop (Akçakaya 1998, 2005) was used to project future (within the next 20 to 50 years) population growth and to assess extinction risks in different management scenarios (I, V, VI). Population viability was examined using three modelling approaches: scalar models (I), projection matrices (I, V) and habitat

specific meta-population models (VI). Scalar models, describe population growth with the Pradel- λ in a single stage matrix (I).

The scalar models and matrices that include immigration, assume density-dependent immigration (I). This fits the dynamics of populations of species where immigration is largely determined by conspecific attraction, such as the Temminck's Stints. Only areas that already have occupied territories receive immigrants despite available areas of good habitat within our study area (own unpublished data). The assumption of density dependent immigration can be unrealistic in scenarios with λ exceeding one. This approach was used for the Temminck's stint (I), which has a declining population and a large potential source population. It was not used for the Dunlin, because all of the Dunlin populations around the Baltic region are declining rapidly. Instead, the introductions mode provided in RAMAS was used with a fixed number of immigrants directed to the fourth age group (V, VI).

Matrices were parameterised with survival and fecundities estimated from the data (I, V, VI). Sensitivities of extinction risks to parameter changes were examined by matrix projections to get insight into the importance of different vital rates and potential management targets (I). Ranges of possible values were chosen based on observed life history (*e.g.* clutch size) and related literature (survival rates, *e.g.* Hildén 1978, Sandercock 2003). Additionally, a model was parameterised with mean vital rates of the Temminck's stint presented by Hildén (1978) to evaluate the effects of historical changes in life history to viability (I).

Models parameterised with average life history of the Dunlin (V) and local recruitment estimated with the re-nesting model were used to assess the effects of different stocking rates and the timing of grazing on viability. A habitat specific metapopulation model consisting of two spatially non-explicit habitats (LG and HG) was used to examine possible effects on extinction risks caused by movement to the putative ecological trap habitat (HG) (VI).

Density dependence was modelled only as a ceiling type, because of lacking information (see *e.g.* Beissinger & Westphal 1998, Ralls *et al.* 2002, I, V, VI). Density dependence of long distance migratory waders is difficult to measure because the group of individuals affecting individuals differs between life cycle stages and density dependent factors may play a more significant role at the non-breeding sites compared to breeding areas (Evans 1991). Fecundities and survival rates were assumed to correlate because local recruitment (juvenile survival) and adult survival are most likely largely determined by the same factors at the non-breeding sites.

Due to assumed constant (V, VI) or density dependent (I) immigration, the uncertainty regarding possible changes in vital rates in the future and the assumption of no density dependence, population growth was projected only for the next 20 or 50 years. A quasi-extinction threshold of 20 individuals (I) and a threshold of a 50% decline (V, VI) were used (Beissinger & Westphal 1998, White 2000). When immigration was not included, an extinction threshold was one (V, VI).

Catastrophes were not incorporated. This was because, to a large extent, variation by the most imminent “catastrophe”, flooding of meadows, is already included in the parameter variances. In RAMAS, environmental stochasticity was modelled with a standard deviation matrix of the corresponding matrix transitions and by repeating projections for 1000 times. Demographic stochasticity was modelled by drawing survival and dispersal rates from a binomial distribution and the number of offspring (I, V) and immigrants (I) from a Poisson distribution (Akçakaya 2005). Estimates of standard deviation for fecundities considering only yearly process variance (SD_{PROCESS}) were calculated with approach described by White (2000). For adult survival (V, VI), recruitment parameter (I) and population growth rates (I), the variance approach in MARK was used. Due to methodological reasons SD_{PROCESS} for adult survival in (I) was taken from published estimates for closely related semipalmated sandpipers (Hitchcock and Gratto-Trevor 1997). Initial population sizes were set to the population sizes derived in the studies V and VI or according to Rönkä *et al.* (2006) (I). The populations were assumed to be at the stable stage distribution.

3 Results and discussion

3.1 Life history overview

Both species had little temporal variation in apparent adult survival rates and elasticity of adult survival was high (Temminck's stint 75 - 86% (I, II), Dunlin 66% (V). The contribution of fecundity to population growth was low (Temminck's stint, 7.4%, II; Dunlin 18.5%, V). Thus, life histories of Temminck's stint and Dunlin fit to that of bet-hedging strategists (Saether *et al.* 1996, Piersma & Baker 2000). This means that mechanisms affecting survival and movement of adults have strong impacts on local population dynamics and viability. Both populations were dependent on immigration, which formed ca. 7 – 15% of the population growth rates (II, V).

3.1.1 Nesting success

There is evidence that breeding success at the Bothnian Bay has decreased during the past decades in both species. In this study, nest success of Dunlin varied between years (range 7 – 81%), being roughly similar on average (42%) to the Swedish (Jönsson 1991, 30%; Pauliny *et al.* 2008, 41%) and Danish (Thorup 1998, 47%) populations, but much lower than nest success in Finland in the 1960s (Soikkeli 1970b, 59%). Nest success of Temminck's stints varied less and was generally poor (23%). There has been a declining trend in nest success starting from the 1960s (III, Rönkä *et al.* 2006, Figure 3).

