

Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis

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Abstract

Many shorebirds that breed in North America are declining. These trends reflect global patterns in shorebird populations. Here we ask what factors make some shorebird species more prone to decline than others. Specifically, we test the influence of migratory behaviour (route and distance), biogeography (population size and range), life history (body size, clutch size) and sexual selection (social mating system and testis size) on population trends in North American breeding shorebirds. Using phylogenetic comparative methods, we show that species that migrate across continental North America are more prone to decline than species that do not. Our finding that continental migrants are associated with population decline indicates that intrinsic factors may play an important role in predisposing a species to decline. Previous studies within the class Aves have failed to identify migration route as a correlate of decline or extinction risk. Two other intrinsic factors (oceanic migrants and threats on the non-breeding grounds) were also important in our overall models, although neither was significant alone. The moderate explanatory power of our variables indicates that other factors are also important for explaining shorebird declines. We suggest that contemporary threats, most notably habitat loss and degradation at migratory stopover sites, are likely to be important.

Introduction

Birds have suffered greatly from the current extinction crisis. Recent estimates suggest that 1211 bird species (12% of the worldwide total) are at risk of extinction (BirdLife International, 2004). Among birds, shorebirds worldwide have suffered alarming recent declines. Forty-eight per cent of 200 populations with known trends are in decline whereas only 16% are increasing (International Wader Study Group, 2003). Analyses of migration monitoring data collected since 1974 (International and Maritimes shorebird surveys; Howe, Geissler & Harrington, 1989; Morrison, Downes & Collins, 1994) suggest that declines are also occurring in shorebirds that breed in North America (Alaska Shorebird Group, 2000; Donaldson *et al.*, 2000; Brown *et al.*, 2001). Recent population declines may provide an early warning of potential local and regional extinction in the future. Furthermore, these declines are of particular conservation concern because the reliance of shorebirds on wetland ecosystems suggests that they may be important indicators of wetland health on a global scale (CHASM, 2004).

Numerous hypotheses have been proposed to explain differences in both population decline and extinction risk between species (Purvis *et al.*, 2000; Bennett & Owens, 2002; Morrow & Pitcher, 2003; Reynolds, 2003; Cardillo *et al.*, 2004; Fisher & Owens, 2004). Here, we focus on four major

intrinsic factors that may predispose species to decline. First, extinction risk may be related to migratory behaviour. For instance, species that migrate are more prone to decline (Zöckler, Delany & Hagemeyer, 2003) or become extinct than resident species (Pimm, Jones & Diamond, 1988). Second, species with small population sizes or ranges (including island dwelling taxa) may be at greater extinction risk than those with large populations or broad geographic distributions (BirdLife International, 2004). Third, species with traits associated with slow life histories, such as large body size (Pimm *et al.*, 1988; Gaston & Blackburn, 1995) and small clutch size (Pimm *et al.*, 1988), are more likely to become extinct than those with traits associated with fast life histories (Owens & Bennett, 2000). Fourth, more intense sexual selection is associated with higher extinction risk (Møller, 2000). Here, sexual selection puts pressure on species to evolve traits that enhance mating opportunities. These traits may reduce or compromise benefits normally accrued through natural selection (see Andersson, 1994), and in a changing environment, these sexually selected species may be less able to adapt and are thus more prone to going extinct (Tanaka, 1996).

The spatial scale at which meaningful comparative studies addressing extinction risk should be conducted has been debated (Fisher & Owens, 2004). In many cases, the utility of the putative correlates as a predictive tool to identify

declines or extinctions in poorly known species may be limited in global, class-wide studies because of the lack of explanatory power. More importantly, large-scale studies are likely to miss idiosyncratic drivers of decline that may be unique to particular geographic regions or taxonomic groups. Thus, although there is great value in large-scale studies of decline, many of the putative correlates cannot be readily applied to conservation management (Fisher & Owens, 2004). Consequently, studies conducted at smaller taxonomical and geographic levels are urgently needed to better inform conservation efforts. Here, we use phylogenetic comparative methods to elucidate factors that make North American breeding shorebirds prone to decline. The fact that shorebirds use a variety of migratory strategies, exhibit diverse life histories and display an exceptional range of breeding behaviours (Pitelka, Holmes & MacLean, 1974; Figuerola, 1999; Székely, Freckleton & Reynolds, 2004; Thomas & Székely, 2005) implies that there are many potential intrinsic drivers of decline and makes them an ideal group to study the effects of evolutionary predisposition on population declines. North American breeding shorebirds are particularly good for such a study because extensive data on the biology and population trends are readily available. We ask how migratory behaviour, biogeography, life history and sexual selection influence population trends. In addition, we test whether the level of extrinsic threats on the wintering and breeding grounds can explain recent population declines in North American shorebird populations.

