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

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**Genetic differentiation between
Dutch Black-tailed Godwit breeding sites
re-examined using D statistics**

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Abstract

In previous research genetic structure between different breeding areas in The Netherlands was investigated. Between 9 different breeding areas no genetic differentiation was found calculating F_{ST} values only. However these calculations were based on highly polymorphic microsatellite data, which could pose the problems for traditional, F_{ST} , genetic differentiation calculations. Therefore we re-analyzed our previous dataset using Jost's D statistics to assess genetic differentiation. The re-assessment of genetic differentiation between Dutch Black-tailed Godwit breeding areas, using D statistics, indicated that these areas are not genetically different from each other. Like in the previous study these data yet again indicate that the Dutch Black-tailed Godwit breeding areas should be considered and managed as one panmictic unit.

Keywords Molecular ecology · Genetic population structure · F statistics · *Limosa limosa* · Breeding population · Isolation · Habitat fragmentation



Introduction

The assessment of population genetic structure has proven to be a powerful descriptive tool in the field of conservation genetics, molecular ecology, evolutionary studies and forensics. The method most frequently used to assess genetic population structure to date is F statistics, introduced by Sewall Wright (1943; 1965). However, recent reports point at the limitations of F-statistics for genetic differentiation calculations in studies using highly variable loci (Gregorius *et al.* 2007, Gregorius 2010, Jost 2008). Jost (2008) points out that the dependency of these statistics on within-population diversity gives unreliable results using these statistics when diversity and differentiation are high. Using F-statistics, similarity between subpopulations (F_{ST}) is measured as the ratio of within-population heterozygosity (H_S) to total heterozygosity (H_T). F_{ST} was originally developed for bi-allelic markers, with F_{ST} values close to zero supposedly indicating high similarity among populations, while values close to unity supposedly indicate nearly complete differentiation (Wright 1943; 1965). However, with multi-allelic markers the maximum possible value equals to $1 - H_S$ (Hedrick 2005). Highly variable loci result in a high H_S value that will reduce the possible range of F_{ST} considerably. For example when within-population heterozygosity is 0.9, which is a common value when using microsatellite markers, the maximum possible value of $F_{ST} = 0.1$, which is generally interpreted as representing weak population subdivision. However, in this example it represents the case with no shared alleles among populations, and maximum divergence (Meirmans and Hedrick 2011). Jost (2008) indicates that this dependency of F_{ST} on the level of within population diversity will cause difficulties in its interpretation, for example when comparing F_{ST} values of groups with different genetic diversity, markers exhibiting different mutation rates, or species with different effective population sizes. Another problem indicated by Jost (2008) is that the expected heterozygosity alone is unsuitable for describing the genetic diversity. Jost (2008) developed a new statistic for estimating differentiation which he termed 'D', avoiding these problems by using the effective number of alleles instead of heterozygosity. Jost (2008) shows that assessing datasets with D that were formerly assessed with F_{ST} might give very different results.

In response to agricultural intensification, which began its rise around 1900 in western Europe, the Black-tailed Godwit, increased in population numbers. However, continuing agricultural intensification has resulted in decreasing population numbers in most of the Black-tailed Godwit's European breeding range (Beintema *et al.* 1995, Bijlsma *et al.* 2001). From 1967 an annual and steady decline in population numbers has also been reported in The Netherlands, one of the remaining Black-tailed Godwit strongholds in Europe (Teunissen and Soldaat 2005). The Black-tailed Godwit shows high breeding site fidelity and some degree of natal philopatry. It was shown that 90% of the adult breeding birds returned within 700 m of the previous nest site. Natal philopatry was demonstrated to be high as well, with 75% of the birds returning within 18 km of their previous hatching site (Groen 1993). With such limited dispersal in a fragmenting landscape, breeding areas could become isolated from each other, resulting in isolated populations. These isolated populations might have small effective population sizes which might affect genetic diversity through genetic drift and might increase inbreeding. Isolation might also affect population dynamics, resulting in a metapopulation structure including source-sinks dynamics. To get some more insight into the population dynamics of



Black-tailed Godwit breeding populations, we assessed genetic structure between different breeding areas in The Netherlands in a former study (Trimbos *et al.* 2011). Between 9 different breeding areas no genetic differentiation was found calculating F_{ST} values only. However these calculations were based on highly polymorphic microsatellite data, which could pose the problems pointed out by Jost (2008). Therefore we re-analyzed our previous dataset using Jost's D (2008) to assess genetic differentiation. Results of both statistics will be compared and discussed here.