Nest predation was the main cause for nest failure in both species (Dunlin 74%, V; Temminck's stint 80%, Rönkä *et al.* 2006), but daily predation rates are much higher for Temminck's stint nests (IV) suggesting higher susceptibility to predators. It is likely that processes related to breeding habitats (large vs. narrow shores, occurrence of sentinel birds), timing of breeding (early vs. late), nest characteristics such as nest concealment (open vs. concealed), breeding system (uniparental vs. biparental care) or anti-predator behaviour are behind the difference (Evans & Pienkowski 1984, Rönkä & Koivula 1997, Koivula & Rönkä 1998).

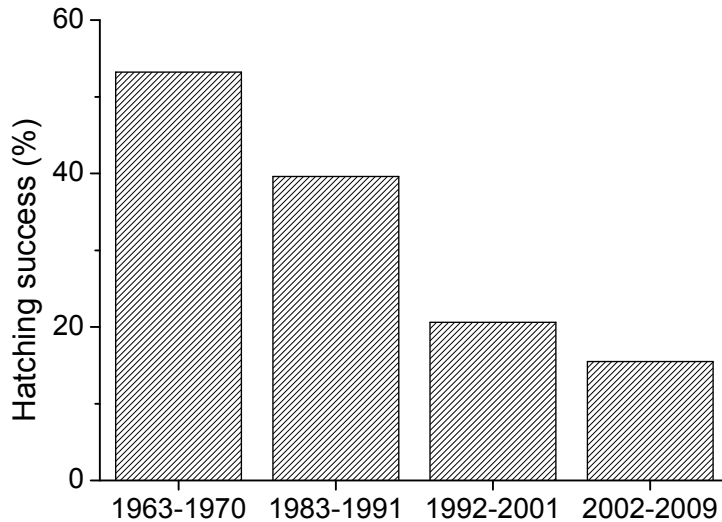


Fig. 3. Nest success of Temminck's stints during the last 50 years calculated from daily nest survival rates of unprotected nests from 1963–1970 (Ill), 1983–2001 (Rönkä *et al.* 2006) and 2002–2009 (Pakanen *et al.* unpublished data).

Predation rates of Dunlin nests decreased strongly with nest age. This may simply mean that vulnerable nests are predated first (Dinsmore *et al.* 2002), but it may also reflect seasonal changes such as shifts in predator diet and increasing nest cover from grass.

3.1.2 Apparent juvenile survival

Nearly one fifth of the hatched Dunlin chicks recruited to the population (apparent juvenile survival: 0.199 ± 0.026). The return rate (0.155) is close to those reported for other populations (Soikkeli 1970b, Jönsson 1991). Juvenile survival was rather high compared to other small or medium sized wader species (*e.g.* 0.09 in Kentish Plover *Charadrius alexandrius*, Sandercock *et al.* 2005; 0.18 in *C. a. nivosus*, Stenzel *et al.* 2007; 0.09 in Semipalmated sandpiper *Calidris pusilla*, Sandercock & Gratto-Trevor 1997; 0.048 in Semipalmated plover, *Charadrius semipalmatus*, Nol *et al.* 2010). The high estimate may reflect the fact that practically all suitable habitats and thus movements within the large study

area were controlled. Mean natal dispersal distance was 9.3 km and the distribution was strongly skewed to short distances, because most of the birds recruited to the natal site. Nevertheless, 46% of returning individuals changed the local populations and mean natal dispersal distance for that group was 15 km.

In contrast to the Dunlin, the apparent juvenile survival of Temminck's stints was low, 0.061 ± 0.02 (I) and 0.106 ± 0.022 (II). These are close to estimates for other similar-sized species (see above). Low returns may reflect permanent emigration from the study area, which is expected especially when study areas are small and when there is suitable habitat available elsewhere (Koenig *et al.* 1996, Nol *et al.* 2010). However, Hildén (1978) reports a return rate of 15% for juvenile Temminck's stints in the 1960s from a very small and isolated study area (12 ha). This suggests that local recruitment has declined strongly in the Bothnian Bay. The decline may be even steeper because the return rates are minimum estimates. This difference, together with the adult survival patterns (no decline, see below) and low pre-fledging survival (0.13–0.35; Pakanen 2004), suggest that the low estimate is largely caused by lowered pre-fledging survival. In contrast to Dunlin, only 3 out of 44 Temminck's stints bred outside their natal site. 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 here. Therefore, a reasonable conclusion is that in the Bothnian Bay, Temminck's stints natal dispersal is minimal at a regional scale and the apparent survival estimates fairly well represent true survival. Still, long distance emigration cannot be ruled out. In fact, genetic analyses suggest strong past or present gene flow between the study population and the northern main range (Rönkä *et al.* 2008). However, because of the robustness of these analyses, the magnitude and significance of emigration to estimates of juvenile survival is difficult to evaluate.

3.1.3 Apparent adult survival

Average apparent survival rates were similar for the Dunlin (0.75 ± 0.020 , V) and the Temminck's stint (1994–2009, 0.7 ± 0.020 (I, II, III); 1962–1970, 0.75 ± 0.036 (III) and resemble those published for other small arctic waders (Jönsson 1991, Warnock *et al.* 1997, Summers *et al.* 2001, Sandercock 2003, Johnson *et al.* 2010, Zöckler *et al.* 2010). No apparent change has occurred in the Finnish populations during the population declines of the late 1900's. Soikkeli (1970b) reported the same return rate 0.75 for Dunlin breeding in Pori. In the Temminck's stint, there was some support for a negative survival trend (I), but detailed

analysis (III) revealed no significant survival difference between the recent data and the data collected in 1960's and in the 1970's (see below).

