

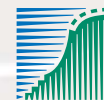
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Waterbirds around the world

A global overview of the conservation,
management and research of the
world's waterbird flyways

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Population declines and the risk of extinction in waders: genetic and ecological consequences of small population size

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ABSTRACT

World-wide population declines in waders are of great concern because many species have not yet recovered from loss of genetic variation caused by population bottlenecks in the late Pleistocene. Therefore genetically effective population sizes are much smaller than census population sizes. Genetic drift can be more important than selection in determining the fate of new mutations in small populations, in which case populations are expected to accumulate deleterious mutations. The fixation of such deleterious alleles is expected to reduce reproductive success of a species and lead to extinction unless new beneficial mutations are fixed by selection and help restore part of the lost fitness. Critical effective size could be as small as a few hundred individuals, above which a population will persist without extinction due to genetic load. However, this requires an approximately 10-fold higher census population size because of the variance in breeding success and fluctuations in numbers in different generations. In populations such as the Red Knot *Calidris canutus rufa* which is currently undergoing a drastic decline in numbers due to bad ecological conditions, the risk of extinction is exacerbated. This paper reviews genetic and ecological evidence of why the population is declining, and argues that an increasing number of species may be in the same risk category.

INTRODUCTION

Wader species and their constitutive populations are of international conservation concern, following a recent review of population trends around the world (International Wader Study Group 2003, Stroud *et al.* 2006). For those species in which population trends were reported, three times as many are in decline as are expanding. Forty-two of 214 species (19.6%) listed by the International Wader Study Group were assessed as either Globally Threatened or Near Threatened. Although this number includes some species that are already thought to be extinct, it is a strong indication that the loss of biodiversity in this charismatic group of birds is accelerating. The causes of this increasing risk of extinction in waders are poorly understood, and raise important issues in conservation management

generally, as well as specific questions about how to halt global declines and engage in population restoration.

While the loss of wetlands and destruction of associated food supplies is likely implicated in most population declines, it is often not appreciated fully that the risk of extinction involves both genetic and ecological consequences of small population size. The purpose of this paper is to bring to the attention of wader biologists some recent theoretical work on the genetic risks of extinction of small populations (Whitlock 2000), and to emphasize that ecological and genetic risks operate in different time frames. However, both need to be considered in the restoration of small populations if we are to try to give them a future in other millennia.

LOW GENETIC VARIATION IN WADERS

Assays of genetic variation in waders have uncovered the rather surprising fact that many species and populations are genetically impoverished, relative to other groups of birds such as passerines. This was first reported by Baker & Strauch (1988) using protein electrophoresis (see Table 1). Low genetic variability is evident not only in small populations of threatened endemics such as the African Black Oystercatcher *Haematopus moquini* and Mountain Plover *Charadrius montanus*, but also in migratory species with much larger population sizes (e.g. Purple Sandpiper *Calidris maritima* and Willet *Catoptrophorus semipalmatus*). The latter implies that at some time in their recent past, Purple Sandpipers and Willets were reduced to small ancestral populations, thereby losing genetic variation, and have expanded subsequently to larger populations. Not enough time has elapsed since the populations expanded for many mutations to accumulate in the genomes of these species and restore the genetic variation expected in equilibrium populations.

HISTORICAL DEMOGRAPHY AND GENETIC BOTTLENECKS

One source of loss of genetic variation in wader populations dates back to previous episodes of population declines in the last glacial maximum (LGM) about 22 000 years ago in the Northern

Table 1. Estimates of genetic variability at 30 loci of some wader species based on protein electrophoresis.

Species	N	No. alleles/locus	% Polymorphic loci	Average heterozygosity
African Black Oystercatcher <i>Haematopus moquini</i>	13	1.1	8.3	0.019
Grey Plover <i>Pluvialis squatarola</i>	13	1.1	7.5	0.011
Mountain Plover <i>Charadrius montanus</i>	10	1.0	0.0	0.000
Red Knot <i>Calidris canutus</i>	25	1.3	17.9	0.020
Purple Sandpiper <i>Calidris maritima</i>	35	1.1	6.9	0.006
Dunlin <i>Calidris alpina</i>	25	1.1	13.8	0.009
Willet <i>Catoptrophorus semipalmatus</i>	23	1.1	5.0	0.002
Passerine average				0.053

