Genetic patterns of Black-tailed Godwit populations and their implications for conservation

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Summary

When raised bogs were converted to wet grasslands and hay lands, for the purpose of dairy farming, the opportunistic Black-tailed Godwit shifted from their former breeding habitat to these newly formed culture lands. From 1900 on the Black-tailed Godwit was mostly present in these damp hay lands, which were the major part of The Netherlands back then. Black-tailed Godwits profited from the increasing usage of artificial fertilizer at these damp hay lands, which in turn increased food availability. Consequently, Black-tailed Godwit population numbers increased drastically in these habitats during the first half of the 20th century. However, increased agricultural intensification, urbanization and decrease of available grassland areal, led to a decrease in habitat quality and the fragmentation of suitable grassland, in turn decreasing Black-tailed Godwit recruitment since the late 1960s. Population numbers have declined ever since with an annual rate estimated at 5%. Different management strategies, such as nest protection, creating reserves and mosaic management have been formulated and adopted to halt these decreases by improving nest success and habitat quality. However, up till now it remains unclear if these measurements do indeed have the desired effect on habitat quality and in turn habitat fragmentation. Furthermore, it remains ambiguous if habitat fragmentation is affecting Black-tailed Godwit populations at all.

Habitat fragmentation and changes in habitat quality might affect the population dynamics of a species. For instance decreasing habitat quality might cause a species to adopt a different dispersal pattern, or a breeding population might get isolated as a result of habitat fragmentation. These kind of population dynamic changes might in turn affect the genetic pattern of the species. In this thesis genetics were used to investigate long term population dynamic processes in Black-tailed Godwit populations resulting from increasing habitat fragmentation on three different spatial scales. However, before genetic research could be conducted genetic markers and easy sampling methods were needed. Therefore, microsatellite markers were developed and the usefulness of egg shell membranes as a source of DNA was assessed.

In chapter 2 we used the developed microsatellite markers to test egg shell membranes as an alternative sampling method to blood samples in population genetic research. We showed that genetic information within eggshell membrane DNA in comparison to blood DNA was not affected by degeneration or possible cross-contamination. Furthermore, neither degeneration nor cross-contamination was apparent in total genotypic comparison of eggshell membrane DNA and blood sample DNA. Our research clearly demonstrated that eggshell membranes can be used for population genetic research.

In chapter 3 we re-examined the findings of a previous study that demonstrated intronic variation in the CHD1-Z gene (Z*) in Black-tailed Godwits was correlated with habitat quality on a local scale. The previous study suggested that Black-tailed Godwit breeding populations were differentially structured at habitat of different quality as a result of positive selection pressures on Black-tailed Godwits breeding at habitat of high quality. We demonstrate that the presence of the Z* allele was not correlated with habitat quality. Other calculations on fitness correlates show that there might be a tendency towards female adults with the Z* allele laying earlier clutches than adult females without the Z* allele. Also the occurrence of the Z* allele was associated with a higher chick body mass and return rate. Interestingly, return rates of chicks that had hatched on herb-rich agricultural

land were higher than return rates of chicks that had hatched on intensively managed meadows, which demonstrates the importance of high quality habitat for breeding Black-tailed Godwits.

In chapter 4 and 5 we investigated if Black-tailed Godwit breeding populations were genetically structured as a result of habitat fragmentation on the scale of The Netherlands. We demonstrated that genetic diversity was moderate and no genetic clustering was visible between Dutch Black-tailed Godwit breeding populations. Gene flow estimates were larger than "one migrant per generation" between sample locations, and no isolation by distance effect was demonstrated. These findings indicated the maintenance of moderate levels of genetic diversity throughout the Dutch Black-tailed Godwit population through appropriate levels of gene flow between different breeding areas. Dutch Black-tailed Godwit breeding areas did not seem to be affected genetically by habitat fragmentation.

In chapter 6, we expanded our focus on the effects of habitat fragmentation to a global scale. The genetic population structure and phylogeny of the Black-tailed Godwit was assessed entailing DNA samples ranging from Iceland to Lake Baikal in eastern Russia and including all three currently known subspecies of Black-tailed Godwit. A historic explanation was given for the genetic patterns found in both microsatellites and newly developed mtDNA markers. We demonstrated only very marginal patterns of genetic structure within the *L. l. limosa.* Furthermore genetic differentiation between subspecies *L. l. limosa* and *L. l. islandica*, but not between *L. l. limosa* and *L. l. melanuroides was* shown. However, the genetic patterns in the mtDNA seemed inconsistent with the nuDNA pattern. The mitochondrial DNA did support a split between *L. l. melanuroides* and *L. l. limosa*/*L. l. islandica* and also demonstrated two *L. l. limosa* haplotype clusters that were not geographically isolated. The genetic patterns probably resulted from a scenario of isolation of *L. l. melanuroides* from *L. l. limosa* in Beringia during the Last Glacial Maximum, possibly followed by recent introgression. During the Pleistocene separation of *L. l. islandica* from *L. l. limosa* occurred, followed by colonization of Iceland by the *L. l. islandica* during the Holocene. Founder events within *L. l. limosa*, followed by population expansion, took place during the Holocene also.

The aim of this thesis was to investigate long term population dynamic processes in Black-tailed Godwit populations resulting from habitat fragmentation on three different spatial scales by using genetics. We demonstrated that egg shell membranes provide a good alternative DNA source for population genetic studies compared to blood samples. Through the usage of egg shell membranes we could conduct the genetic studies in this thesis a large spatial scales. Genetic population structuring was studied here because Black-tailed Godwit breeding areas seemed geographically fragmented and it was unclear if this had led to genetic separation and inbreeding as well. On a local scale we did not detect any genetic populations structuring as an effect of habitat fragmentation. We showed that habitat fragmentation, although geographically visible, has not yet lead to genetic differences between Dutch breeding populations. As such it seems that Dutch breeding areas of the Black-tailed Godwit consist of a single panmictic population. On a global scale this thesis confirmed the presence of three genetically distinct groups now recognized as subspecies. However, no clear genetic differences were found between *L. l. limosa* across most of its current breeding range. Possibly, there is some genetic differentiation between *L. l. limosa* breeding areas in the Netherlands and Sweden.