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The evolution of sexual bill-size dimorphism in shorebirds: a morphometric test of the resource partitioning hypothesis

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ABSTRACT

Question: Is sexual dimorphism in shorebirds an adaptation to reduce resource competition between males and females?

Hypothesis: If selection for resource partitioning between the sexes has contributed to dimorphism, then the degree of sexual size dimorphism (SSD) in resource-exploiting characters – such as those related to feeding – should exceed that expected from sexual selection alone.

Data: Morphometric data from 151 species of shorebirds (Charadriiformes).

Methods: We compared the degree and direction of SSD between a resource-exploiting trait (bill length) and a non-resource-exploiting trait (body size). If bill-SSD exceeds body size-SSD, then resource partitioning may contribute to morphological differentiation of the sexes in shorebirds. We also tested whether SSD is more pronounced in migrant than non-migrant species.

Conclusions: From species level data it appears that bill dimorphism is more pronounced than body size dimorphism, and is more common in migrant than non-migrant shorebirds. This observation from extant taxa suggests a role for resource partitioning in promoting SSD. The phylogenetic effect on both of these correlations is significant, however, to the extent that shared ancestry, rather than contemporary selection, is sufficient to explain why resource-exploiting traits and migrants are more sexually dimorphic.

Keywords: bird migration, resource partitioning hypothesis, sexual bill-size dimorphism, sexual selection, shorebirds.

INTRODUCTION

In many animal species, males and females are not noticeably different in size, yet in others the sexes are dramatically different. Sexual size dimorphism (SSD) occurs in a wide range of invertebrates and vertebrates (Fairbairn *et al.*, 2007). Variation in SSD is often attributed to sexual selection – either in response to female choice or in response to male–male competition, with males typically larger than females (Andersson, 1994).

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However, sexual selection does not underlie all instances of SSD. For example, female sea kraits tend to have relatively larger heads than males, and they forage on larger sized prey (Shetty and Shine, 2002). Cases where sexual dimorphism is functionally associated with resource use suggest that natural selection rather than sexual selection is a driving force. An alternative explanation for SSD is therefore that the sexes are selected to reduce inter-sexual competition by specializing on different ecological niches (Shine, 1989), particularly foraging niches (Selander, 1966; Slatkin, 1984; Hedrick and Temeles, 1989).

Sexual size dimorphism is common in birds. In fact, the discovery of the astonishing range of bill sizes and shapes in the *Geospiza* finches played a major role in developing Darwin's theory of evolution by natural selection. Since then, studies on intra- and inter-specific variation in bill morphology have contributed to our understanding of natural and sexual selection for SSD (Price, 1984; Smith, 1993; Grant and Grant, 2003; Temeles *et al.*, 2010). Despite this understanding, large-scale tests of the resource partitioning hypothesis remain rare because data on measures of natural versus sexual selection are not typically available for whole clades, and even for single species it is difficult to link sexual differences in trophic morphology to sexual differences in resource use (Shine, 1989; Temeles *et al.*, 2000, 2010).

Once sexual selection has given rise to body size differences between males and females, further divergence in bill morphology may occur as a result of competition for trophic resources (Price, 1984). Thus, any selection for sex-biased foraging to reduce intra-specific competition should affect bill morphology in particular, and thus the degree of SSD for this trait should exceed that explained by sexual selection on body size alone (Selander, 1966, 1972).

Here we test the resource partitioning hypothesis in shorebirds, which represent several clades within the order Charadriiformes. Besides shorebirds, the Charadriiformes include gulls, terns, and alcids (Thomas *et al.*, 2004). Shorebirds predominantly use inland and coastal wetlands, while species in the other clades are marine birds, and as such are not included in our analyses. Shorebirds are a suitable model to test the idea that resource partitioning is important to sexual dimorphism because species in this clade show extreme variation in SSD (Jehl and Murray, 1986). Moreover, the clade is species-rich and an estimate of the complete phylogeny is available, making a large-scale comparative analysis possible.

We define SSD as dimorphism between the sexes in any body size metric, not just body size *per se*, which differs from prevailing usage, which tends to refer to dimorphism in body size only. Sexual size dimorphism in body size in shorebirds has been attributed to sexual selection (Székely *et al.*, 2000). However, if bill-SSD exceeds that observed for other measures of body size, or if the direction of dimorphism is opposite between trophic (bill) and non-trophic (tarsus) characters, then sexual selection alone is unlikely to account for the full range of size dimorphisms. Moreover, if natural selection is important for generating SSD in bill length, then we predict that bill-SSD will vary as a function of migratory status.