Males had higher apparent survival than females in both species. However, the difference was pronounced only in the Temminck's stints (III, V). Sex differences in survival are rare in monogamous species such as the Dunlin, but if they exist, males tend to survive better (Sandercock & Gratto-Trevor 1997). Low female survival may reflect higher reproductive costs caused by the production of energetically demanding clutches. However, males tend to brood, which should balance these to some degree (Sandercock & Gratto-Trevor 1997). The sex differences are most easily explained by dispersal of females (Soikkeli 1970a). Lower recapture probabilities and higher between habitat movement rates of female Dunlin compared to males supports the dispersal explanation (VI).

In the Temminck's stint, moving between successive clutches (Breihagen 1989, Hilden 1975) may expose Temminck's stint females to energetic stress and predation, and thus decrease survival. There was strong evidence suggesting that females exhibit higher dispersal propensities than males (III, Hildén 1979). Transience effects for females were clear, especially in the 1960's data (Hildén 1978, III). Recapture rates were also lower for females than for males, which suggests that females move more or are less easily observed. Most importantly, females responded stronger to nest failure (III, see below). These observations are in accordance with results from molecular data suggesting female-biased dispersal between the study population and Fennoscandian inland populations (Rönkä *et al.* 2008). All fragments of evidence above point to the conclusion that lower female survival can be explained by permanent emigration.

3.1.4 Population viability analysed from average life history

Both study populations had insufficient local recruitment to maintain stable population growth. The Temminck's stint population declined during the study (I, Pradel- $\lambda = 0.892$). Available censuses also show a recent and abrupt decline (35%) in the Bothnian Bay area during the same period (Rönkä 1996, Rönkä *et al.* 2006). The process is a continuation of the historical decline that started already earlier in the 20th century (Rönkä 1996, Rönkä *et al.* 2006). The prospective estimates of λ for the Temminck's stint comprised by local dynamics (immigration excluded) was unrealistically low ($\lambda = 0.758 - 0.765$, I, II), suggesting a drastic decline. However, they remained low even when immigration was considered ($\lambda = 0.911$) (I, II). Models predicted 39 to 50% probabilities of quasi-extinction in the next 20

years. After 50 years, extinction was almost certain. Without immigration the decline was predicted to be fast, with an extinction probability of ~ 1 in the next 20 years.

Sensitivity of λ suggests that there is no single remedy to increase the population. Even a change in adult survival to 0.8 would not turn the population to increase. If the immigration rate is considered density-dependent, a change of more than 0.25 would be needed to turn the population to increase and juvenile survival needs to rise fourfold.

The matrix model parameterized using Hildén's (1978) data suggested that in the 1960s the coastal population was quite stable. Considering the fact that the survival estimates in Hildén's (1978) data were return rates and that his study area was relatively small, survival, as well as recruitment, may have been underestimated.

The population growth rate for the Dunlin also indicated a strongly declining population in the absence of immigration ($\lambda = 0.856$). However, immigration was sufficient to keep the population growth stable ($\lambda = 1.01$). Accordingly, the model including immigration predicted a stable or a slightly increasing population with a low probability to decline 50% within the next 20 years (V). However, a model without immigration predicted a high extinction risk within the next 20 years (V).

3.1.5 Sink populations maintained by rescue immigration

It is evident that these study populations are dependent on rescue migration. Immigration covered roughly 61% (V) to 70% (I) of total recruitment. Hence both of the study systems represent sink populations *sensu* Pulliam (1988). However, the productivity estimates can be biased due to permanent emigration, if the sample does not cover the whole meta-population (Runge *et al.* 2006). Following Runge *et al.* (2006), total emigration rates needed for the Temminck's stint population to become a source population are extremely high for juveniles (>0.84) and adults (>0.25), requiring also extremely high survival. The same parameters for the Dunlin are lower (juveniles >0.64 and adults >0.18). Emigration of this magnitude is within a realistic range only for adult Temminck's stint (III). Therefore, the sink nature of the populations is highly probable (I, V).

3.2 Life history correlates of dispersal

The study illustrates a striking example of how immigrants can comprise a large portion (>50%) of an isolated local population. The results indicate that immigrants are essential for the viability of the local populations, and that the population dynamics of Temminck's stints is driven to a large degree by dispersal. The impact of dispersal was further illustrated by the difference in apparent adult survival probabilities between immigrant and philopatric individuals. This was found to be associated with different breeding dispersal strategies of immigrant and philopatric individuals. While immigrant birds apparently have lower lifetime reproductive success than locally born birds, reliable fitness comparisons of these strategies cannot be made. However, immigrants and locally born birds are not equally valuable in terms of local population growth.

3.2.1 Nest success and dispersal status

Reproductive success was not clearly associated with dispersal status in the Temminck's stint (II). The nests of philopatric individuals and those incubated by males survived best (II). The difference in nest success did not translate into hatchling production per breeding attempt. This can be explained in part by a decrease in the resolution of the analysis when nests not found (assumed breeding attempts) are included (II). On the other hand, because first captures are bound to nests or broods that are found, first attempts may weigh more in the success of immigrants than in that of philopatric individuals. Higher nest success of philopatric Temminck's stints could have been caused by benefits from site familiarity, *i.e.* knowledge about site specific resources (*e.g.* Pärt 1994). However, the same should apply for immigrants in the seasons following settlement, provided that they do not choose to emigrate. If immigrants are more likely to select poor territories due to *e.g.* restricted knowledge of site quality and are later faithful to their territories as Temminck's stints are, nest success and even adult survival can be consistently lower (*e.g.* Pärn *et al.* 2009).