Methods

We based our analyses on the population trend scores for North American breeding shorebirds from the US Shorebird Conservation Plan (USSCP, 2004) because this is the best data currently available. Scores for population trends are given as follows: 1 = significant population increase, 2 = apparent population increase, 3 = stable population, 4 = apparent population decline and 5 = significant population decline. Data on breeding and non-breeding ranges, and the perceived degree of threat on the breeding and non-breeding ranges were obtained from USSCP (2004; an explanation of scores can be found in Donaldson *et al.*, 2000; Brown *et al.*, 2001). Breeding range followed a five-point scoring system based on the area of North America occupied by a species: 1 = more than 20%, 2 = 10–20%, 3 = 5–9.9%, 4 = 2.5–4.9% and 5 = less than 2.5%. Geographic area alone may be a poor measure of non-breeding range for species that disperse along a coastline; hence non-breeding distribution was scored based on measures of both area and length of coastline. Here, 1 = very widespread, 2 = widespread, 3 = intermediate, 4 = local and 5 = highly restricted (see Donaldson *et al.*, 2000; Brown *et al.*, 2001 for full details). Both threats during the breeding season and threats during the non-breeding season were scored as 1 = demonstrably secure, 2 = threats assumed to be low, 3 = no known threats, 4 = significant potential threats exist but have not actually occurred and 5 = known threats are

actually occurring and can be documented. Migration route was split into three dichotomous variables based on data in *The birds of North America* (Poole & Gill, 2003): (1) continental migration (i.e. migrate overland), (2) coastal migration and (3) oceanic migration. Each species was assigned a score of 1 if they used the route and a 0 if they did not. A species could be scored a value of 1 on two different variables if they, for example, used a coastal route in one part of its range and a continental route in another. The advantage of this scoring system is that we can differentiate the effects of each route on population trends. Migration distance was taken as the difference in degrees latitude between the midpoint of the breeding range (estimated from the most northerly and most southerly breeding latitude) and the midpoint of the wintering range (estimated from the most northerly and most southerly wintering latitude; Hayman, Marchant & Prater, 1986). Population size estimates were taken from R. I. G. Morrison *et al.* (unpubl. data). Data on mean body mass and clutch size were obtained primarily from *The birds of North America* series (Poole & Gill, 2003; see Supplementary Material Appendix S1 for full details). Body mass fluctuates throughout the year, so we restricted our body mass measurements to those taken during the breeding period. We note that clutch size variation in shorebirds is restricted relative to the class Aves, and thus analyses may lack statistical power. Nonetheless, it is the mostly widely used and reliable method of quantifying life-history variation in birds because within-species variation is more tightly constrained than other measures such as indices of mortality. The social mating system was used as a proxy for pre-mating sexual selection. The intensity of sexual selection is expected to be highest in males within polygynous species and females within polyandrous species (see a similar logic in Székely, Reynolds & Figuerola, 2000; Dunn, Whittingham & Pitcher, 2001). The social mating system was scored based on descriptions in the literature: 0 = social polygyny, 1 = social monogamy and 2 = social polyandry. An alternative scoring system (0 = social monogamy 1 = social polygamy) does not qualitatively alter our results. Testis mass was used as a proxy for post-mating sexual selection (i.e. sperm competition; Dunn *et al.*, 2001) as large testis mass is expected to reflect intense sexual selection. We used testis masses presented in Dunn *et al.* (2001). Because testis size is expected to be associated with body size, we controlled for this by including body mass in multiple regression analyses. Although recent studies have highlighted the importance of interactions between extinction risk and the type of threat on a species (e.g. habitat loss, human persecution, predation; see Owens & Bennett, 2000; Cardillo *et al.*, 2004), there were insufficient data on the type of threats for most shorebird species to include such variables. Altogether, we were able to gather data on 51 species and five subspecies of shorebirds that breed in North America. This information and the associated reference materials are available as Supplementary Material Appendix S1.