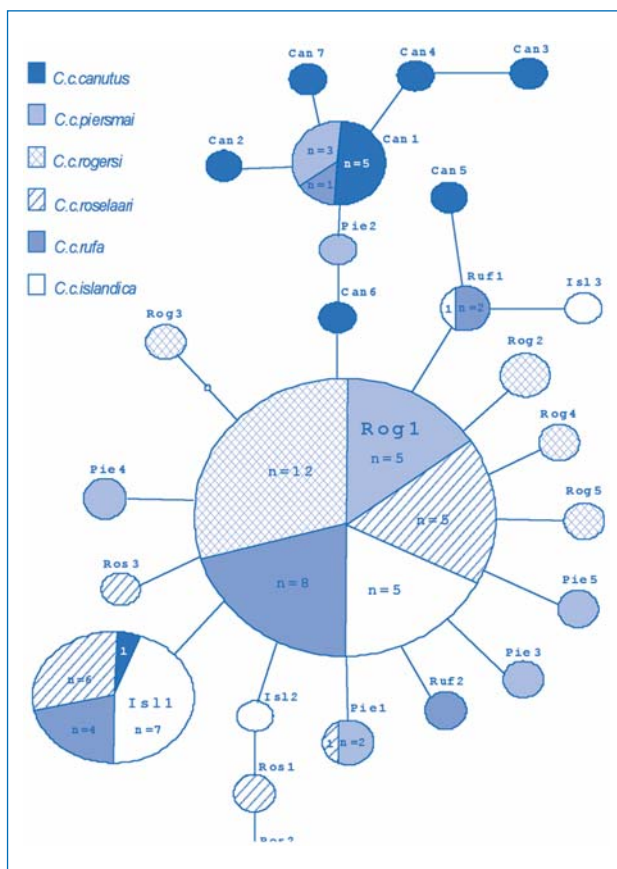


Fig. 1. Minimum spanning network connecting 91 haplotypes found in 657 bp of the mitochondrial DNA control region in globally distributed populations of the Red Knot *Calidris canutus*. The star-like pattern is created because most haplotypes differ by one mutation from the common haplotypes. From Buehler & Baker (2005).

Hemisphere, or possibly earlier glacial maxima in the Pleistocene. Especially for migratory waders breeding in the high Arctic tundra, such as the Red Knot *Calidris canutus*, the genetic footprint of a small population that survived the LGM is readily apparent in the very limited variation in mitochondrial DNA sequences of the six subspecies (Baker *et al.* 1994). Only 25 haplotypes were found in 675 bp sequences of the control region, the fastest evolving part of the mtDNA molecule. Furthermore, the 91 individuals that were sequenced were sampled over the global range of the species (Buehler & Baker 2005). The minimum spanning network has the pattern expected under a demographic contraction and population bottleneck in the LGM: a few ancestral common haplotypes that survived the bottleneck, and most of the remainder arising by mutations of one or a few bases subsequently as the population expanded (Fig. 1).

Such a star-like phylogeny is typical of small populations of recently bottlenecked species. Although such a pattern can also be generated by selection acting on linked genes in the nucleus, this is unlikely in Red Knots because (1) the same star-like pattern has been found in other species of waders suggesting a general demographic contraction in response to harsh Pleistocene environmental conditions, and (2) a similarly low level has been found in nuclear loci (Table 1) and in genomic scans of Red Knots using amplified fragment length polymorphisms (AFLP, Table 2). The scans also show that waders such as the Red Knot and Dunlin *Calidris alpina* have less genetic

variation at hundreds of nuclear loci than a range of other bird species. The lowest value was recorded in the Red Knot (all subspecies included), even though a larger number of loci (836) were scanned than in passerine taxa.

POPULATION PERSISTENCE AND THE GENETIC RISK OF EXTINCTION IN SMALL POPULATIONS

In a seminal paper, Whitlock (2000) assessed the genetic risk of extinction in small populations in which he not only considered the fixation of deleterious alleles that thereby affect the fitness of all individuals, but also factored in the fixation of beneficial mutations that can reduce this genetic load. Beneficial alleles are more likely to be lost and deleterious alleles are more likely to be fixed in small populations because random genetic drift is more important relative to selection. Thus small populations have a high probability of extinction because of the inexorable decline in fitness.

However, Whitlock showed that there is a critical threshold size ($N_e, crit$) above which populations are expected to persist indefinitely because the loss of fitness from the fixation of deleterious alleles is countered by the fixation of beneficial alleles. This critical effective size in populations varies according to a number of factors. First, if the rate of beneficial mutation is large relative to the rate of deleterious mutation, the loss of fitness will be restored in smaller populations than would be the case if the rates were reversed. Second, when the mean effects of mutation are high, the importance of genetic drift of nearly neutral alleles is decreased, and thus critical effective size is lower. Third, if beneficial mutations are likely to be more frequent or have a larger effect in compensating for a previous decline in fitness, then $N_e, crit$ will be lower. Fourth, a high ratio of effective population size (and hence the number of breeding adults) to census population size will decrease the critical threshold size for population persistence. Finally, sexual selection could also lower this threshold by removing deleterious alleles, as alleles that decrease productivity are also likely to reduce mating success (Whitlock 2000).

Due to uncertainty and lack of empirical estimates of these parameters, the critical effective size can only be approximated, but is thought to be in the range of hundreds of individuals. However, the ratio of effective population size to census population size in waders (Buehler & Baker 2005) is typically about 0.1, as it is in other wildlife (Frankham 1995). Therefore, as Whitlock (2000) pointed out, census population size for population persistence in the longer term needs to be at least 10 times larger than the critical effective size, typically in the thousands.