Material and methods

Samples, sample locations (Zuid-West Fryslân (ZWF), Eemnes/Arkemheen/Vinkeveen (EAV), Zoeterwoude (ZOE), Idzegea (IDZ), Middelie (MID), Normerpolder (NOR), Vijfheerenlanden (VIJF), Uitdam (UIT) and OVE (Overijssel) and the according PCR fragment dataset from Trimbos *et al.* (2011) was used for genetic differentiation calculations. Pairwise F_{ST} values between locations were previously calculated using ARLEQUIN 3.11 and are used here again (Excoffier *et al.* 2005). If significant values were obtained, Bonferroni correction was applied. D values between different locations were calculated using the Species Prediction And Diversity Estimation (SPADE) program with 2000 bootstrap replications (Chao and Shen 2009). Confidence intervals (CI), calculated by the program, were used to assess if D values differed from zero.

Results

Nearly all pairwise F_{ST} values between locations were not significantly different from zero, except ZWF and VIJF (Table 1). However, after Bonferroni correction this significance did not hold. Most D values were 0. Three D values, between UIT and NOR, ZWF and VIJF and between EAV and VIJF were apparently higher than 0. However, their confidence intervals overlapped with 0.

Table 1. Pairwise F_{ST} below the diagonal, and D values above the diagonal for pairs of Dutch Black-tailed godwits populations. Uncorrected P values smaller than 0.05, for F_{ST} , or CI's not overlapping with zero, for D values, are indicated with *.

	ZWF	EAV	ZOE	IDZ	MID	NOR	VIJF	UIT	OVE
ZWF	--	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000
EAV	0.005	--	0.000	0.000	0.000	0.000	0.003	0.000	0.000
ZOE	0.000	0.000	--	0.000	0.000	0.000	0.000	0.000	0.000
IDZ	0.000	0.004	0.000	--	0.000	0.000	0.000	0.000	0.000
MID	0.000	0.001	0.000	0.000	--	0.000	0.000	0.000	0.000
NOR	0.002	0.000	0.000	0.003	0.000	--	0.000	0.016	0.000
VIJF	0.013*	0.015	0.008	0.003	0.000	0.000	--	0.000	0.000
UIT	0.000	0.000	0.000	0.000	0.000	0.013	0.000	--	0.000
OVE	0.003	0.006	0.000	0.001	0.000	0.000	0.005	0.000	--

Discussion

The re-assessment of genetic differentiation between Dutch Black-tailed Godwit breeding areas, using D statistics, indicates that these areas are not genetically different from each other. Most D values were 0 or close to 0 indicating no differentiation. The D value of 0.016, between UIT and NOR, might indicate very slight genetic differentiation between these sites. However, the CI indicated that this value was not different from 0. In general these results seem comparable to the earlier calculated pairwise F_{ST} values between Dutch Black-tailed Godwit breeding sites. Pairwise F_{ST} values were low and only one pairwise comparison, between VIJF and ZWF, was significantly different from 0, indicating that these 2 locations might be genetically differentiated from each other. However this significant F_{ST} value was lost after Bonferroni correction.

Does this mean that F_{ST} and D performed equally and that both statistics indicate that there is no genetic differentiation? Jost (2008) seems to argue that only D should be used to assess genetic differentiation. Meirmans and Hedrick (2011) point out that while D performs better at measuring the actual differentiation between demes, F_{ST} is better at describing the influence of demographic events on the distribution of alleles and suggest to use both statistics simultaneously to get a better comprehension of population structure. In this view, D values indicates an absence of genetic divergence while F_{ST} values indicate a lack of allele fixation between breeding areas. This more complete assessment of genetic structure demonstrates that the Dutch Black-tailed Godwit breeding areas are still genetically similar or have become isolated from each other too recently for lineage sorting to become complete. These data yet again do not indicate that the Dutch Black-tailed Godwit breeding areas should not be considered and managed as one panmictic unit.

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