Habitat Selection, Nest Predation and Conservation Biology in a Black-tailed Godwit *(Limosa limosa)* Population

BY

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Dissertation for the Degree of Doctor of Philosophy in Population Biology presented
at Uppsala University in 2001

Abstract

Johansson, T. 2001. Habitat selection, nest predation and conservation biology in a
black-tailed godwit (*Limosa limosa*) population Acta Universitatis Upsaliensis.
*Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and
Technology* 610. 38 pp. Uppsala. ISBN 91-554-4958-1.

This thesis focuses on a black-tailed godwit (*Limosa limosa*) population, consisting of
35-40 pairs, that breeds on a grazed shore meadow on SE Gotland, Sweden. The small
size of the population makes it more prone to extinction due to chance events, than a
larger population.
   The godwits showed microhabitat preferences when choosing nest sites. Godwit
nests had higher vegetation over the nest cup, lower surrounding (1-3 m) vegetation
and different plant species composition, as compared to random sites. Breeding near
conspecifics or other wader species, especially lapwings (*Vanellus vanellus*) and
further away from potential predator perches were the most important factors in
decreasing nest predation. A comparison between different shore meadows along the
east coast of the island revealed that large, open areas suffered less from nest
predation. Thus, shore meadows suitable for breeding godwits should be large and
without trees or other predator perches and have a grazing regime that favours
variation in vegetation height.
   Over 80% of previously ringed adults returned each year, but very few birds
ringed as chicks were recovered. Hatching success was 55-60% for all observed nests.
To predict the future of the current population, demographic data were used in an
ecological risk analysis. The simulations showed that the Gotlandic population will not
survive the coming 40 years without immigration.
   Black-tailed godwits are divided into three subspecies. Genetic analyses
(mtDNA) revealed that all subspecies had unique haplotypes and there was a clear
geographic structure among subspecies. Within the *limosa* subspecies, godwits on
Gotland and Öland showed a high proportion of rare haplotypes, but no genetic
variation was found in Dutch birds. These results imply that black-tailed godwits on
Gotland and Öland have high conservation value.

Key words: Black-tailed godwit, *Limosa limosa*, nest site selection, nest predation,
philopatry, phylogeography, risk analysis.

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"Hennes hållning och det lilla smala hufvudet till den långa halsen äro en smärtsam påminnelse om att storken är så lite efterlängtad här i landet"

(Bengt Berg 1916)

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals **I-V.**

I.   Johansson, T. Nest site selection in black-tailed godwits (*Limosa limosa*): implications for conservation. Submitted manuscript.

II.   Johansson, T. and Thuman, K. Nest predation in black-tailed godwits: an experimental study. Submitted manuscript.

III.   Thuman, K., Johansson, T. and Höglund, J. Large open areas and high bird densities decrease predation on artificial nests. Submitted manuscript.

IV.   Höglund, J., Johansson, T., Beintema, A. and Schekkerman, H. Phylogeography of the black-tailed godwit *Limosa limosa*: substructuring revealed by mtDNA control region sequences. Submitted manuscript.

V.   Johansson, T., Svensson, M. and Ranta, E. Philopatry and risk analysis of a Swedish population of black-tailed godwit (*Limosa limosa*).

The order of the authors of the papers reflects their involvement in them. I have personally written papers I, II and V, and performed most of the analyses. Co-authors performed some of the analyses, discussed ideas and commented on the text. My co-authorship of papers III and IV reflects this as well.

CONTENTS

INTRODUCTION

The distribution of species can be fragmented. Small and more or less isolated populations often occur at the fringe of a species distribution. Such small populations run a higher risk of extinction, as compared to larger ones (Gilpin & Soulé 1986, Burgman et al. 1988). In this thesis, I have studied one such small population; the black-tailed godwits (*Limosa limosa*) on Gotland. I have focused on nest predation, because this is an important factor affecting breeding success and hence the growth rate of a population (**II** and **III**). I have also studied habitat choice, because this is of prime importance in defining where organisms breed (**I**). In paper **IV**, I studied the mtDNA genetic structure of black-tailed godwits. There were two aims with this genetic study: 1) to obtain an indirect measure of migration between Gotland and other populations, 2) to study whether the Gotlandic population is genetically different from other godwit populations. This is potentially important, when deciding on conservation measures. If the population does not differ from other populations, then the extinction of the Gotlandic godwits could be considered less of a problem. If unique, an argument for the preservation of this particular population is strengthened. Lastly, I have studied the demography of the current population and performed an ecological risk analysis to determine the survival prospects of the population (**V**).

Habitats differ can differ in for example, food availability, vegetation structure and composition, intra- and interspecific competition, predator abundance, access to mates and suitable breeding sites (Cody 1981, 1984, Skeel 1983). Habitat selection is the choice made by individuals of a species on where they spend their time (e.g. Partridge 1978). This is likely to affect individual choices at several levels. First, a general habitat has to be chosen, second, the individual has to decide exactly where to breed within this general habitat. Previous studies have shown that, although many wader species share a general habitat, they vary in their specific habitat choices (e.g. Skeel 1983, Berg 1992a, 1993, Pampush & Anthony 1993, Johansson & Blomqvist 1996). Nest site selection can be divided into two main categories; access to food and anti predator strategies. An example of how food supply may affect nest site choice is when the food required by chicks is different to the food required by adults (Blomqvist

& Johansson 1995). The anti predator tactics can include, for example, breeding a long distance from perches used by avian predators (Sullivan & Dinsmore 1990, Berg et al. 1992), breeding in higher vegetation and thus hiding from predators (Hill 1984, Sugden & Beyersbergen 1986, Crabtree et al. 1989), and breeding near aggressive species or conspecifics (Stamps 1988, Göransson et al. 1975, Dyrcz et al. 1981). However, a nesting site, minimising nest predation and maximising foraging, may not exist, and therefore a conflict (trade-off) between these two demands may arise.

Nest predation is one of the major factors decreasing nesting success in birds (e.g. Nolan 1963, Johnson et al. 1989, Martin 1993a). In many bird species, the possibility to decrease nest predation may therefore have an important role for habitat selection (Martin 1993b). The different wader species show different behavioural tactics to avoid nest predation (Cramp & Simmons 1983, Gochfeld 1984). Some species, like black-tailed godwits, lapwings (*Vanellus vanellus*) and curlews (*Numenius arquata*) are very aggressive towards predators and often attempt to chase them away (Lind 1961, Cramp & Simmons 1983, Berg 1992b). Other species are less aggressive, instead of chasing, more often they only use alarm calls. Small species, such as ringed plovers (*Charadrius hiaticula*) can use distraction displays ("broken wing") to lead the intruder away from the nest or young (Gochfeld 1984). The most timid species rely upon vegetation cover and camouflage when protecting their nests. The intensive mobbing behaviour of aggressive species can reduce predation risk (Göransson et al. 1975), not only for the mobbing species, but also for timid species nesting nearby (Dyrcz et al. 1981, Eriksson & Götmark 1982). For species nesting on the ground, like waders, it is possible that the vegetation structure will affect the intensity of nest predation. A nest in a meadow of homogeneous, close-cropped vegetation will be more obvious than a nest in taller and heterogeneous vegetation (Bowman & Harris 1980, Hill 1984, Baines 1990).