Two migration scenarios are possible: a high degree of bill-SSD evolves more often in resident species where males and females share feeding habitat throughout the year, and where competition is thus likely to be more persistent. Alternatively, bill-SSD may evolve as a result of selection due to differential habitat use in differential migrants, where males and females spend most of the annual cycle foraging at geographically separated habitats (Cristol *et al.*, 1999). The current lack of data on differential migration in shorebirds (Nebel, 2007) does not allow us to test for the degree of bill-SSD in differential migrants only. However, a difference in the degree of bill-SSD between residents and migratory shorebirds (including

non-differential migrants) would nevertheless provide support for the resource partitioning hypothesis.

To explore the role of migration in promoting SSD in shorebirds, we perform a comparative test of whether SSD in bill-size differs between migrant and non-migrant species. If so, then migration may be a life-history trait that affects the evolutionary likelihood for sexual size dimorphism. For all comparative tests, we use the most recent complete species-level phylogeny available for shorebirds (Thomas *et al.*, 2004).

METHODS

Estimating sexual size dimorphism from morphometric data

We used previously published morphometric data for 151 shorebird species (from Lislevand *et al.*, 2007). From these data, we estimated male and female bill and tarsus length for each species. From species' mean values, we estimated the degree of SSD for both traits by calculating the 'size dimorphism index' (SDI). The SDI is calculated as the female-to-male size ratio, minus 1 (Lovich and Gibbons, 1992). This index provides an ideal estimate of size dimorphism because, unlike raw ratios, it is linear (a doubling in magnitude of dimorphism is reflected in a doubling of the SDI score), it is symmetrical (changes in male or female size yield the same absolute SDI score), and it contains directional information (positive SDI scores indicate females are larger, whereas negative scores indicate males are larger). We used the absolute values of SDI when we were interested in the degree of dimorphism, but not in its direction.

We used morphometric data from *bill length* to represent the SDI for a specific trophic character, and data from *tarsus length* to represent the SDI for a non-trophic character. This characterization is imperfect, but reasonable. First, tarsus morphology may not be strictly a non-trophic character for every species; female bar-tailed godwits have longer legs that permit them to forage in deeper mud than males (Smith and Evans, 1973), but in general variation in bill morphology is more directly related to variation in feeding habitats than tarsus morphology. Second, among shorebirds tarsus shows some variation with environmental conditions on the breeding grounds (Cartar and Morrison, 2005). Despite its limitations, tarsus is the best indicator of a non-trophic character available to us because other characters, like body mass, show strong variation with season and individual condition (Piersma and Davidson, 1991; Witter and Cuthill, 1993), and wing length varies with migratory status (Voelker, 2001; Milá *et al.*, 2008), one of the main factors in our analysis. We then compared SDI values for trophic and non-trophic characters between migrants and residents, using the migratory classification of del Hoyo *et al.* (1996).

Phylogenetically informed methods

Comparisons of characters across species can result in statistical bias if related species are similar as a result of common ancestry (Felsenstein, 1985). However, applying phylogenetically corrected methods to characters that are not phylogenetically autocorrelated can create problems of statistical non-independence where none existed initially (Gittleman and Luh, 1994). We therefore first assessed whether absolute SDI in bill, tarsus, wing, and body mass were phylogenetically correlated by implementing the test for serial independence (Abouheif, 1999) using the computer program Phylogenetic Independence v.2.0 (Reeve and Abouheif, 2003; see Abouheif, 1999). As all characters showed significant phylogenetic autocorrelation (bill:

$P = 0.001$; tarsus: $P = 0.002$; wing: $P = 0.001$; mass: $P = 0.001$), we used a supertree of shorebirds and the Pdtree module (Midford *et al.*, 2005) of Mesquite (Maddison and Maddison, 2006) to calculate phylogenetically independent contrasts (Felsenstein, 1985). Paired *t*-tests were then used to determine if absolute SDI (log-transformed) differed between bill, tarsus, wing, and body mass for both raw (uncorrected) data and independent contrasts using the statistical software SYSTAT (SYSTAT, 2007). Owing to availability of morphometric data, there are minor differences in sample size between tests. We used the Bonferroni correction to adjust the significance threshold for multiple comparisons.