POPULATION PERSISTENCE AND THE ECOLOGICAL RISK OF EXTINCTION IN SMALL POPULATIONS

Ecological and demographic factors such as breeding failure and low recruitment rates, low adult annual survival and worsening environmental conditions present much more immediate risks of extinction than genetic factors (Lande 1998). This is because ecological pressures can operate on a much shorter time frame of a few generations in long-lived organisms such as waders, whereas genetic problems accumulate slowly through time. In the *rufa* population of Red Knots, for example, the immediate threats are more likely to be ecological. Late arrival at Delaware Bay in spring and inadequate refuelling at this last stopover before migrating to the Arctic breeding grounds have resulted in

Table 2. Genomic diversity in bird taxa estimated with amplified fragment polymorphisms (AFLP).

Species	No. amplified loci	No. polymorphic loci	% polymorphic loci
House Finch <i>Carpodacus mexicanus</i>	363	223	61.4
Chiffchaff <i>Phylloscopus collybita</i>	251	141	56.2
Bluethroat <i>Luscinia svecica</i>	232	81	34.9
Willow Flycatcher <i>Empidonax traillii</i>	708	197	27.8
Dunlin <i>Calidris alpina</i>	900	203	22.6
Red Knot <i>Calidris canutus</i>	836	129	15.4
Average	585.4	150.2	31.4

decreased annual survival of adults and low recruitment rates in the period 2000-2001 (Baker *et al.* 2004). The further loss of 13 000 birds from the over-wintering population in Tierra del Fuego, as recorded by an aerial census in February 2005, considerably increases the risk of extinction of this population. In the short period of five years, the population has declined from about 53 532 to 17 653.

The large-scale losses of birds could, in part, be a lag effect of inadequate refuelling at stopover sites, increased risk of breeding in unpredictable climatic conditions in the Arctic due to global climate change, and increased susceptibility to pathogens and parasites. In small populations, the latter can be associated with the loss of adaptive variation and the accumulation and fixation of deleterious mutations which reduce fitness. We therefore expect such populations to be more prone to large mortalities in unfavourable ecological circumstances such as annual food failures, increased incidence of pathogens, and pollution. The joint effects of environmental stochasticity and genetic processes could increase the risk of extinction even further, as appears to be the case in the Red Knot. Not only have refuelling problems and late arrival at stopover sites been implicated in the severe decline in the Tierra del Fuego population, but also spring migrants passing through Lagoa do Piexe in southern Brazil in 1997 were observed dying in small flocks after foraging on ocean beaches. The cause of this mortality could not be determined, but was possibly due to a viral pathogen.

The interaction of genetic and ecological risk factors was the basis for the “parasite” hypothesis of wader migration which predicted that long-distance migrants such as the Red Knot have to winter in low-parasite marine environments (Piersma 1997), because they trade-off increased energy expenditure for immune system suppression. This in turn was also predicated on the observation that many species of waders are genetically impoverished as a result of population bottlenecks in the late Pleistocene (Baker & Strauch 1988, Baker *et al.* 1994), and thus have reduced levels of adaptive variation. The salient point about species that have survived a prolonged bottleneck (as in the millennial duration of glacial maxima) is that a population must exist at a much larger size for a very long time to recover from the negative effects on fitness suffered when the population was small (Whitlock 2000).

Migratory waders are vulnerable not only because of their life history characteristics and specialized ecologies, but also because of the genetic erosion of adaptive genetic variation from small population size in the past (Piersma & Baker 1999). We should thus not be surprised that so many migrant waders are declining world-wide and many species will be in the same risk



Dunlin *Calidris alpina* surface-tension feeding. Dunlins have lower genetic diversity than many other bird species. Photo: Rob Robinson.

category, and must be cognizant that restoration of their populations probably depends on managing for larger census population sizes than implied in the old 50 : 500 rule of thumb. This rule suggests that an effective population size of 50 breeding adults may be adequate in avoiding inbreeding depression, whereas an effective size of about 500 is required to prevent the loss of genetic variation in quantitative traits with high heritability (Harris *et al.* 1987, Simberloff 1988). This rule implies a census population size of about 5 000 adults for minimum viable population size, but if the ratio of beneficial to deleterious mutations is low, then it is wise to manage for at least double this population size to increase the chances of long-term persistence.

Although critical threshold size for population persistence has large uncertainties associated with it, larger census populations are good insurance in mitigating ecological and genetic risk factors. Finally, it is better to act earlier in declaring species or populations threatened or endangered. Rather than waiting until numbers have dwindled to hundreds or a few thousands, population restoration has to be attempted much sooner when the population is correspondingly bigger. Not only will this decrease adverse genetic effects, but it will also increase the prospects for a demographic expansion and reduce the risk of extinction.

REFERENCES

- Baker, A.J. & Strauch, J.G. 1988. Genetic variation and differentiation in shorebirds. Proceedings of XIX International Ornithology Congress, Ottawa, June 1986. Symposium 27: 1639-1645.
- Baker, A.J., Piersma, T. & Rosenmeier, L. 1994. Unraveling the intraspecific phylogeography of knots (*Calidris*