Small populations, as compared to large, suffer from a much higher risk of extinction, due to demographic and environmental stochasticity (Burgman et al. 1988). Demographic uncertainty can be defined as the chance variation in individual birth and

death rates. In small populations extinction can occur accidentally and the population will not be safe until a large enough number of individuals are reached (Gilpin & Soulé 1986). Environmental stochasticity can be referred to as any changes in the habitats, and includes both decrease in habitat quantity and deterioration in environmental quality (Gilpin & Soulé 1986, Ranta et al. 1996). Small populations may also be negatively affected by inbreeding depression and genetic drift (e.g. Burgman et al. 1988).

Several terrestrial vertebrates are faithful to their natal and/or breeding areas (Greenwood 1980). Among waders, several species have been shown to have strong breeding area fidelity (adult philopatry) (Soikkeli 1970, Skeel 1983, Gratto et al. 1985, Thompson & Hale 1989, Groen 1993). In the wader family Scolopacidae (sandpipers and allies), adults are more likely to return to the same breeding area, than are juveniles breeding for their first time (Oring & Lank 1984). Between the sexes, females often disperse more, both as adults and juveniles (Greenwood 1980). There can be different advantages of a strong philopatry, e.g. greater familiarity with environmental factors (e.g. food, cover, predators) and/or familiarity with conspecifics (mates and relatives) and other species (e.g. Hinde 1956). However, since philopatric populations remain in the same breeding area, there might be a higher extinction risk for such local populations (Kruk et al. 1998).

The phylogeography of any species is of interest because it aids in identifying the processes that may lead to genetic differentiation between local populations (Avise et al. 1997, Avise 2000). Studying genetic variation and its geographic structure is thus of major importance in understanding how populations evolve to become separate species. From a conservation point of view, it is not always the case that a current single species is the "unit" worth considering for conservation, but instead subspecies or local populations may have a high conservation value. Subspecies or isolated populations may have very limited gene flow with other different geographic areas and

may therefore be regarded as individual taxa (Rojas 1992, Barrowclough & Flesness 1996).

METHODS

Natural History of the Black-tailed Godwit

The black-tailed godwit belongs to the family Scolopacidae (sandpipers and allies), subfamily Tringinae. They breed in loose colonies (semi-colonial) and seem to be strictly monogamous (Lind 1961). The female is slightly larger and paler than the male. The males perform different ceremonial flights to attract females and/or to advertise their presence to other males. They are active and aggressive nest defenders against predators. Both parents incubate the, usually four, eggs and both also take care of the young until fledging (Lind 1961, Green et al. 1990). Incubation time is 22-24 days (Lind 1961). The chicks are nidifugeous and leave the nest within 24 hours after hatching, to forage on insects in higher grass vegetation (Beintema et al. 1991).

The black-tailed godwit is divided into three discrete subspecies. The nominate subspecies (*L. l. limosa*) breeds in western and central Europe; from England in the west to the Yenisey River in Russia in the east, and from southern Norway and Sweden in the north, to Italy in the south (Cramp & Simmons 1983, Beintema & Melter 1997). The preferable breeding habitats are grassland, moorlands, (shore) meadows and fens. They over-winter in freshwater habitats in western Africa (Mali, Senegal, Guinea-Bissau and Mauritania). About half of the European population, 130 000 – 250 000 breeding pairs, inhabit the Netherlands (Beintema & Melter 1997). The *islandica* subspecies, 5 000 – 15 000 pairs, are found on Iceland, Scotland, northern and central Norway (Cramp & Simmons 1983). Their appearance differ little from the nominate subspecies, but the bill and tarsus are slightly shorter. They breed on subarctic tundra and over-winter along the Atlantic coast, from Britain to Morocco (Beintema & Melter 1997). The subspecies *melanuroides* breeds in Siberia, from east of the Yenisey River and to the Pacific Ocean. These godwits are larger than their

European conspecifics (Groen & Yurlov 1999) and they over-winter in India, SE Asia and Australasia (Beintema & Melter 1997).

There is a negative population trend for most of the European black-tailed godwits (Beintema & Melter 1997). The decrease in numbers is mainly due habitat destruction; drainage or changes in agricultural activities, which leads to lower hatching success. The vegetation in abandoned grazing areas has been taken over by tall grass vegetation and bushes.

In Sweden, there are no more than 275 breeding pairs (Svensson et al. 1999). They are mainly divided among three small fringe populations; on the two large islands (Öland and Gotland) in the Baltic and in the province of Scania in the south. The black-tailed godwit is categorised as "vulnerable" in the red list of Swedish species (Gärdenfors 2000), most likely due to the decline of grazed shore meadow areas during the last decades (Johansson et al. 1986). The godwits on Gotland used to breed on bogs, but many of these habitats were drained in the 1960s, so most of the godwits switched to grazed shore meadows (Högström 1975). At present, there are about 50 breeding pairs, of which 35-40 breed at the same shore meadow – Faludden.