Closely related species tend to be more similar to one another than would be expected by chance as a result of

shared ancestry (Harvey & Pagel, 1991). Thus, under a non-directional random walk model evolution (sometimes called Brownian motion), traits are expected to diverge proportionally with the branch lengths of a phylogeny. It is therefore important to account for phylogeny in cross-species comparative analyses. However, although some traits, such as body size, are tightly related to phylogeny, others are more labile and may not be as similar in closely related species as predicted by the underlying phylogeny (Freckleton, Harvey & Pagel, 2002; Blomberg, Garland & Ives, 2003). This presents a problem for analyses including phylogenetically labile traits because standard species regressions fail to account for statistical non-independence due to phylogeny, whereas standard phylogenetic comparative techniques such as independent contrasts (Felsenstein, 1985) may over-compensate for phylogeny.

Here, we use a recently developed statistical technique that estimates the degree of phylogenetic correction required for comparative data. The parameter λ (Pagel, 1999; Freckleton *et al.*, 2002) estimates the most appropriate branch length transformation for the given data and phylogeny by maximum likelihood estimation, with values ranging from 0 (equivalent to a star-shaped phylogeny indicating that no phylogenetic correction is required) to 1 (traits evolved as predicted by the phylogenetic tree). λ can be used to estimate the degree of phylogenetic dependence of a single trait or to estimate, and simultaneously correct for, phylogenetic effects in correlations among multiple traits. The log likelihood for λ at its maximum-likelihood value can be compared with λ at a fixed value (e.g. 0 or 1) using the likelihood ratio statistic with one degree of freedom. It is important to note that the maximum-likelihood estimate of λ for a single trait may differ from the maximum likelihood of λ of a regression analysis involving that trait. We therefore estimated λ separately for each analysis to ensure we used the appropriate degree of phylogenetic correction. For a full description and discussion of the applications of this method, see Freckleton *et al.* (2002). We used the phylogenetic supertree of shorebirds (Thomas, Wills & Székely, 2004) for our comparative analyses. The tree was pruned to include only the 51 North American breeding species where we had collected relevant information. The additional subspecies were included by adding them as polytomies with zero length branches to the appropriate species tip in the original tree.

We first tested whether population trends were associated with shorebird phylogeny by estimating λ . We then constructed minimum adequate models (MAMs; Purvis *et al.*, 2000) while simultaneously estimating and implementing the λ branch length correction. MAMs were constructed using backward elimination of predictors from the full model. The predictor that contributed the least amount of explanatory power to the full model was removed and the model was fitted again. We repeated this procedure until we developed a model in which all the remaining predictors were statistically significant ($P \leq 0.05$). The excluded predictors were then reintroduced to the model in turn and remained in the model only if they added significant explanatory power (i.e.

$P \leq 0.05$ for the predictor). This was repeated until a final MAM was obtained. Note that we also estimated MAMs using a forward stepwise approach, beginning from single predictors, and the final MAM was identical to that obtained using the backward elimination approach. We could not use Akaike's information criterion (AIC_c) (Burnham & Anderson, 2002) model selection method for the full set of alternative models because of variation in sample size across models. All analyses were performed in R 2.1.0 (Ihaka & Gentleman, 1996) using code written by R. P. Freckleton and modified by G.H.T.

Results

Of the 56 species and subspecies in our dataset, 30 are declining and only one species is currently increasing in number (*Limnodromus scolopaceus*). Despite the large number of declining species, we found no evidence that closely related species are any more likely to share population trend indices than distantly related species (maximum likelihood estimate of λ for population trend = 0; likelihood ratio test against $\lambda = 1$: $\chi^2 = 582.396$, $P < 0.001$).