3.2.2 Higher apparent survival for philopatric individuals

Philopatric individuals of both sexes had considerably higher apparent adult survival probabilities than immigrants in two independent life history data (called the low and high predation periods in III) separated by a time gap of 25 years (II,

III). This pattern, reflecting survival or emigration rates specific to the individual's dispersal status, is so far reported only for few animal populations (Doligez & Pärt 2008, II).

It is reasonable to expect that site familiarity and territory quality are relevant to reproductive success, however not so applicable to survival. Instead, in a long distance migratory species such as the Temminck's Stint, spending less than two months in the breeding areas, processes operating outside the breeding areas are probably more significant in determining survival (*e.g.* Evans 1991, Baker *et al.* 2004).

Only a few avian studies have reported an association between adult survival and dispersal status, and about half of them actually report higher survival for dispersers (see II and references). Higher adult survival of philopatric individuals has been reported only in a few studies concerning dispersal distance or dispersal status (Greenwood & Harvey 1976, Pärt & Gustafsson 1989, Verhulst & van Eck 1996, Daniels & Walters 2000, Hansson *et al.* 2004, Postma & van Noordwijk 2005, but see Pärn *et al.* 2009). Most of these studies are from small, geographically separated populations (Verhulst & van Eck 1996, Altwegg *et al.* 2000, Marr *et al.* 2002, Hansson *et al.* 2004, Postma & van Noordwijk 2005). In such conditions, genetic or phenotypic local adaptations might become important. In cases of high immigration, like in this study population, the descendants of immigrants comprise a large part of the philopatric individuals. This suggests that the existence of phenotypic adaptations is more likely than genetic effects that are prevented by gene flow. Alternatively, it is possible that immigrants are simply of lower quality, which can result for example from low quality natal habitats, (*e.g.* Marr *et al.* 2002) or from representing inferior phenotypes that have failed to mate or acquire territories in their natal areas (*e.g.* Altwegg *et al.* 2000).

This study examined correlates of dispersal, and thus cannot evaluate the consequences of dispersal for immigrants. The analysis does imply, however, that at least immigrants seem to do poorly when compared to philopatric individuals. However, the evolutionary stability of dispersal requires that immigrants must receive compensating benefits or reproduce somewhere else in later years (Lemel *et al.* 1997).

Dispersal-status and breeding dispersal strategies

Unsuccessful breeding Temminck's stints had a lower probability of returning than successful individuals. This suggests that unsuccessful individuals are more

prone to disperse (III). The choice to leave after failing to produce chicks was especially prominent among the immigrants, *i.e.* individuals that had chosen to move already in their natal phase. In contrast, the return rates of successful and unsuccessful philopatric breeders were similar (III). Thus, the immigrants' lower apparent adult survival (II, III) is partly explained by differences in breeding dispersal propensity (Doligez & Pärt 2008). The difference in apparent adult survival between philopatric individuals and immigrants was smaller during the period of high nest success (III), giving further support for the role of reproductive success on dispersal behaviour. Although previous movement has been shown to predict future dispersal in some avian populations (see Doligez & Pärt 2008), no evidence of behavioural responses to cues triggering breeding dispersal exists for individuals of specific dispersal status. These patterns provide an example of a mechanism on how the evaluation of consequences and correlates of dispersal can be biased by within-individual consistency in dispersal behaviour (Doligez & Pärt 2008).

In contrast to immigrants, philopatric individuals seem to be more fixed to their overall dispersal strategy, or at least do not cue on their reproductive success. The observed pattern may be based on a genetically determined sensitivity to environmental factors (Ronce 2007), but may also be affected by environmental factors experienced early in life or benefits gained from prior experience. The dispersal response of immigrants to breeding success was weaker among second time breeders compared to first time breeders (III). This could suggest that the experience gained within the first breeding year may weigh in decision making in the future (see also Schjørring *et al.* 2000).

The near absence of natal dispersal events (II) together with effects of dispersal status and breeding success suggest that dispersal distances of Temminck's stints are either long (outside the study area) or extremely short (philopatry). Hence, the dispersal distance distribution is probably bimodal instead of the unimodal flat tailed distribution described for a variety of taxa (*e.g.* Clobert *et al.* 2001). A bimodal distribution again suggests the existence of two migration morphs (Lemel *et al.* 1997). The discrete variation could be maintained by spatio-temporal variation in costs and benefits of movement (*e.g.* Bowler & Benton 2005). In the present study system, nest predation could be the main cause of this variation (Hildén 1978, Rönkä *et al.* 2006). In fact, long dispersal distances are expected when dispersal is a response to poor habitat conditions (Clobert *et al.* 2001).

3.2.3 Population growth and dispersal status

It is evident that the prognosis of the study population's future depends on whether immigration is considered in a demographic analysis (II). The results demonstrate that dispersal affects population dynamics also indirectly through vital rates associated with dispersal status (Vindenes *et al.* 2008). The low apparent survival of immigrants decreases their demographic impact. When dispersal status was considered in the models, predicted λ was higher. This was visible already from the λ derived from philopatric individuals (model C, $\lambda = 0.929$). The model including immigration and dispersal status (model D) gave the highest estimate for λ with nearly stable population growth ($\lambda = 0.972$), which is close to the λ 's derived from the number of territories ($\lambda = 0.974 \pm 0.144$).