Study Area and Population

The main study area has been Faludden (57°10'N, 18°20'E), on the east coast of southern Gotland, Sweden, in the Baltic. (Fig. 1) It is an open shore meadow, predominantly grazed by cattle, but also by sheep in some smaller areas and to a lesser extent, by horses. This peninsula of 450 hectares is dominated by different grass species (*Agrostis* ssp, *Bromus* ssp, *Festuca* ssp, *Poa* ssp) and sedges (*Carex* ssp, *Luzula* ssp), intermixed with a few isolated trees and bushes. Faludden has a long tradition of farming activities and has been used for grazing and harvesting for many centuries (L. Jakobsson, pers. comm.).
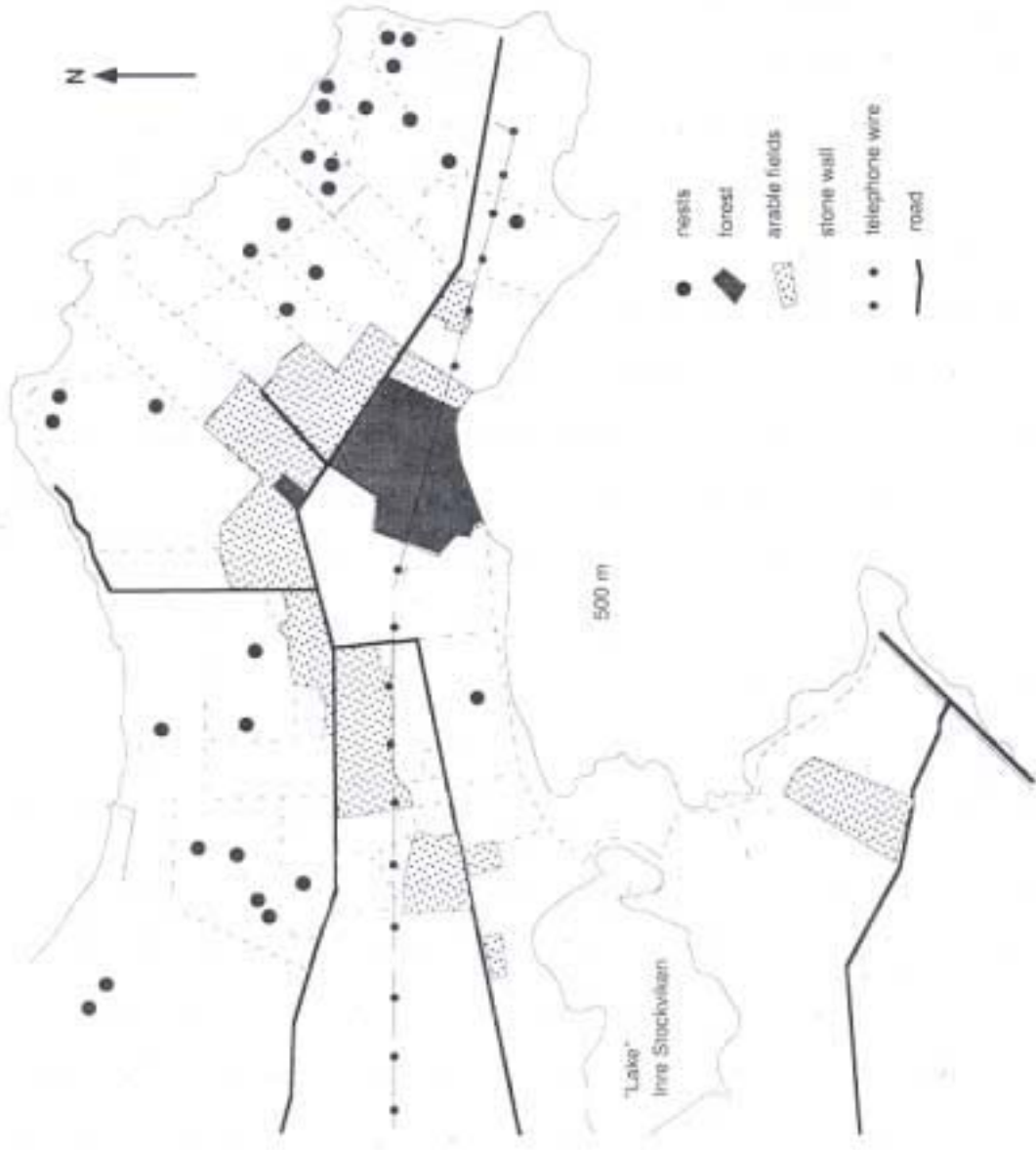
Figure 1. Map over the study area on SE Gotland. Last years' (2000) nests plotted, as an example of where the godwits breed.

Many other wader species also use this large shore meadow for breeding, such as avocets (*Recurvirostra avosetta*), common snipe (*Gallinago gallinago*), curlews, dunlins (*Calidris alpina*), lapwings, oystercatchers (*Haematopus ostralegus*), redshanks (*Tringa totanus*), ringed plovers, ruffs (*Philomachus pugnax*) and turnstones (*Arenaria interpres*). The adult godwits arrive to Faludden in late March/early April. The eggs are mainly laid in the second half of April, so most of the clutches hatch in the middle of May. However, a few nests (re-nesting) can still remain until the middle of June.

General Methods

The field studies were performed from mid-April to mid-June, during 1996-2000. When searching for nests, the birds were followed from a distance using binoculars and telescopes and a few times a hide was used. Each nest found was marked with 1-4 yellow tags (5.8 cm in diameter), five meters from the nest. In addition, I sometimes used natural landmarks (stones, bushes etc). The adults were caught by using a trap placed above the nest. The trap had the shape of a cylinder (about 75 cm in diameter) with a small entrance. Most of the incubating birds were possible to catch and no negative effects of the handling were detected during the rest of the (or following) breeding season(s). Since both sexes incubate the eggs (at least during daytime), it was possible to ring both parents. Each adult bird was ringed with a metal ring and three colour rings, for individual recognition from a distance. Shortly after hatching (within 6-24 hours), the chicks were marked with a metal ring only.

Godwit Nests

At each nest found, vegetation height and plant species composition was recorded (**I**). For measuring vegetation height, I used a piece of cardboard (28.5 x 19 cm; 18.9 grams) with a hole in the middle and a measuring stick (Ekstam & Forshed 1996). The stick was inserted through the loosely fitting hole in the cardboard. The cardboard was dropped from one meter and slided down the stick. Vegetation height was measured

(to nearest cm) from where the cardboard rested against the vegetation. This was done above the nest cup, one and three metres east, south, west and north, respectively. A mean vegetation height was calculated from these eight measurements. The difference between vegetation height over the nest cup and around each nest was also calculated. Plant species composition was checked 1 m^2 around each nest (**I**). The species were scored as either present or absent and only higher plants were included. This procedure was done, during 2-3 days, in the beginning of June. The data was analysed by using canonical correspondence analysis (CCA) in CANOCO (Ter Braak 1987). A CCA computes eigenvalues along the first canonical axis for all nests in the study. I tested whether the eigenvalues differed between the two nest categories (godwit nest or random site) by running 1000 Monte-Carlo simulations within the CANOCO package. Other measured parameters were distances to potential avian predator perches and distance to nearest neighbouring godwit nest (**I-III**). A comparison of hatching success between nests classed as clustered or dispersed was also performed (**I**).

Artificial Nest Types

In paper **I** godwit nests were compared to random sites. These sites were not actual nests but just sites where the same measurements were made, as for godwit nests. This comparison was performed to see if godwits had specific demands when choosing nest sites. In paper **II**, artificial nests were placed in tussocks at three different locations; "nest site", "territory" and "study area". "Nest site" nests were placed 1 m north, "territory" nests 175 m east of a godwit nest and "study area" nests were randomly placed within the study area. All these artificial nests were marked, as godwit nests.

Two experiments were conducted. The first was designed to test if the choice of nest place within the shore meadow was important, i.e. if predation rates differed between "nest site" and "study area" nests. The second experiment was created to see if active nest defence by godwits could prevent other nests from being depredated. Since the maximum attack-distance by godwits is suggested to be 150 m (Lind 1961), we placed the artificial nest just outside the defensive range. By comparing artificial

nests inside the territory with nests outside, the effect of nest defence was investigated, In paper **III**, the intensity of nest predation in six different shore meadows along the southeast coast of Gotland was studied. On each meadow, five lines, constituting five artificial nests, were placed at random. The nests within each line were separated by 15 meters. This experimental set-up allowed us to use a nested ANOVA analysis. Three of the shore meadows were regarded as narrow (< 300 m) and three were wide (> 400 m). Furthermore, within each category (narrow and wide), there was one site with high, one with intermediate and one with low bird density.