The MAM (Table 1; maximum likelihood estimate of $\lambda = 0$; likelihood ratio test against $\lambda = 1$: $\chi^2 = 589.918$, $P < 0.001$) indicates that species that migrate along either continental or oceanic routes have a higher risk of decline. In addition, high levels of threat in non-breeding ranges are associated with more severe population decline. However, it should be noted that only the continental migration route remains statistically significant when all other predictor variables are removed ($b = 0.664$, $P = 0.009$, $n = 55$; Fig. 1). The significance of continental migration is further corroborated using non-parametric statistical tests without phylogenetic correction (Mann-Whitney test: $U = 212.5$, $P = 0.010$). Neither the oceanic migration route ($b = 0.121$, $P = 0.644$, $n = 55$) nor non-breeding threats ($b = 0.179$, $P = 0.210$, $n = 56$) are statistically significant correlates of population declines in North American shorebirds when considered as single explanatory variables. The fit of the MAM is better than that of any other combination of its three contributory predictors, as evidenced by a comparison of r^2 , adjusted- r^2 and AIC_c (Table 2). Continental migration explains only 12% of the variation in population trends; this increases to 27.7% of variation when non-breeding threats and oceanic migration are included in the MAM. None of

Table 1 Minimum adequate model explaining population trends (response variable) in North American shorebirds ($n = 55$ taxa)

Predictor variable	Slope \pm SE	t	P
Intercept	1.768 \pm 0.558	0.558	0.003
Continental migration	1.047 \pm 0.257	4.078	< 0.001
Oceanic migration	0.574 \pm 0.250	2.300	0.026
Non-breeding threats	0.372 \pm 0.132	2.809	0.007

Full model: $r^2 = 0.277$, $F_{4,51} = 6.516$, $P < 0.001$.

Excluded variables include breeding distribution, non-breeding distribution, population size, coastal migration, migration distance, testis size, mating system, body mass, clutch size and breeding threats.

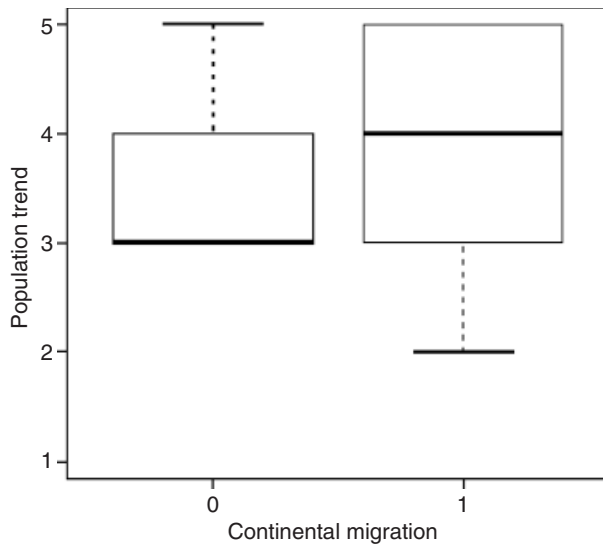


Figure 1 Boxplot of population trends against continental migration route in North American shorebirds. Species that use continental migration routes (value of 1) have a median population trend of 4 (declining), whereas species that do not use continental routes (value of 0) have a median population trend of 3 (stable).

Table 2 Comparison of the minimum adequate model (MAM) with alternative models including the predictors continental migration (cont), oceanic migration (ocean) and non-breeding threats (nb-threat)

Model	r^2	Adjusted- r^2	n	P	AIC _c
MAM	0.277	0.235	55	<0.001	140.494
cont, nb-threat	0.202	0.171	55	0.003	142.525
cont	0.121	0.105	55	0.009	144.510
cont, ocean	0.165	0.133	55	0.009	145.010
ocean	0.004	-0.015	55	0.644	151.429
ocean, nb-threat	0.041	0.004	55	0.334	152.621
nb-threat	0.029	0.011	56	0.210	152.555

Note that the AIC_c statistic for the model including only non-breeding threat as a predictor is not directly comparable with the other models because the sample sizes differ.

AIC_c, Akaike's information criterion.

the other tested variables contributed significant explanatory power to the model and are thus excluded (Table 1).

Discussion

Our analyses indicate that shorebird species that migrate through interior portions of North America, and to a lesser extent those that migrate over the ocean and have threats on their non-breeding grounds, are associated with recent population declines. Previous studies have shown that migratory behaviour may be an important predictor of population decline (Pimm *et al.*, 1988; Prinzing *et al.*, 2002), but the causal effect has been associated with the fact the species migrates, not where it migrates. To our knowledge, ours is the first phylogenetic comparative study to

show explicitly a link between the route a species migrates and the likelihood of it declining.