3.2.4 Implications to local population dynamics

The results show clear links between vital rates, dispersal behaviour and conservation of populations. Irrespective of the causes of the observed survival pattern, the consequences to local (and regional) population dynamics are the same. Philopatric individuals had roughly three times higher reproductive values than immigrants. Indeed, pooled elasticities for adult survival stages were considerably higher for philopatric individuals (0.73) than for immigrants (0.13, II). Elasticity analysis also implied that an increase in local recruitment has a larger relative impact on λ than an increase in immigration (II).

Reproductive success has a major impact on the future trajectory of local populations. Increases in fecundity parameters, particularly in nest success, result in a stabilising population through an increased amount of philopatric individuals with high survival and a lowered rate of emigration of immigrants. However, such dynamics driven by reproductive success may increase extinction risks of small local populations through temporal autocorrelation of vital rates, *i.e.* making poor periods of reproduction also periods of low local survival (*e.g.* Morris & Doak 2002). These results, however, illustrate the potential for improving local adult survival through an increase in site fidelity for management purposes, which should be a profitable way to influence population growth.

3.3 Habitat management and ecological traps

3.3.1 Risks of grazing management

In a pasture with relatively low stocking rates, the trampling probability of artificial nests was almost 80% for a three week incubation period (IV). Daily trampling rates were high compared to ones reported elsewhere (IV). Trampling rates of course correlate with stocking rates (*e.g.* Jensen *et al.* 1990, Fondell & Ball 2004) but depend also on pasture specific factors (*e.g.* Ausden 2007, IV). High trampling rates are expected, when both nest sites and cattle are non-randomly distributed and coincide in their space use (Guthery & Bingham 1996). This is probably the case in the present Dunlin study area (IV). Additionally, productivity of the coastal meadows at Bothnian Bay are many times lower than that of temperate salt marshes in Europe (Niemelä *et al.* 2008), which may affect cattle behaviour, and hence trampling rates.

Trampling rates of Dunlin nests decreased as a function of time after the initiation of grazing (IV). This was probably due to high movement of the cattle during the first grazing days, but may also reflect drying of the meadow and spatial variation in suitable grazing areas for the cattle. In contrast to other studies comparing predation and trampling of wader nests, this study found trampling rates to be higher than predation rates (*e.g.* Beintema & Müskens 1987, Liker & Székely 1997, Ottvall 2005). Trampling has often been considered inconsequential due to high nest predation levels (Liker & Székely 1997, Ottvall 2005). Present results show that this is not general and even low stocking rates can cause detrimental effects on nesting success.

There was no support for the hypothesis that the presence of cattle increases nest predation (IV). Cattle can cause additional movement of parent birds to and from the nest, which may help predators to locate nests (Hart *et al.* 2002). Disturbance may also influence nest attendance and therefore the length of the incubation period, and thus increase exposure time to predators. Therefore, grazing is expected to cause increased nest predation for species that are easily flushed from their nest (Hart *et al.* 2002), and for species whose nests become more easily exposed (Baines 1990). The effect of disturbance on parents' behaviour was not quantified and therefore it is possible that the assumption of increased activity was false. However, if movement increased, the secretive behaviour of Dunlin when leaving the nest (no warning calls, generally short flushing distances) might lower the effect of nest predation.

3.3.2 Habitat specific life history: is there an ecological trap?

Settling Dunlins preferred intensively grazed pastures with short sward height (HG) over less grazed (LG) high sward habitat (VI). Individuals born in the HG habitat primarily returned there (86%) while more than half of the individuals born in the LG habitat dispersed to the HG habitat (54%). Of the 28 dispersing individuals, 68% selected HG habitat. Adults were philopatric, but 60% ($n = 10$) showed between site movements from LG to HG. Dunlins seem to prefer highly grazed pastures that because of the potential negative direct impacts caused by the grazers have the potential to work as ecological traps.

Results suggest that most Dunlins make ideal habitat selection decisions (Arlt & Pärt 2007). The more preferred habitat produced 1.8 times more recruits per female when trampling was prevented. This was due to higher hatching success which may be a result of lowered predator activity or susceptibility to predation associated with low vegetation (Koivula & Rönkä 1998, Wallander *et al.* 2006, MacDonald & Bolton 2008, Salo *et al.* 2008, Schekkerman *et al.* 2009). Juvenile survival, in turn, tended to be higher in the LG habitat. This may reflect unfavourable feeding conditions or higher visibility for avian predators at the HG habitat (Bellebaum & Bock 2009, Schekkerman *et al.* 2009).

The results suggest that the proximate cues used by Dunlin in habitat selection are adaptive (Schlaepfer *et al.* 2002). However, because Dunlins are not capable of recognising abrupt changes in habitat quality with the introduction of cattle (at least in the short term), they are susceptible to negative effects of cattle (Schlaepfer *et al.* 2002, Battin 2004). This ecological trap scenario was evaluated by simulating production of local recruits with a re-nesting model under varying grazing practices (timing, grazing pressure). All stocking rates had a substantial effect on reproductive success, but the higher reproductive success at the HG habitat somewhat buffered against trampling. The HG habitat was found to be an ecological trap for breeding Dunlin in terms of local recruitment in two grazing scenarios (high and moderate stocking rates), but the emergence of traps was largely determined by the timing of grazing (VI).