The artificial nests contained fresh, light-brown chicken eggs and plasticine eggs, similar in colour and size. The plasticine eggs had a wooden centre with a wire loop attached to a 15-cm metal hook, securing the eggs to the ground. The imprints made by the predators on the plasticine eggs were used for predator identification.

Bird censuses

A bird census was done to obtain data on the number of nesting waders in the immediate area around the artificial nests (**II** and **III**). The count was done by walking up to each artificial nest or line and counting the number of waders that were seen or heard. The following species were present in one or more nesting areas: avocet, black-tailed godwit, common snipe, curlew, dunlin, lapwing, oystercatcher, redshank, ringed plover, ruff, and turnstone. Only lapwings and redshanks were included when calculating the effects of nesting bird density (**III**), as these two species were the most common and widespread in the study areas. Their combined numbers were highly correlated with total bird density (r = 0.95, p < 0.0001). Including all species did not affect the outcome of the analyses.

Phylogeography (IV)

To study whether Gotlandic godwits are genetically different from other populations and therefore potentially a "conservation unit", blood or tissue samples were collected

from breeding birds from a large part of the breeding range. All three subspecies (*islandica*, *limosa* and *melanuroides*) were included, together with two hudsonian godwits (*Limosa haemastica*) breeding in northern Canada. We sequenced 334 base pairs of the mitochondrial control region for 109 birds and analysed the phylogeographic pattern within this sample by calculating population subdivision, migration rates and an intra-specific phylogeny.

Risk Analysis (V)

An ecological risk analysis was performed to predict the risk of the Gotlandic population going extinct. Risk analysis is a widely used method in conservation biology (Burgman et al. 1993) and has recently been shown to be an accurate method to assess the future of threatened populations (Brook et al. 2000). Demographic parameters in the models below were taken from data of ringed birds. The models were run with broad ranges of the included parameters. Stochasticity was included by assuming that the number of deaths, the number of hatched eggs and the number of surviving chicks, will vary randomly within the binomial distribution. The purpose of these models was to determine the relative significance of demographic stochasticity for the Gotlandic godwit population. The following model was used:

$$N_{t+1} = (N_t * p_{sa}) + (N_t * f * p_h * p_{sj})$$

Here p_{sa} is the proportion of adults surviving to the next year, f is fecundity (the number of eggs laid per female), p_h proportion of eggs that hatch and p_{sj} proportion of juveniles surviving their first year. The model used female bias; meaning only females were taken into account and assumed that all females laid four eggs of which two were females. The model used discrete time steps and no density dependent effects were included.

Another model was aimed to quantify the needed number of recruits for population persistence. Recruits could be immigrants or individuals produced within

the population. This exploration was done by two differing approaches. In the first attempt, recruits were added as constant numbers each year. The number of adults surviving each year was assumed to vary within the binomial distribution. In the second attempt, recruits were added randomly within the negative binomial distribution (negbin n, 0.5). The usage of this distribution was to mimic different numbers of recruits added between years. Most years lower numbers than average were added, but in some good years, larger numbers were recruited to the population.

RESULTS AND DISCUSSION

Nest Site Selection (I)

Black-tailed godwits showed microhabitat preferences when choosing nest sites. In the comparison between godwit nests and random sites, 73 nests of each category were analysed. All measured parameters, except plant species composition were entered into a Log Likelihood logistic regression (Table 1). The godwit nests had higher vegetation over nest cup and the surrounding vegetation was lower, as compared to the random sites. Apparently, the godwits do not seem to maximise the concealment of their nests. The lower vegetation around the nest may allow the incubating bird to have better view of the surroundings and thereby possibility to detect predators in advance (Dyrcz et al. 1981, Burger 1987). I also found that Godwit nests tended to be further away from potential avian predator perches than expected by chance.

Plant species composition in the 1 m^2 surrounding area of the godwit nests differed significantly from that of random sites. The probability of achieving a higher than observed eigenvalue along the first canonical axis by chance was 0.001, as obtained from the Monte-Carlo simulations. Six plant species were exclusively found at godwit nests, while 35 species were found only at random sites. If the godwits should have had no preferences when selecting a nest site, the number of exclusive plants would be more or less equal between godwit nests and random sites.

Table 1. Mean and ± SD of parameters for godwit nests (*n* = 73) and random sites (*n* = 73). Logistic regression with nest type (godwit nest or random site) as dependent variable. Df = 1 in all cases. Goodness of Fit = 147.18. The final model was significantly different from the null model (no variables included), (χ^2 = 111.49, *n* = 146, df = 4, *P* < 0.00001). There was no difference in mean vegetation height or distance to neighbours, these parameters were therefore omitted from the final model. The model classified 88.4% of the cases correctly.

Included Variables	Godwit Nests (mean ± SD)	Random Sites (mean ± SD)	-2 Log LR	p-value
Vegetation height over nest (cm)	12.10 ± 3.55	8.85 ± 6.96	12.84	0.0003
Diff. between veg. height over nest cup and surroundings (cm)	5.15 ± 2.66	-0.97 ± 3.56	85.07	< 0.00001
Distance to perches (m)	312.3 ± 172.1	211.6 ± 170.9	3.74	0.053
Difference between years			3.56	0.059
Not Included Variables				
Distance to neighbours (m)	193.0 ± 247.4	300.7± 192.6		0.11
Mean vegetation height (cm)	7.52 ± 2.65	9.71 ± 6.10		0.49

The plant species that predominated at godwit nests, and were less abundant at random sites, were species preferring fertile and/or mesic habitats (Mossberg et al. 1992). Most of the plant species that were predominantly found at random sites, and were less abundant at godwit nests, were species that either prefer dry and sandy habitats or mesic/moist habitats (Mossberg et al. 1992). It thus appears that the black-tailed godwits on Faludden prefer fertile and mesic, over dry and sandy habitats and they seem to avoid extremely wet or moist environments.

There were no differences between hatched and depredated godwit nests in any of the vegetation parameters, including plant species composition (Table 2). However,

hatched nests were more often clustered and further away from potential avian perches. A cluster of aggressive conspecifics and other species may be more efficient to chase predators away (Elliot 1985, Berg et al. 1992). Breeding away from predator perches also seems to decrease nest predation.

Table 2. Mean and ± SD of variables for hatched and depredated godwit nests ($n = 40$ and $n = 33$, respectively). Logistic regression with hatched versus depredated godwit nests as dependent variable. Df = 1 in all cases. Goodness of Fit = 70.47. The final model was significantly different from the null model (no variables included), ($\chi^2 = 14.26$, $n = 76$, df = 2, $P < 0.001$). There was no difference in any of the vegetation height parameters and no difference between years, these parameters were therefore excluded from the final model. The model classified 64.4% of the cases correctly.