We suggest that continental migrants may be declining because of large-scale habitat change. The conversion of upland areas (along with suppression of fire) into agriculture is one of the main reasons for the extinction of the Eskimo curlew *Numenius borealis*, a continental migrant whose numbers plummeted during the late 1800s and early 1900s (Gill, Canevari & Iverson, 1998). Contemporary declines in shorebirds may be a result of continued modification of upland and wetland areas (Jorgensen, 2004). The decrease in the number of small farms has led to larger fields covered predominantly with corn, soybeans or other single-species crops. In many cases, the remaining wetlands are being degraded from sediments and contaminants in the surrounding fields and from the growth of formerly uncommon plant species when herbivores are removed. Earlier planting of crops and the use of no-till agricultural practices may have also decreased the value of upland areas to shorebirds (L. Morris, pers. comm.).

An alternative explanation for why continental migrants may be declining could be the increase in avian predators across North America since the late 1970s (Hoffman & Smith, 2003). Predation pressure may be especially acute when individuals aggregate at migratory staging and stop-over sites (Reed, 1999). However, this is unlikely to explain declines associated with continental migrants for two reasons. First, raptor numbers have increased throughout North America (Hoffman & Smith, 2003) and yet declines in shorebird numbers are only associated with continental and, to a lesser extent, oceanic migrants. Second, detailed studies on western sandpipers *Calidris mauri* at stopover sites on the Strait of Georgia indicate that increased raptor numbers are not actually leading to declines in this species (Ydenberg *et al.*, 2004). Rather, the length of stay of western sandpipers at this stopover site is decreasing with increasing predator numbers, suggesting that the birds have adapted their migration strategy in response to the heightened predation risk. Of course, this does not preclude predation by raptors as a cause of decline in other shorebird species.

In contrast to coastal migrants, protection of habitats in interior regions is complicated because many shorebirds rely on small, often ephemeral, wetlands scattered over a large area (Skagen & Knopf, 1993; Skagen, 1997; Brown *et al.*, 2001). These sites are seldom recognized by the Western Hemisphere Shorebird Reserve Network and Important Bird Areas initiatives, which seek to highlight and thereby protect larger stopover sites (Myers *et al.*, 1987; see <http://www.manomet.org/WHSRN/> and http://www.audubon.org/bird/iba/iba_intro.html). These wetlands have been lost extensively during the past and present centuries (Senner & Howe, 1984). Only a few, large interior sites have been protected (e.g. Cheyenne Bottoms and Quivira National Wildlife Refuge, Kansas) and these may be of little value to species that require ephemeral wetlands or uplands during migration.

Declines in shorebirds that migrate over the ocean may be related to climatic factors that affect the successful passage

of the migrants. The length of the ocean passage and the frequency of unfavourable weather have been associated with declines in North American songbirds that cross the Atlantic Ocean and Gulf of Mexico (Butler, 2000). The effects of unfavourable weather may be less on shorebirds as they migrate before most of the poor weather begins and earlier than landbirds. Nevertheless, global climate change models suggest that weather systems have and will intensify in the North Pacific (Inkley *et al.*, 2004). It is unclear how long-distance oceanic migrants, especially those near their physiological threshold for successfully completing their migrations (Gill *et al.*, 2005), have suffered or will adapt to these changing conditions.

Habitat loss or degradation on the non-breeding areas may also explain declines in continental and oceanic migrants. This is supported by the increase in explanatory power of our model with the introduction of the variable 'threat on the non-breeding grounds'. Although the scores given in USSCP (2004) describe only the intensity of the threat, it is evident from *The birds of North America* species accounts and regional conservation plans that habitat loss and degradation are likely major contributors. In contrast, the fact that species that migrate along coastal areas were not associated with population declines implies that the protection of key, and much more notable, large stopover sites along the Pacific and Atlantic coasts may be helping to reduce the number of species declining that use these migration routes. A notable exception to this are the recent declines in red knots associated with over-harvesting of horseshoe crabs in Delaware Bay (Baker *et al.*, 2004). In this case, it appears that the habitat was protected but the food resource was not.