A negative effect on a life history parameter in a certain environment can be compensated by improvement caused by another effect or in another trait (Flaspohler *et al.* 2001, Battin 2004). In the present system, it is possible that the high density of cattle reduced predation by increasing the anti-predator value of the habitat. Due to the possibility of compensating effects, ecological trap studies should cover the complete life history of the population involved, *i.e.* λ

(Schlaepfer *et al.* 2002, Battin 2004, Pärt *et al.* 2007). Population growth rate of the putative trap habitat (HG) was higher than that in the LH habitat even under the worst management scenarios (VI). This was because adult survival, a parameter with high elasticity (66%), was 10% higher in the HG habitat than in the LG habitat (VI). There is no information on possible compensating effects on mortality at the breeding habitats. A lower cost of reproduction is not an option in this case, because nest success was higher in the HG habitat due to nest protection.

The answer to the existence of a trap is dependent on whether the survival difference reflects differences in adult survival or adult site fidelity. Site fidelity could explain the survival difference, if adults also considered the HG habitat to be a better and more attractive (Robertson & Hutto 2006). However, adults were generally philopatric, which is congruent with studies reporting high site fidelity, with occasional breeding dispersal after mate death, nest failure or divorce (Soikkeli 1970a, Thorup 1999, own unpublished data). Thus, it could be that the lower reproductive success at the LG habitat results in permanent emigration (III). While a correlation between adult survival and nest success could indicate also habitat differences from on-nest adult predation (Low *et al.* 2010), only few adults have been found to be killed at their nests. As described earlier, waders spend only two months at the breeding sites and are largely dependent on resources of the non-breeding sites, which suggest that causes of mortality reside outside the breeding sites (Evans 1991, Baker *et al.* 2004). It seems that if there are potential differences in site fidelity, compound estimates such as λ cannot be reliably used to compare habitat specific fitness. Thus, using the reproductive output can be considered indicative of a trap.

3.3.3 Grazing and population viability

The Dunlin population managed mostly by grazing was considered stable when nest trampling did not reduce breeding success (V). However, the fact that the stability owed to immigration suggests poor viability and that such habitat management alone is insufficient to maintain viable populations. Due to the sink nature of the study population, it was vulnerable to the additive reduction in breeding success caused by trampling. Trampling altered population growth from stable to decline, the extent varying with the stocking rates and timing of grazing. Without the rescue effect of immigration, the population had no chances of coping with any degree of trampling and faced imminent danger of extinction within the projected 20 years (V). Thus, results suggest that grazing can be

considered safe only if the immigration remains stable and if the negative impacts are reduced.

While being a trap in terms of lower reproductive success for individuals settling to the HG habitat, its impact on metapopulation viability was not drastic (VI). This was because the HG habitat had higher population growth despite the trampling effect. Higher adult survival in the HG habitat buffered against the trap. However, population persistence was dependent on the extent of immigration, which defined the final population sizes.

Examination of population persistence under no immigration and equal adult survival among habitats suggested that the observed juvenile movement rate towards the trap does increase extinction risks. However, high movement rates and a large difference in reproductive success were needed for strong increases in the extinction risk within a period of 20 years. The observed magnitude of juvenile movement (ca. 50%) from the LG habitat to the HG habitat raised extinction risks by 7% when local recruitment to HG was half of that in LG. The results can be primarily explained by the low elasticity of fecundities. Of course, longer projections would give larger differences, but then all populations would perish if immigration was zero. Instead, the movement of adults, that comprise the largest portion of the population, caused a stronger response in the extinction risks.

This result suggests that the generally high adult site fidelity among long lived wader species buffers against traps. Long lived species should also be resistant to ecological traps if individuals rely on plastic habitat choice rules such as experience based learning (Kokko & Sutherland 2001). Although, birds are known to cue on both individual and patch reproductive success when making breeding habitat choices (Lima 2009), individual characteristics such as dispersal status or site familiarity may affect decisions (Schjørring *et al.* 2001, III), and thus their resistance to ecological traps.

3.4 Validation for the re-nesting and PVA models

The predictions of models are only valid to the extent to which the data and the model structure accurately describe the system (*e.g.* Reed *et al.* 2002). In studies I, V and VI, both the re-nesting and the PVA models are based on long term life history data, and should therefore model the system well. Results from the re-nesting models are sensitive to the probability of nest replacement, information which was available in this study.

Uncertainty in the PVA model predictions resulting from simplifications (no density dependence, no genetic stochasticity) and assumptions (*e.g.* constant immigration, vital rates remain unchanged) may affect the reliability of the projections (*e.g.* Beissinger & McCullough 2002). This was controlled by using the PVA to assess management options by covering relatively short periods (20 or 50 years) and using thresholds (20 individuals or a 50% decline threshold).

Predictions from models used to examine effects of trampling on viability may be biased, if some aspect affecting the breeding success of Dunlin changes in relation to grazing, *e.g.* compensating effects caused by grazing (V). However, this aspect was controlled for in the habitat based model (VI).