Included Variables	Hatched (mean ± SD)	Depredated (mean ± SD)	-2 Log LR	p-value
Distance to predator perches (m)	280.3 ± 153.1	205.8 ± 105.3	5.64	0.018
Clustered or Dispersed			8.30	0.004
Not Included Variables				
Vegetation height over nest cup (cm)	11.83 ± 4.01	12.42 ± 2.92		0.52
Mean vegetation height (cm)	7.48 ± 2.90	7.56 ± 2.35		0.82
Diff. between veg. height over nest cup and surroundings (cm)	4.89 ± 2.55	5.47 ± 2.80		0.49
Difference between years				0.14

Nest Predation (II and III)

In these two studies, I conclude that high bird densities, higher vegetation height over the nest cups and longer distances to potential avian predator perches increase the probability of avoiding nest predation.

It seems reasonable to assume that artificial nests can be used to estimate nest predation on shore meadows, as there was very similar predation rates between godwit nests and artificial nests placed one meter away ("nest site"). In four out of five occasions, both nest types were depredated at the same time or at least during the same three day period. However, there was a significant difference in the risk of predation between artificial nests placed close to godwit nests ("nest site") and artificial nests at random sites ("study area"). The main differences, except for the immediate proximity of the breeding godwits, was that there were many more breeding waders of other species around, and the higher vegetation over the nest cup in "nest site" nests, as compared to "study area" nests.

Among the wader species breeding in the area, the number of lapwings showed the highest correlation with decreasing nest predation, since successful nests had significantly more lapwings in the vicinity of their nests. Lapwings are aggressive nest defenders and their intensive mobbing may reduce predation risk (Göransson et al. 1975), not only for themselves, but also for timid species nesting nearby (Dyrcz et al. 1981, Eriksson & Götmark 1982). Surprisingly, no such effect of black-tailed godwits was detected when comparing "nest site" nests and "territory" nests (just outside the defensive range of the godwits), because there was no significant difference in predation rate between these two categories. The mean distance to potential avian perches was significantly longer for successful, as compared to depredated artificial nests (Mann-Whitney U-test, N=53, z=53, p<0.0001, Fig. 2). This result indicates that avian predators can detect a nest or nesting activities from perches and thus waders nesting further away have a better nesting success.
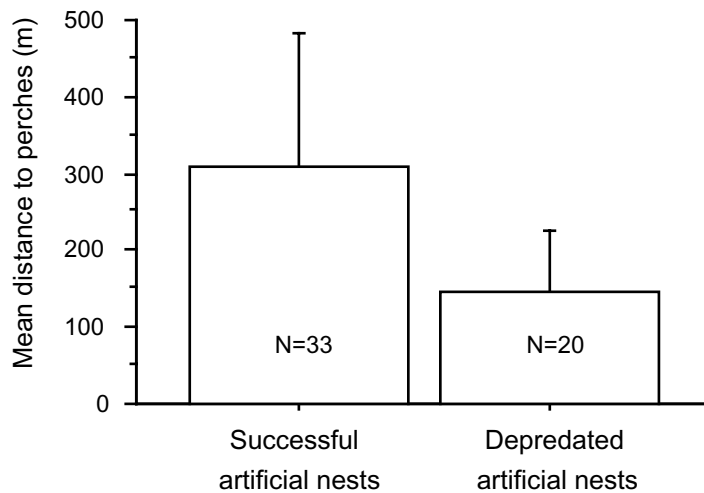
Figure 2. The difference in mean distance to perches between successful and depredated nests (mean ± SD). Only artificial bird depredated nests were included ("nest site", "territory" and "study area"). There was a significant difference ($P < 0.0001$), such that depredated nests were closer to perch sites (trees and telephone poles).

When comparing different shore meadows on Gotland, both a high bird density and large size were important factors in decreasing nest predation. Thus, wide meadows suffered less from nest predation as compared to narrow ones. Furthermore, nest predation was negatively correlated with bird density on both wide and narrow shore meadows, implying that the presence of aggressive wader species deters potential predators, concurring with the results above (Fig. 3).

Crows and gulls seemed to be the main nest predators on shore meadows on Gotland. They depredated equal numbers on wide meadows, but crows depredated more nests on narrow ones. If assuming that gulls enter the meadows from the shoreline, it does not matter how wide the meadow is. Crows, on the other hand often enter from inland, therefore the size of the meadow may have an effect of decreased nest predation. Since crows often use trees and other perches when searching for nests, a wide meadow may provide a larger distance between perch site and wader nests. Mammalian predators are very scarce on Gotland. Foxes (*Vulpes vulpes*) depredated only a few of the artificial nests.
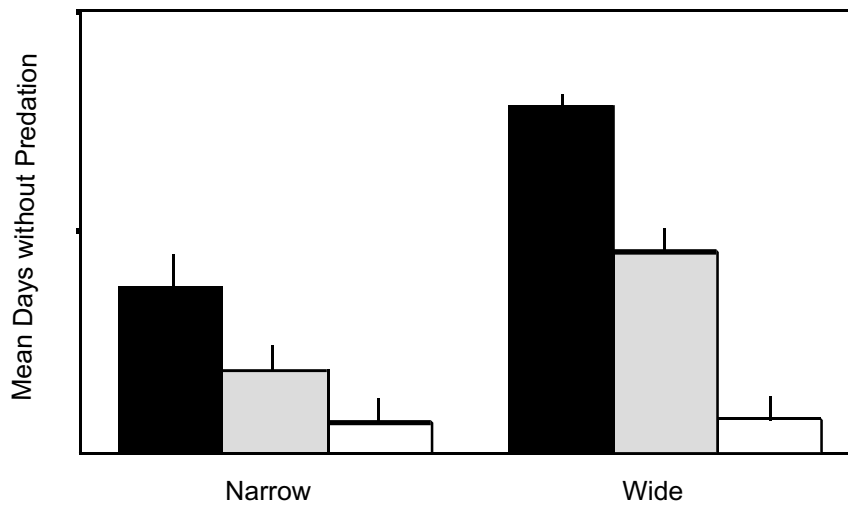
Figure 3. Days without predation (mean ± SE) in relation to the 2 categories wide and narrow shores and bird density. Black bars indicate high, grey bars intermediate and white bars low bird density.

Phylogeography (IV)

In total, we found 13 unique haplotypes among 109 sequenced individuals. Three of the haplotypes were common and each of these was unique to one of three subspecies (*islandica*, *limosa* and *melanuroides*). Other haplotypes were rare, i.e. found in four individuals or less, and were private to each one of the sampled populations. These results suggest that the three black-tailed godwit subspecies are clearly separated with little, or no gene flow among them. All intraspecific variation was due to either one or two base substitutions. The difference between hudsonian godwit and *limosa* subspecies was 14 substitutions (4.6%), which suggests that hudsonian godwits have been genetically isolated from the black-tailed godwits for a long time. Haplotypes were clearly geographically structured. Within *limosa*, most individuals (87%) had the common haplotype, regardless of geographic origin. However, 8 out of 23 (35%) of the birds sampled from Öland and Gotland, had haplotypes unique to these locations. All four birds sampled within the *melanuroides* subspecies (from eastern Siberia) had

a unique substitution that differentiated them from the other populations and subspecies.