Although we have identified statistically significant correlates of recent population declines in North American breeding shorebirds, the overall explanatory power is only moderate. Twelve per cent of the variation in population trends among species was explained by continental migration alone, and a much smaller percentage was explained by oceanic migration and threats on the non-breeding grounds. Altogether, these three variables explained almost 28% of the variation. Why is the explanatory power of our model not higher? We offer three possible explanations. First, the data on population trends were at times relatively unsophisticated. For example, when survey data were unavailable population trend data were based on the opinion of scientists familiar with the species (Donaldson *et al.*, 2000; Brown *et al.*, 2001). Nonetheless, the trend estimates used in our analyses represent the best available information and new data are not likely to be present soon. The recently developed North American shorebird monitoring program (PRISM; Harrington *et al.*, 2002) is projected to take a minimum of 7–10 years to provide population trend data once it is fully implemented (J. Bart, pers. comm.). As more precise data on population status, including estimates of annual decline, become available, the relationships between extent of decline and these explanatory factors may be stronger. Second, it was not always easy to classify a species' migration pattern. For example, species that use different

patterns of movement within the continental flyway (e.g. narrow band, widespread, narrow band and widespread, jumps and crossband; see Skagen *et al.*, 1999) were clumped together, and species that use multiple migration routes were classified as using two patterns (e.g. American golden-plovers *Pluvialis dominica* migrate continentally during northward migration but over the ocean during southward migration). Increasing the resolution of our data may further elucidate the relationship between migration routes and population trends. Third, our models are based primarily on potential intrinsic correlates of population declines, whereas it is likely that extrinsic factors are important and indeed may interact with intrinsic factors (Owens & Bennett, 2000; Cardillo *et al.*, 2004). We found weak evidence that the intensity of threat on the non-breeding grounds influenced population trends. However, detailed species-specific data on putative environmental correlates of decline are not readily available for our dataset and additional studies are needed to determine how habitat loss and degradation, climatic conditions and other factors (e.g. conditions on the breeding grounds; Morrison *et al.*, 1994) affect the survival of shorebirds throughout their range. Furthermore, these types of potential extrinsic threat may be spatially aggregated rather than specific to any given species; thus it may be more fruitful to investigate these types of issues at a spatial rather than species or phylogenetic level.

An important additional outcome of our analyses is that population trend was unrelated to phylogeny in our sample of North American shorebirds. Most cross-species studies of population declines and extinction risk assume that complete phylogenetic correction is necessary (see Fisher & Owens, 2004). However, as our analyses show, this is not necessarily the case. Phylogenetic correction may be appropriate but cannot be assumed a priori for many traits. Although the results of phylogenetic and species regressions are often qualitatively similar, this raises the issue of whether correlates of extinction risk and population declines have been correctly identified in some previous studies.

Taken together, our results indicate that the route a shorebird migrates in North America, especially if via a continental route, is associated with more severe population decline. However, the low explanatory power of our models demonstrates that other factors require consideration, and we suggest that extrinsic factors are likely to be important and should be investigated. Finally, our results also highlight the taxonomic and regional idiosyncrasies of population declines as migration route has not previously been identified as a correlate of decline.