3.5 Management implications

High elasticity of adult survival implies that both the Temminck's stint and the Dunlin reside at the slow end of the "slow-fast continuum" of animal life histories (Sæther *et al.* 1996, Sæther & Bakke 2000). From the management point of view, the "fast" species respond to improved reproductive success while the "slow" species respond better to improved adult or juvenile survival (Heppel *et al.* 2000, Sæther & Bakke 2000). Even though adult survival has the highest elasticity, it does not prove that it is the most promising target for management (*e.g.* Benton & Grant 1999). It is possible that management cannot enhance survival, because it is already so high or because its variance is too low (Green & Hirons 1991). In these cases management efforts should concentrate on the vital rates with smaller elasticity but higher potential for improvement (*e.g.* de Kroon *et al.* 2000).

Because of the important role of adult survival, favourable environments on migration routes and wintering sites are important for the persistence of long distance migratory waders (Piersma & Baker 2000). Recent developments suggest drastic changes in wader populations due to changes at the wintering sites (*e.g.* Baker *et al.* 2004) emphasising the need to find out specific wintering sites (Thorup *et al.* 2009).

3.5.1 Conservation of the Baltic Temminck's stint population

Life history parameters of the currently endangered Temminck's stint population seem to have declined when compared to a stable population of in the 1960s (I, Hilden 1978). Hildén's (1978) high return rates compared to the recent apparent survival estimates suggest that the population decline is best explained by a

decrease in adult survival (I). However, when return rates are replaced by more accurate apparent survival, the decrease in survival is not statistically significant (III). Moreover, the survival asymmetry can be partly explained by a decrease in the frequency of locally born birds that have higher apparent adult survival (are less prone to disperse) and a higher emigration rate of immigrants during the period of high nest predation (III).

The results suggest that the recent population decline of Baltic Temminck's stints reflects a multilevel response to increased nest predation at the Baltic region through a decrease in local recruitment and an increase in emigration (Rönkä *et al.* 2006). Thus, management of breeding sites, directed particularly to the enhancement of reproductive output is likely to have a wide impact on population dynamics. Such effects can be expected also in other populations.

The low reproductive success and low apparent survival rate of immigrants indicate that gene flow to the study population is not accurately estimated by the immigration rate (see Peery *et al.* 2009). Estimated immigration rates can be higher than 'effective' immigration, gene flow (meaning that immigrants recruit and produce recruits in the population). Reduced gene flow is in line with findings from microsatellite data, which also describe low but significant differentiation from other Fennoscandian populations (Rönkä *et al.* 2008). The impact of stochastic genetic processes will become more pronounced if the population decline continues as predicted (I). Furthermore, high natal philopatry and long life span of adults further subject local populations to inbreeding. In fact, the degree of inbreeding is higher within the Baltic population than elsewhere in Fennoscandia (Rönkä *et al.* 2008).

3.5.2 Management options for the Temminck's stint

Good visibility from the nest and presence of sentinel birds would improve the anti-predator strategy of Temminck's stint, and thus decrease the vulnerability of nests to predation (Koivula & Rönkä 1998). This can be achieved by creating or maintaining large, open and peaceful areas with low and sparse vegetation. Increasing the amount of suitable habitat in unoccupied areas would give the opportunity for colonisation. If promotion of the settlement of immigrants via conspecific attraction using decoys (Hahn & Silverman 2007) is possible, improving immigration to unoccupied areas can also be a feasible management option.

Nest success can be most efficiently increased by reducing predation pressure. Nest protection was found to substantially increase hatching success (II). However, nest protection works only in areas with specific predator fauna (Rönkä *et al.* 2006). Nest protection has the potential to cause increased adult mortality (Smith *et al.* 2011) and thereby needs constant follow-up and checking of protected nests (Isaksson *et al.* 2007, Pauliny *et al.* 2008). This makes the method costly and unrealistic in large scale conservation work. Thus, predator eradication would be the most safe and effective measure (Smith *et al.* 2010).

3.5.3 Grazing management

This study provides an example where the use of density as a proxy for the effectiveness of management may lead to false conclusions. Based on density, the highly grazed habitat (HG) would have been mistakenly classified a source. This stresses the importance of viewing management consequences in terms of not only attracting birds to managed sites (immigration) but also to examine the properties influencing life history (reproduction) (IV, V, VI). The fact that low sward habitat produced by intensive grazing (without trampling) resulted in higher reproductive success indicates that cattle grazing can be used as effective management tool for coastal meadows.

However, the results also suggest that the trampling rates caused by density recommendations of livestock (0.5–2 LSU / ha) should be applied with caution. Local pasture conditions should be taken into account when planning stocking pressure. For example, the effective pasture area, the part of the pasture actually intensively used by cattle, should be clearly identified, and stocking rates calculated accordingly.

The Dunlin population was dependent on immigration and thus susceptible to the additive destruction caused by trampling of nests. Because immigration is largely dependent on processes acting at their origin, management should be designed safely so that no immigration is assumed. This underlines the need for specific consideration of the stocking rates and the timing of grazing in relation to the life histories (nesting location, demography and breeding phenology) of the management targets.

When adjusting grazing regimes, managers fall into trade-off situations (Sabatier *et al.* 2010). Trampling can be primarily avoided by reducing stocking rates or by postponing grazing to a later date, but this may be uneconomical from the cattle owners point of view. Further, timing and intensity of grazing have also

significance in achieving habitat management goals (Tichit *et al.* 2007, Durant *et al.* 2008, Sabatier *et al.* 2010).