An analysis of the molecular variance among black-tailed godwits revealed significant genetic structuring at all levels of analyses. About half of the genetic variation was accounted for between subspecies. Only about three percent of the variation was accounted for within subspecies, which however, was significantly more than expected by chance (Table 3). However, we only had access to extensive geographic sampling within the *limosa* subspecies; birds from the other two subspecies were sampled at closely situated geographic locations. Furthermore, 46 % of the genetic variation was accounted for within populations.

Table 3. Analysis of molecular variance (Distance method: Tajima & Nei 1984).

| Source of Variation	df	Sum of Sq	Fixation index	% of Var.	P-value
Among subspecies	2	20.70	0.51	50.53	0.05
Among pop. within subspecies	4	3.82	0.07	3.47	0.000
Within populations	104	44.72	0.54	46.00	0.000
Total	110	69.24	1.12	100	

The two subspecies *islandica* and *melanuroides* showed very limited gene flow with all other populations. Within the *limosa* subspecies, the population breeding on Öland and Gotland was significantly differentiated to all other populations, except for the Estonian/Moscow population. Between the other *limosa* populations, there seem to be extensive gene flow. These results indicate that the black-tailed godwits breeding in the Baltic basin and especially on Gotland may harbour unique genetic variation not found elsewhere. Thus, Gotlandic godwits tentatively qualify as a "conservation unit".

However, such a conclusion should ideally await further analyses, when more data on mt-DNA and also nuclear genetic variation should be sampled.

**Philopatry and Risk Analysis (V)**

During the field periods (1996-2000), 34 males and 36 females have been individually colour marked. Most (>80%) of these ringed adults returned each year. Hatching success was also high; 56.8% of all observed nests were successful. However, the return rate of ringed chicks was very low, provided that all chicks return to their natal area as adults. Only two individuals breeding as adults have been caught and a few more adults with just a metal ring have been seen in the study area, meaning that only 2-3% of all ringed chicks returned to their hatching area. The same return rate was found in the Netherlands (Groen 1993). The mate faithful pairs laid next years' nest significantly closer to previous years' nest, as compared to pairs with new mates (Fisher's Exact test $p=0.0058$, Fig. 4). One reason for this difference may be due to that females with new mates follow the males to their respective "breeding territory", as female birds often disperse more (Greenwood 1980).

Figure 4. The distance between the previous and the new nest site for different pair constellations. Numbers above bars are sample sizes.
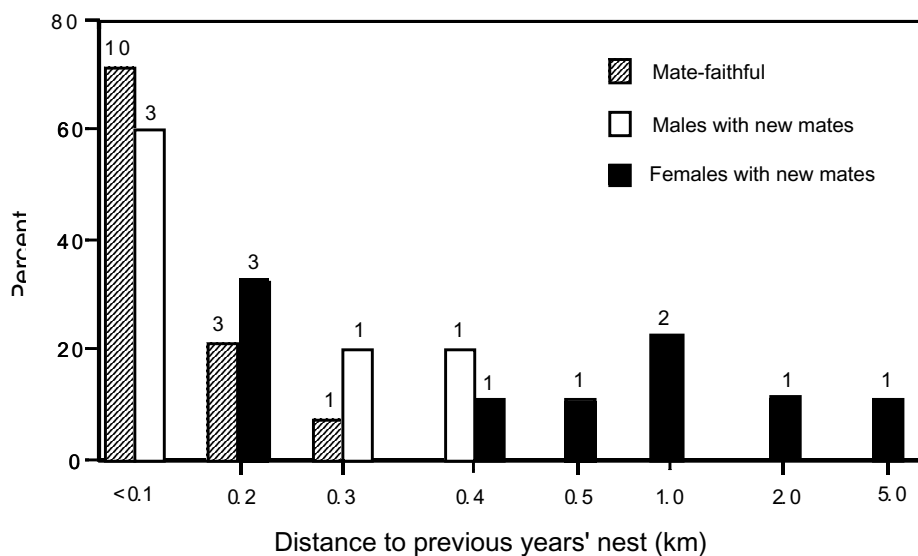
Successful pairs laid the following years' nest closer, as compared to depredated nests (G-test: χ^2=34.00, df=7, p<0.001, Fig. 5). Also in this respect, were the results in concordance with Dutch studies (Groen 1993).

Figure 5. The distance between the previous and new nest site for hatched and depredated nests. Numbers above bars are sample sizes.
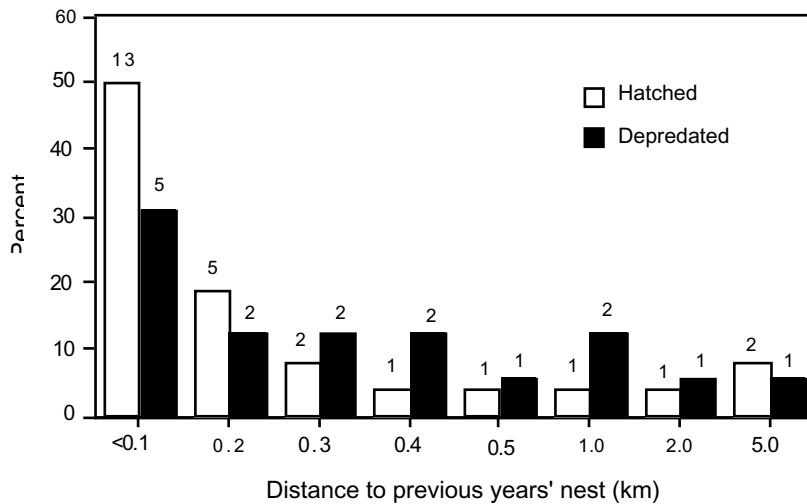

Most risk analysis simulations we have performed concern hypothetical conditions, although certain features of this actual black-tailed godwit population can be assessed. We have no data on survival from hatched eggs to fledged juveniles from the current godwit population, but at least two individuals ringed as chicks have returned as breeding adults. When knowing adult survival and hatching success, juvenile survival (from hatched young to the following breeding season) can be estimated for population persistence. With an adult survival of about 80%, juvenile survival has to be at least 0.2 for a 10% risk of population decrease (Fig. 6 A). In a similar way, with a hatching success of 0.55-0.6, the juvenile survival has to be 0.2 for a low risk of population decrease (Fig. 6 B). Thus, there is a high risk of population decline for the estimated values of the demographic parameters. To maintain the population at the current level there is a need for external number of recruits.