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References

- Alaska Shorebird Working Group (2000). *A conservation plan for Alaska Shorebirds*. Unpublished report, Alaska Shorebird Working Group. Available through U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Baker, A.J., González, P.M., Piersma, T., Niles, L.J., de Lima Serrano do Nascimento, I., Atkinson, P.W., Clark, N.A., Minton, C.D.T., Peck, M.K. & Aarts, G. (2004). Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proc. Roy. Soc. Lond. Ser. B* **271**, 875–882.
- Bennett, P.M. & Owens, I.P.F. (2002). *Evolutionary ecology of birds: life history, mating system and extinction*. Oxford: Oxford University Press.
- BirdLife International (2004). *State of the world's birds 2004: indicators for our changing world*. Cambridge, UK: BirdLife International.
- Blomberg, S.P., Garland, T. Jr. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.
- Brown, S., Hickey, C., Harrington, B. & Gill, R. (2001). *The United States shorebird conservation plan*. 2nd edn. Manomet, MA: Manomet Center for Conservation Studies.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. New York: Springer-Verlag.
- Butler, R.W. (2000). Stormy seas for some North American songbirds: are declines related to severe storms during migration? *Auk* **117**, 518–522.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004). Human population density and extinction risk in the world's carnivores. *Publ. Lib. Sci. Biol.* **2**, 909–914.
- Committee for Holarctic Shorebird Monitoring (CHASM) (2004). Monitoring Arctic-nesting shorebirds: an international vision for the future. *Wader Study Group Bull.* **103**, 2–5.
- Donaldson, G., Hyslop, C., Morrison, R.I.G., Dickson, H.L. & Davidson, I. (2000). *Canadian shorebird conservation plan*. Ottawa: Canadian Wildlife Service.
- Dunn, P.O., Whittingham, L.A. & Pitcher, T.E. (2001). Mating systems, sperm competition, and the evolution of sexual size dimorphism in birds. *Evolution* **55**, 161–175.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Figuerola, J. (1999). A comparative study on the evolution of reversed size dimorphism in monogamous waders. *Biol. J. Linn. Soc.* **67**, 1–18.
- Fisher, D.O. & Owens, I.P.F. (2004). The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391–398.
- Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of the evidence. *Am. Nat.* **160**, 712–726.
- Gaston, K.J. & Blackburn, T.M. (1995). Birds, body size and the threat of extinction. *Philos. Trans. Roy. Soc. Lond. Ser. B* **347**, 205–212.
- Gill, R.E. Jr., Canevari, P. & Iverson, E.H. (1998). Eskimo curlew (*Numenius borealis*): number 347. In *The birds of North America*: 1–28. Poole, A. & Gill, F. (Eds). Philadelphia: The Birds of North America, Inc.
- Gill, R.E. Jr., Piersma, T., Hufford, G., Servrancks, R. & Riegen, A. (2005). Crossing the ultimate ecological barrier: evidence for an 11,000-km-long nonstop flight from Alaska to New Zealand and Eastern Australia by bar-tailed godwits. *Condor* **107**, 1–20.
- Harrington, B.A., Brown, S.C., Corven, J. & Bart, J. (2002). Collaborative approaches to the evolution of migration and the development of science-based conservation in shorebirds. *Auk* **119**, 914–921.
- Harvey, P.H. & Pagel, M.D. (1991). *The comparative method in evolutionary biology*. Oxford series in ecology and evolution. Oxford: Oxford University Press.
- Hayman, P., Marchant, J. & Prater, T. (1986). *Shorebirds: an identification guide to the waders of the world*. Boston: Houghton Mifflin Co.
- Hoffman, S.W. & Smith, J.P. (2003). Population trends of migratory raptors in western North America. *Condor* **105**, 397–419.
- Howe, M.A., Geissler, P.A. & Harrington, B.A. (1989). Population trends of North American shorebirds based on the International Shorebird Survey. *Biol. Conserv.* **49**, 185–199.
- Ihaka, R. & Gentleman, R. (1996). R: a language for data analysis and graphics. *J. Comput. Graph. Stat.* **5**, 299–314.
- Inkley, D.B., Anderson, M.G., Blaustein, A.R., Burkett, V.R., Felzer, B., Griffith, B., Price, J. & Root, T.L. (2004). *Global climate change and wildlife in North America*. Wildlife Society Technical Review 04-2. Bethesda, MD: The Wildlife Society.
- International Wader Study Group (2003). Waders are declining worldwide. Conclusions from the 2003 International Wader Study Group Conference, Cádiz, Spain. *Wader Study Group Bull.* **101/102**, 8–12.
- Jorgensen, J.G. (2004). *An overview of shorebird migration in the Eastern Rainwater Basin*. Nebraska Ornithologists' Union occasional paper number 8, Nebraska.
- Møller, A.P. (2000). Sexual selection and conservation. In *Behavior and conservation*: 55–90. Birkhead, T.R. & Møller, A.P. (Eds). London: Academic Press.
- Morrison, R.I.G., Downes, C. & Collins, B. (1994). Population trends of shorebirds on fall migration in eastern Canada 1974–1991. *Wilson Bull.* **106**, 431–447.
- Morrow, E.H. & Pitcher, T.E. (2003). Sexual selection and the risk of extinction in birds. *Proc. Roy. Soc. Lond. Ser. B* **270**, 1793–1799.