Determination of excessive bill-SDI

To determine whether trophic characters differ in magnitude or direction of SSD from non-trophic characters, we identified those species for which bill-SDI was exceedingly large (defined below) relative to tarsus-SDI, or for which bill-SDI showed the opposite sign to tarsus-SDI. While the sign is easily identified directly from each SDI-value (positive vs. negative), there is no inherent cut-off to recognize differences in magnitude. Accordingly, we devised a two-step test for significance. First, we subtracted absolute tarsus-SDI from absolute bill-SDI to obtain a body-size-corrected value of bill-SDI – hereafter 'residual bill-SDI'. We then compared this residual value to the null expectation if trophic and non-trophic traits are perfectly co-dimorphic – that is, if residual bill-SDI equals zero. If any residual bill-SDI value deviated from the null expectation by more than two standard deviations (0 ± 2 S.D.), we inferred that dimorphism in the trophic character does exceed that for the non-trophic character. Although this cut-off is arbitrary, it is suitable given that two standard deviations approximate 95% of the variance. We also considered a less (±1 S.D.) and more (±3 S.D.) conservative cut-off to recognize excessive trophic trait dimorphism (Fig. 1).

Testing for correlated evolution between SSD and migratory status

We used the most complete phylogenetic hypothesis available for shorebirds (Thomas *et al.*, 2004) to test for correlation between SSD (using residual bill-SDI) and migratory status. We then used the program TreeEdit (Rambaut and Charleston, 2001) to prune the shorebird supertree of taxa for which morphometric data were unavailable. From this pruned tree structure [including 135 of an original 366 taxa (Thomas *et al.*, 2004)], we again used TreeEdit to randomly resolve polytomies and assign to these resolutions a marginally positive branch length. We used Pagel and colleagues' (2004) comparative method to test for correlated evolution between SSD and migratory status by comparing the fit (log-likelihood) of two models; one corresponding to independent evolution, the other to correlated evolution such that changes in one trait depend on the background state of the other (Pagel *et al.*, 2004; Barker and Pagel, 2005). If the dependent model is no more likely than the independent model, as evaluated by likelihood ratio tests, then there is no evidence for correlated evolution. We implemented this test under maximum likelihood criteria using the program BayesTraits [available at www.evolution.rdg.ac.uk (Pagel and Meade, 2006)].

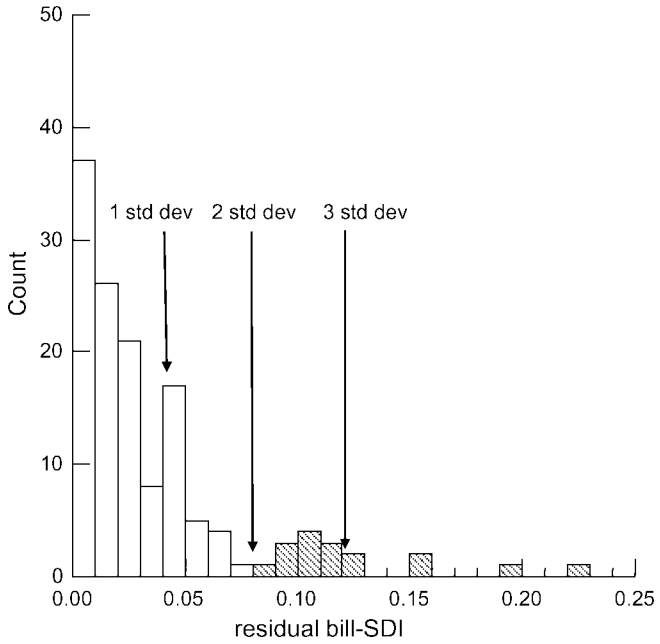

Fig. 1. Frequency distribution of residual bill-SDI. Species that exceeded two standard deviations (hatched bars) were considered to show excessive trophic trait dimorphism.