Figure 6. Simulation of demographic stochasticity for different parameters. Curves indicate isoclines for population decrease. Thus, in the area below the 90% isocline (p = 0.9) the population declined in 90% of all simulations, below the 50% isocline (p = 0.5) this occurred in half of the simulations, while above the 10% isocline (p = 0.1) a decline was observed in 10% of the simulations. **A)** Simulated for 40 years and hatching success of 0.567, and **B)** Simulated for 20 years and adult survival of 0.808.
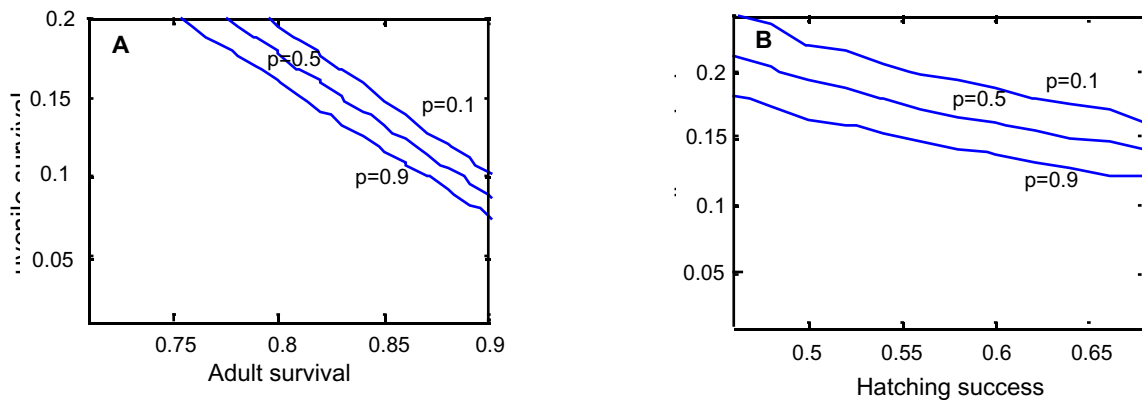
If adding a constant number of recruits to the population each year, the population need at least 17-18 recruits, given an adult survival of 0.8 (Fig. 7 A). If instead, recruits are added annually from a negative binomial distribution, at least 24 individuals are needed each year. Furthermore, the increase is unproportionally higher at lower adult survival rates (Fig. 7 B).

Figure 7. Number of recruits needed to maintain the population. Curves indicate probabilities of population decrease, p = 10%, 50% and 90% respectively (see Fig. 6 for explanation). The initial population size was 80 individuals. **A)** Recruits added as constant number each year, and **B)** Recruits added randomly from a negative binomial distribution (negbin *n*, 0.5).
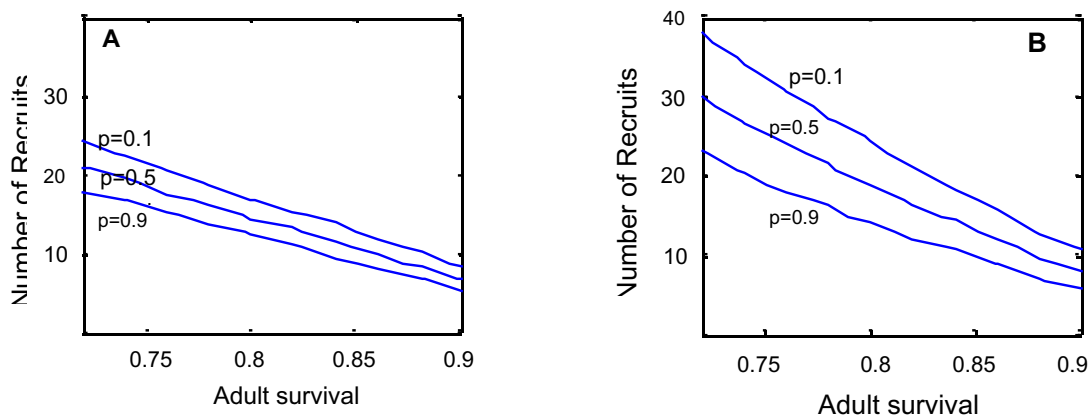
CONCLUSIONS

Black-tailed godwits showed specific nest site preferences within the shore meadow. Godwit nests, as compared to random sites, had higher vegetation over the nest cup but the surrounding (1-3 m) vegetation was lower. Plant species composition 1 m^2 around the nests was also different. It seems as the godwits prefer to breed in fertile and mesic, over dry and sandy habitats and avoid wet or moist environments. Furthermore, the successful godwit nests were more often clustered and further away from potential avian predator perches, as compared to depredated nests.

The nest predation experiments using artificial nests revealed almost the same results, as for godwit nest. The main factors for decreasing nest predation were high bird density, high vegetation over nest cup and longer distances to predator perches. Among the breeding waders, the number of lapwings had the highest correlation of decreasing nest predation. We could not detect such an effect for black-tailed godwits. Crows and gulls were the main nest predators.

The adult godwits showed a strong breeding area fidelity; over 80% of the colour-ringed birds returned each year. There was no difference between the sexes. More than half of the nests hatched each year. However, the return rate of ringed chicks was very low; only 2-3% was seen breeding as adults in their natal shore meadow (Faludden). Mate-faithful pairs laid next years' nest significantly closer to previous years' nest, as compared to pairs with new mates. The ecological risk analysis concluded that the Gotlandic population will not persist without immigration. To maintain the population at current level, there is a need for at least 17 recruits every year.

From the genetic study, it seems that the Gotlandic godwits harbour unique genetic variation, not found in the mid-European godwits or other populations. Therefore, the black-tailed godwits on Gotland tentatively qualify as a "conservation unit" and the preservation of this population is strengthened.

ACKNOWLEDGEMENTS

Despite living in Stockholm, I have to admit that Uppsala is a great place, at least when doing your PhD, otherwise I prefer many other places, in more temperate climate zones.

First of all, I would like to thank my supervisor Jacob Höglund, for always having time for my 1000 and one questions, reading manuscripts and for being a good friend. We have had many discussions, not necessarily about science, but more often about football, bandy and music. I am also grateful to the former head of the department, Staffan Ulfstrand, for his inspiration and fascination about evolution, birds and elephants. When Staffan retired, Mats Björklund took over, and I suddenly became a hybrid, belonging to both (or neither?) the department of animal ecology and population biology. I am pleased that Mats and Jacob solved the practical problems with this peculiar situation.

To my bald-headed brother, Måns – "the crazy diamond"- I am indepted for sometimes letting me stay in his minimal apartment (the submarine) when life was a struggle, and for all the fun in California and Africa, on Gotland, and in Uppsala, and for the "Nick Cave-mys". Johan W – thanks for reading and giving comments on some of the manuscripts, and for all discussions about life and everything. In you I have found a real friend. Another good friend; Jobs-Kalle ("Piglet") should also be thanked for the golf-tournaments, for sometimes lending me a mattress and for the violin.

The weeks in Namibia, Botswana and Zimbabwe with Staffan, Janne, Sami, Susanne, Camilla, Ineke, Sara, Anna and Måns are not easily forgotten. Thank you all for a tremendous time. I shall never forget MAP Ives for his great knowledge about African nature.