- Myers, J.P., Morrison, R.I.G., Antas, P.Z., Harrington, B.A., Lovejoy, T.A., Sallaberry, M., Senner, S.E. & Tarak, A. (1987). Conservation strategy for migratory species. *Am. Sci.* **75**, 19–26.
- Owens, I.P.F. & Bennett, P.M. (2000). Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl. Acad. Sci. USA* **97**, 12144–12148.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988). On the risk of extinction. *Am. Nat.* **132**, 757–785.
- Pitelka, F.A., Holmes, R.T. & MacLean, S.F. Jr. (1974). Ecology and evolution of social organization in arctic sandpipers. *Am. Zool.* **14**, 185–204.
- Poole, A. & Gill, F. (Eds) (2003). *The birds of North America*. Philadelphia: The Birds of North America, Inc.
- Prinzing, A., Brändle, M., Pfeifer, R. & Brandl, R. (2002). Does sexual selection influence population trends in European birds? *Evol. Ecol. Res.* **4**, 49–60.
- Purvis, A., Gittleman, J.L., Cowlshaw, G. & Mace, G.M. (2000). Predicting extinction risk in declining species. *Proc. Roy. Soc. Lond. Ser. B* **267**, 1947–1952.
- Reed, J.M. (1999). The role of behavior in recent avian extinctions and endangerments. *Conserv. Biol.* **13**, 232–241.
- Reynolds, J.D. (2003). Life histories and extinction risk. In *Macroecology: concepts and consequences*: 195–217. Blackburn, T.M. & Gaston, K.J. (Eds). Oxford: Blackwell Publishing.
- Senner, S.E. & Howe, M.A. (1984). Conservation of Nearctic shorebirds. In *Shorebirds: breeding behavior and populations. Behavior of marine animals*. Vol. 5: 379–421. Burger, J. & Olla, B. (Eds). New York: Plenum Press.
- Skagen, S.K. (1997). Stopover ecology of transitory populations: the case of migrant shorebirds. *Ecol. Stud.* **125**, 244–269.
- Skagen, S.K. & Knopf, F.L. (1993). Toward conservation of midcontinental shorebird migrations. *Conserv. Biol.* **7**, 533–541.
- Skagen, S.K., Sharpe, P.B., Waltermire, R.G. & Dillion, M.B. (1999). *Biogeographical profiles of shorebird migration in midcontinental North America*. Biological science report USGS/BRD/BSR – 2000-0003, U.S. Government Printing Office, Denver, CO.
- Székely, T., Freckleton, R.P. & Reynolds, J.D. (2004). Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proc. Natl. Acad. Sci. USA* **101**, 12224–12227.
- Székely, T., Reynolds, J.D. & Figuerola, J. (2000). Sexual size dimorphism in shorebirds, gulls, and alcid: the influence of sexual and natural selection. *Evolution* **54**, 1404–1413.
- Tanaka, Y. (1996). Sexual selection enhances population extinction in a changing environment. *J. Theor. Biol.* **180**, 197–206.
- Thomas, G.H. & Székely, T. (2005). Evolutionary pathways in shorebird breeding systems: sexual conflict, parental care and chick development. *Evolution* **59**, 2222–2230.
- Thomas, G.H., Wills, M.A. & Székely, T. (2004). A supertree approach to shorebird phylogeny. *BMC Evol. Biol.* **4**, 28.
- U.S. Shorebird Conservation Plan (2004). *High priority shorebirds – 2004*. Unpublished report, U.S. Fish and Wildlife Service, 4401 N. Fairfax Dr., MBSP 4107, Arlington, VA, USA.
- Ydenberg, R.C., Butler, R.W., Lank, D.B., Smith, B.D. & Ireland, J. (2004). Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proc. Roy. Soc. Lond. Ser. B* **271**, 1263–1269.
- Zöckler, C., Delany, S. & Hagemeyer, W. (2003). Wader populations are declining – how will we elucidate the reasons? *Wader Study Group Bull.* **100**, 202–211.

Supplementary material

The following material is available for this article online:

Appendix S1 Population trend, migratory behaviour, biogeography, life history, sexual selection traits, and breeding and non-breeding ground threat scores of North American shorebirds.

This material is available as part of the online article from <http://www.blackwell-synergy.com>