RESULTS

SDI in trophic vs. non-trophic characters

First we examined the raw SDI data. The degree of sexual size dimorphism varied between trophic (bill) and non-trophic (tarsus) characters. The absolute degree of dimorphism was higher for bill length (mean absolute SDI = 0.057) than it was for tarsus length (mean absolute SDI = 0.031; Fig. 2), as indicated by a paired *t*-test ($t_{135} = 5.422$, $P < 0.001$). Dimorphism in bill length was also more variable (S.D. = 0.055; range = 0.266) than for tarsus length (S.D. = 0.028; range = 0.145), as evaluated by the *F*-test for equality of variances ($F_{135,135} = 0.474$, $P < 0.001$).

We also calculated SDI for both wing length and body mass. We were thus able to test whether pronounced SDI in trophic over non-trophic traits is robust against alternate measures of body size. A comparison of absolute SDI values between all three non-trophic traits indicated that tarsus length (mean = 0.031), wing length (mean = 0.029, S.D. = 0.031, $n = 135$), and cubic root (Peig and Green, 2009) of body mass (mean = 0.041, S.D. = 0.0438, $n = 110$) were smaller than bill length (mean = 0.057), suggesting that the trophic characters are generally more dimorphic than the non-trophic traits. A paired *t*-test confirmed that bill-SDI was also more dimorphic than wing-SDI ($t_{134} = 6.276$, $P < 0.001$) as well as body mass-SDI ($t_{109} = 2.753$, $P = 0.021$). We then performed pair-wise comparisons of the standardized independent contrasts of the absolute SDI values of the four morphometric characters, but did not detect any differences among them (bill vs. tarsus: $t_{133} = -1.437$, $P = 0.919$; bill vs. wing: $t_{133} = -0.352$, $P = 1.000$; tarsus vs. wing: $t_{133} = 1.619$, $P = 0.647$; bill

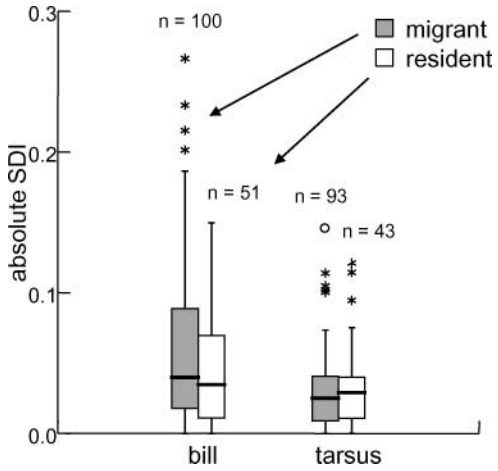

Fig. 2. Absolute size dimorphism index (SDI) for bill and tarsus for migrant and resident shorebird species. The box plot shows the median (thick horizontal line), 50% range (box), range (whiskers), outliers (asterisks), and extreme outliers (circles). The plot shows that the trophic trait (bill) was more dimorphic than the non-trophic trait (tarsus) and that migrants were more dimorphic for the trophic, but not the non-trophic trait, than non-migrants.

vs. mass: $t_{133} = -0.333$, $P = 1.000$; tarsus vs. mass: $t_{133} = 1.097$, $P = 1.000$; wing vs. mass: $t_{133} = -0060$, $P = 1.000$).

Excessive bill-SDI

Of the 136 species used for this test, 17 species (12%) showed a disproportionate degree of dimorphism in the trophic versus non-trophic character, as evidenced by an absolute residual bill-SDI value in excess of the null expectation (see online Appendix at: www.evolutionary-ecology.com/data/2588Appendix.pdf). For these taxa, trophic and non-trophic characters thus appear to differ in the magnitude of dimorphism between males and females. For all of these cases, bill length dimorphism is in excess of the level expected from dimorphism in body size alone. Residual bill-SDI showed significant phylogenetic autocorrelation ($P = 0.001$), as shown by the test for serial independence. Indeed, with reference to the phylogenetic supertree of Thomas *et al.* (2004), 11 of these species are clustered within three genera – *Numenius* (curlews), *Limosa* (godwits), and *Calidris* (sandpipers) – and all of them are migrants. The other six species that show evidence of resource partitioning belong to the oystercatchers (Haematopodini), and include both migrant and non-migrant species.