Thanks to; Fredrik for sharing Faludden with me without too many problems, Putte for playing reggae-music late night at parties, Lisa and Maria for sharing office at Zootis, David for introducing me to the world of computer games and for solving most of the problems with the grey box in front of me, Arne for all the disputes about football and reading manuscripts, Karin for all the parties, Robert for just being

"Lilleman", Marcus for the CD-burner, Sönke for all discussions about nest predation, Michael for great hospitality during the conference in Zürich and the guided tour in Switzerland and Italy, and Stein-Are for the whiskey. Maybe I should thank some of the guys in the other corridor… Martin, Niclas, Per, Mats, Annacarin…. well - Thanks for being a good company during coffee, lunch breaks and evenings.

Nisse is thanked for making some traps, but especially for his "one-eyed-opinions" about sports, especially football, and thanks to Lars-Erik, Mats and Henrik for made practical things going. To Ingela and especially Marianne, I am very indepted for solving all kinds of problems, and always with a smile (even Ingela) – you are fantastic! For those of you not mentioned, you are not forgotten - all of you have in one way or another contributed to this thesis – Thanks!

I have had a very good time during my field seasons on Gotland. All the landowners, especially Lasse and Sonja, Yngve, and Mattsons, showed patience and sometimes even interest (curiosity) for what I have been doing out there, on the shore meadows for such a long time, Thank you all. To Lasse Tydén, thanks for good company and the bird watching trips.

Outside the office, in the real life, I want to thank Camilla and Emma, for being a nice family and I really hope we will spend the future together. For exciting Saturdays, I am grateful to "Tippeligan"; Mange, Dufva, Ricke and Bestefar. Lastly, many thanks to Jack Kerouac, Neil Cassidy, Robert Nesta Marley, Neil Young and Dag Vag for making things easier.

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SWEDISH SUMMARY - SVENSK SAMMANFATTNING

Boplatsval, bopredation och bevarandeekologi hos en rödspovspopulation

För att kunna skydda och bevara en hotad art är det viktigt att veta dess speciella krav på miljö och livsbetingelser. Min forskning har syftat till att klargöra de behov rödspoven (*Limosa limosa*) ställer på sitt habitat. Rödspoven är, med sina 250-275 häckande par, en relativt ovanlig art i Sverige och klassas som sårbar. Den återfinns främst på Öland och Gotland samt i östra Skåne. På Gotland häckar ungefär 50 par rödspov, utav dessa är 35-40 på Faludden, på sydöstra delen av ön (strax öster om Burgsvik). Mellan 1880 och 1930 saknades den helt på Gotland och fanns då bara i liten skala på Öland, men den var förmodligen mer allmän på båda öarna under 1700 och 1800-talet. Tidigare häckade de gotländska rödspovarna på myrar, men p.g.a. den enorma utdikningsiver som rådde under 1900-talet försvann många lämpliga häckningsplatser. Spovarna bytte då främst till betade strandängar.

Jag studerade dessa vadare på Faludden, från mitten av april till mitten av juni, 1996-2000. Under dessa år märktes 73 vuxna och drygt 200 ungar. De vuxna försågs med metallring och tre färgringar, vilket gjorde det möjligt att identifiera de olika individerna på långt avstånd. Ungarna märktes endast med en metallring. Drygt 80% av alla märkta vuxna fåglar återkom året därpå, vilket får anses som en stor andel. Det var ingen skillnad mellan könen i återkomstfrekvens. De allra flesta paren var trogna genom åren och byte av parter skedde nästan uteslutande då en av dem ej återvände till Faludden. Utav ungarna har dock bara några få procent återkommit till Faludden för att häcka. Häckningsframgången var bra; utav de funna bona kläckte 55-60%, vilket också är en hög andel, jämfört med tidigare studier av andra vadare. Utifrån dessa data kan framtidsutsikterna för en population beräknas genom en s.k. ekologisk riskanalys. Dessa datasimuleringar visade att den gotländska populationen behöver tillföras minst 17 individer årligen, förmodligen drygt 20, för att populationen ska kunna bibehålla sin nuvarande storlek.

För att utreda vilka faktorer som är viktiga för rödspovens val av boplats, jämfördes spovarnas bon med slumpvis utvalda platser inom strandängen. Det visade sig att vegetationen var högre vid rödspovens bon medan de omgivande tre m hade lägre vegetationen, än vad man kan förvänta sig av slumpen. Detta tyder på att spovarna inte enbart strävar efter att dölja sina bon. Den lägre vegetationen runt omkring boet kan gynna den ruvande fågelns möjligheter att tidigare upptäcka annalkande faror. Växtartssammansättningen, 1 m^2 runt rödspovarnas bon, skilde sig också från slumpen. Runt spovarnas bon dominerade växter som fördrar friska och näringsrika förhållanden, medan många av växtarterna vid slumpplatserna föredrar sandiga, torra eller alternativt våta miljöer. Vid jämförelse mellan de framgångsrika spovarnas bon och de bon som misslyckades p.g.a. predation var avståndet till träd och telefonstolpar en viktig faktor. De bon där äggen kläcktes, låg längre ifrån dessa utkiksplatser, som ofta används av kråkor och till viss del även av trutar. Dessa framgångsrika bon låg också oftare mer samlade med andra spovars bon, medan de misslyckade sålunda var mer solitära.

Jag gjorde även försök med konstgjorda bon. Dessa artificiella bon innehöll två små bruna hönsägg och två lerägg. Från avtryck i leräggen var det möjligt att identifiera den eventuella predatorn. De två absolut vanligaste boplundrarna på de gotländska strandängarna var kråkor och trutar. En faktor som minskade bopredationen var huruvida tofsvipor fanns i närområdet. De artificiella bon som var placerade bland många vipor, klarade sig betydligt bättre, än bon med få vipor i omgivningen. Uppenbarligen kan många tofsvipor, med sitt aggressiva boförsvar, bidra till att även andra bon klarar sig bättre. Detta kan medföra att mindre aggressiva arter gynnas av att häcka nära aggressiva arter. Stora strandängar visade sig vara bättre än små. Bopredationen var betydligt lägre på de stora ytorna och även i denna analys visade det sig att ett längre avstånd till träd var fördelaktigt.

Genetiska analyser tyder på att de gotländska rödspovarna, tillsammans med de öländska, bär på en unik genetisk variation, vilket skiljer dem från de övriga rödspovarna i Europa.

Sammantaget styrker mina resultat att bevarandevärdet för den svenska beståndet av rödspov är högt. Det största hotet mot rödspoven torde vara att arealen av betade strandängar har minskat de senaste årtionden. Markerna måste hållas öppna, d.v.s. sakna träd och buskar, för att därigenom minska bopredationen. Det är även fördelaktigt med en varierad växthöjd, vilket torde erhållas genom måttligt betestryck.