In the present case, high intensity grazing is needed to maintain, and especially to restore good quality low sward habitat preferred by the Dunlin. Therefore the role of timing of grazing becomes the factor to be optimised. In this specific case optimal timing is recommended, but this is based on extensive data which in general is not available for other sites or populations. Thus, in general one could recommend that the safest way would be to start grazing as late as possible. Using higher densities with late starts could be the most effective way to enhance reproductive success if low sward habitat results to improved nest success, as was found in this study. Postponement of grazing, in turn, may result to a conflict of interests between livestock grazing and conservation because a late start of grazing may not satisfy cattle feeding requirements (Sabatier *et al.* 2010). For example, in terms of beef production, the optimal time for initiating grazing on coastal meadows of the Bothnian Bay would be late May (*i.e.* mid-incubation period for Dunlin). It should not start later than in mid-June to ensure high forage quality (Niemelä *et al.* 2008).

As mentioned, acquiring data such as used in this study to estimate optimal grazing regimes for local conditions is laborious. Other strategies, such as alternating pastures between years or rotational grazing during the season, may provide tools which do not require extensive and detailed species or pasture specific information (Lapointe *et al.* 2000, Sabatier *et al.* 2010). Instead, locating breeding hot spots or otherwise sensitive areas could be possible using conventional inventory data. However, in conservation work of critically endangered species such as the Baltic Dunlin, data on at least breeding success and phenology should be acquired to weigh the impact of livestock and adjust the timing of grazing properly. In extremely critical cases, the use of laborious but effective protective cages preventing trampling and predation may markedly reduce nest losses (Isaksson *et al.* 2007, Pauliny *et al.* 2008).

4 Conclusions and guidelines for future research

Demographic modelling with population specific data indicates that both Temminck's stint and Dunlin populations breeding at the Bothnian Bay are non-viable and unable to produce enough local recruits to compensate for adult mortality or emigration. Instead, they persist through immigration. The results suggest that both species are declining due to lowered local recruitment rather than changes in adult survival. In the Temminck's stint, the recent decline reflects a multiple response to increased nest predation through decreased local recruitment and increased emigration.

Philopatric Temminck's stints born in the study area were found to have higher nest and apparent adult survival compared to immigrants. Apparent adult survival of philopatric individuals was higher in two independent datasets and the difference to immigrants was highlighted during the period of high nest predation. Immigrants had low return rates after reproductive failure suggesting that the difference in apparent adult survival is at least partly caused by different breeding dispersal strategies. Whatever the cause, this means that the demographic impact of immigrants is lower than that of local recruits. Matrix modelling showed that the estimated population growth rate was more realistic when immigration and dispersal status were included in the model. Population ecologists usually assume that dispersal status does not play an important role in demography, but this study encourages acknowledging that in some systems it may play a major role.

Population growth was most sensitive to changes in adult survival as expected in animals with relatively long life span. However, the results suggest that management directed towards reproduction has a higher impact on viability than previously thought because it also has consequences on local dynamics by affecting adult site fidelity. Directing management towards enhancing reproduction is also a more feasible option than trying to affect adult survival, which may prove to be very difficult.

Livestock grazing has been used to restore habitat and aid reproduction on overgrown meadows. While grazing has undoubtedly been vital in the conservation of the Baltic Dunlin and other species inhabiting short-vegetated coastal meadows, the results imply that it may threaten their long term viability by reducing reproduction through trampling of nests. The highly grazed habitat was preferred by young Dunlins. Because this habitat also had the highest trampling risks, it can work as an ecological trap when grazing is started too early.

However, the ecological trap did not increase extinction risks because apparent adult survival was high in the trap habitat.

The results encourage continuation of the use of cattle grazing as a management tool but at the same time they highlight the need for more detailed consideration of local grazing practices especially when sketching management plans for endangered species.

This thesis was based on population ecologist's tools in conservation biology. However, because both study population are close to what is defined as a small population (Caughley 1994), it would pay to concentrate on the role of genetic effects in these declining metapopulations (see for example Blomqvist *et al.* 2010). The small population size results to genetic drift and accumulation of harmful mutations (*e.g.* Lande 2002). Furthermore, within these small populations, observed high site fidelity, low genetic influence of immigrants and possible assortative mating in relation to dispersal status (Verhulst & van Eck 1996, Doligez *et al.* 2009) may lead to inbreeding and further loss of genetic variation, and thus reduced viability.

Genetic data would also give important information on the study of dispersal in the form of parentage analysis. Temminck's stint nests were recently found to have a high frequency of multiple paternity (own unpublished data), a factor that may bias fitness correlates of dispersal (Pärn *et al.* 2009). It is possible, for example, that site familiarity of philopatric males gives advantage in terms of copulations. Furthermore, the local recruitment of young produced by philopatrics may be higher than that of immigrants because of inherited dispersal behaviour (Doligez & Pärt 2008, Doligez *et al.* 2009). In such a case, both ecological and genetic impacts of immigration to local dynamics would be further decreased. The causes of dispersal behaviour including its genetic basis warrants further research.

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Original articles

- I Koivula K, Pakanen V-M, Rönkä A & Belda E-J (2008) Steep past and future population decline in an arctic wader: dynamics and viability of Baltic Temminck's stints (*Calidris temminckii*). *Journal of Avian Biology* 39: 329–340.
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- V Pakanen V-M, Aikio S, Luukkonen A & Koivula K (2011) Modelling the impact of nest trampling on the viability of a meadow bird population. Manuscript.
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