We also identified 19 species (14%) for which the sign of dimorphism (regardless of whether it was considered 'excessive' or not) differed between the trophic and non-trophic trait (see www.evolutionary-ecology.com/data/2588Appendix.pdf). Of these, 14 species had females with larger bills despite males with larger bodies (tarsi), and five species showed the opposite pattern – that is, males with larger bills despite females with larger bodies. While male and female shorebirds typically covary in magnitude (87.5% of species) and direction (86% of species) of trophic and non-trophic traits, there are important exceptions (19 of 129 species) that seem to violate these trends.

SDI and migration

A comparison of mean SDI scores between migrant and non-migrant species indicated that migrants were significantly more dimorphic for the trophic ($t_{149} = 1.995$, $P = 0.048$) but not the non-trophic ($t_{95} = 0.347$, $P = 0.730$) trait than non-migrants (Fig. 2). However, taking phylogenetic relationships – and thus the statistical non-independence of taxa – into account, Pagel's discrete likelihood ratio test indicated that evolutionary changes in migratory status were not good predictors of sexual dimorphisms. Specifically, the fit of the dependent model in which gains and losses in 'excessive' sexual dimorphism were constrained to covary with gains and losses in migrant status is not significantly better than that of the independent model (LRT statistic = 1.88, $P > 0.05$, d.f. = 4). This lack of correlation between migratory status and presence of residual bill-SDI is upheld even when more (LRT statistic = 2.12, $P > 0.05$, d.f. = 4) and less (LRT statistic = 2.36, $P > 0.05$, d.f. = 4) stringent criteria are used to define SSD (referring to 3 and 1 standard deviations, respectively). Thus, shorebirds that migrate appear no more or less likely to evolve excessive bill SSD than resident species.

DISCUSSION

SDI in trophic vs. non-trophic traits

We use morphometric data from shorebirds to test the idea that selection for differential resource use between males and females contributes to sexual bill dimorphism. To do so, we compared the level of dimorphism between two types of morphological characters: bill length as a resource exploiting trophic character, and tarsus length as an overall measure of body size that is not directly related to trophic resource use. Using the conventional size dimorphism index of Lovich and Gibbons (1992) to estimate degree and direction of dimorphism, we found two patterns in the raw (phylogenetically uncorrected) data that support the resource partitioning hypothesis.

First, bill length dimorphism was significantly more pronounced than tarsus length dimorphism, suggesting that characters related to resource exploitation are more sexually dimorphic than character sets unrelated to resource use. Second, sexual bill length dimorphism was opposite to that of tarsus length in 19 species (14%). Assuming that differences in SSD among traits reflect differences in selective pressure, rather than allometric constraints on development, this striking pattern suggests that male–female dimorphisms in resource-exploiting traits and those in overall body size are responding to different selection pressures, and that these differences are not just a matter of degree but a matter of type.

We did not, however, detect a difference in the absolute SDI of bill and tarsus measures of body size when using independent contrasts. The pattern for bill and body size that we observe above is therefore adequately explained by shared ancestry among species rather than contemporary selection on each species independently. If resource partitioning does explain the excessive SSD for resource-exploiting traits (bill), this effect is likely historical rather than contemporary.

Migration and SSD

Our analysis of the raw data showed that bill-SSD was more pronounced and more variable in migrants than residents. The non-trophic trait, by contrast, did not vary between the two groups. These findings support our prediction that bill-SSD evolves through differential use of food resources by differential migrants, where males and females exploit different feeding niches during the non-breeding season. Indeed, all shorebird species that are known to be differential migrants [western sandpiper (Nebel *et al.*, 2002), least sandpiper (Nebel, 2006), spotted sandpiper, ruff (Cristol *et al.*, 1999), curlew sandpiper, eastern curlew, bar-tailed godwit (Nebel, 2007)] show pronounced sexual bill dimorphism. The comparative test for correlated evolution between SSD and migratory status did, however, not support this hypothesis. It is therefore unlikely that migration co-evolves with sexual dimorphism in shorebirds.

CONCLUSIONS

In this study, we show that sexual size dimorphism in shorebirds is more pronounced in trophic than non-trophic traits, and more common in migrants than in non-migrant shorebird species. These patterns are not obvious from single-species studies, and only emerge from large-scale comparative studies of morphometric data. The comparative approach reveals, however, that these patterns are not strictly the result of contemporary natural or sexual selection, but rather reflect the shared ancestry of extant species.

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