Phenotypic divergence in two sibling species of shorebird: Common Snipe and Wilson's Snipe (Charadriiformes: Scolopacidae)

TIAGO M. RODRIGUES,[1,2]* (iD) EDWARD H. MILLER,[3] (iD) SERGEI V. DROVETSKI,[4]† (iD) ROBERT M. ZINK,[5] (iD) JON FJELDSÅ[6] (iD) & DAVID GONÇALVES[1,2] (iD)

[1]*CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, no. 7, Vairão, 4485-661, Portugal*

[2]*Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Rua do Campo Alegre s/n, Porto, 4169-007, Portugal*

[3]*Department of Biology, Memorial University, St. John's, NL, A1B 3X9, Canada*

[4]*Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC, 20004, USA*

[5]*School of Natural Resources, School of Biological Sciences, Nebraska State Museum, Lincoln, NE, 68583, USA*

[6]*Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark*

Natural and social selection are among the main shapers of biological diversity but their relative importance in divergence remains understudied. Additionally, although neutral evolutionary processes may promote phenotypic divergence, their potential contribution in speciation is often overlooked in studies of comparative morphology. In this study, we investigated phenotypic differentiation in two allopatric shorebirds: the Palaearctic Common Snipe *Gallinago gallinago* and the Nearctic Wilson's Snipe *Gallinago delicata*. Specimens of Common Snipe (n = 355 skins, n = 163 skeletons) and Wilson's Snipe (n = 403 skins, n = 141 skeletons) in natural history collections were examined to quantify differences in skeletal and external measurements, and measures of wing and tail plumage variables. The species do not differ in skeletal variables except for the relatively larger sternum of the Common Snipe. The two species do not differ in multivariate wing size or shape (pointedness). Previously known plumage differences between these species were confirmed: the Common Snipe has fewer rectrices, longer and wider outermost rectrices, more extensive white on tips of the secondary feathers, and more white in the axillaries. Between-species variance in skeleton, primary length and plumage variables was greater than expected if drift was mainly responsible for phenotypic divergence, suggesting a role of selective processes. However, drift could not be rejected after adjusting for multiple comparisons. Differences in plumage traits were greater than in skeletal or external measurements. Because snipe use plumage traits in signalling, the results suggest a more rapid divergence in socially selected traits between these species than in traits related to resource use.

Keywords: *Gallinago delicata*, *Gallinago gallinago*, genetic drift, museum collections, natural selection, social selection, speciation.

†Present address: USGS Patuxent Wildlife Research Center, 10300 Baltimore Avenue, BARC-East Bldg. 308, Beltsville, MD, 20705, USA.

*Corresponding author.
Email: trodrigues@cibio.up.pt
Twitter: @TiagoMRodrigues

More than a decade after the publication of his explanation for the evolutionary role of natural selection (Darwin 1859), Darwin devoted an entire book to another mechanism that, along with natural selection, also contributes to descent with

modification. In *The Descent of Man and Selection in Relation to Sex*, Darwin (1871) developed a concept that he had introduced briefly in *The Origin* (Darwin 1859; pp. 87–90): sexual selection, a mechanism that 'depends on the advantage that certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction' (Darwin 1871; p. 256). Sexual selection was later included under the umbrella of social selection (West-Eberhard 1983), a concept that accommodates selection on traits that function in many kinds of intraspecific social interactions (West-Eberhard 1983, 2014, Price 2008, Lyon & Montgomerie 2012, Tobias *et al.* 2012, McEntee *et al.* 2016). The relative contributions of natural and social selection as drivers of biological diversity merit further study (West-Eberhard 1983, 2014, Price 2008, Lyon & Montgomerie 2012, Tobias *et al.* 2012, McEntee *et al.* 2016, Littleford-Colquhoun *et al.* 2019).

In early stages of divergence, when allopatric populations face similar ecological conditions, social selection can be an important cause of morphological change over time (Winger & Bates 2015) because niche conservatism can impede divergence in traits related to resource use (Wiens *et al.* 2010, Zink 2014). The relative importance of natural and social selection can be evaluated with a trait-based approach (Safran *et al.* 2013) by quantifying divergence in traits with probable primary signalling functions and comparing this with divergence in traits more related to resource use. Many sister taxa and allopatric populations differ primarily in display traits related to mate choice and species recognition, so social selection may be the main cause of divergence, particularly in early stages of differentiation (Panhuis *et al.* 2001, Seddon *et al.* 2013). An example of early divergence is afforded by the Barn Swallow *Hirundo rustica*, in which populations with low genetic differentiation show significant phenotypic differentiation in signalling characters but not in ecological traits (Wilkins *et al.* 2016). Socially selected characters also diverged more rapidly than ecologically relevant traits in *Junco* (Friis & Milá 2020).

Natural and sexual selection also play roles in the evolution of differences between the sexes (Darwin 1859, 1871) but disentangling their relative contributions to the evolution of sexual differences in vocalizations, colour or body size is challenging (Littleford-Colquhoun *et al.* 2019, Price 2019). Among birds, the evolution of sexual-size dimorphism (SSD) seems to be a result of intrasexual competition (Székely *et al.* 2000, 2004, 2007, Drovetski *et al.* 2006, Trefry & Diamond 2017). For most species, this led males, the more competitive sex, to become larger than females; however, several taxa evolved in the opposite direction (Székely *et al.* 2007). Among scolopacids, the evolution of reversed SSD seems to be associated with the demands of males' aerial courtship displays (Székely *et al.* 2000, 2004, 2007), as smaller bodies may be advantageous in flight agility (Trefry & Diamond 2017). However, differences in foraging ecology, parental roles or even the needs imposed by egg production may also explain patterns of SSD (Székely *et al.* 2007).

Phenotypic divergence also may be promoted by neutral evolutionary processes, such as drift (Mayr 1954, Lande 1976, 1980) but because their roles in the evolution of phenotypic traits and behavioural isolation seem minor (Coyne *et al.* 1997, Coyne & Orr 2004, Price 2008), their potential contribution in speciation is seldom tested in comparative studies. Drift alone could not explain phenotypic differentiation across populations of House Sparrow *Passer domesticus* (Holand *et al.* 2011, Geue *et al.* 2016, Cohen & Dor 2018, but see Kekkonen *et al.* 2012) but could not be rejected in other studies, suggesting an occasional role for neutral processes in trait divergence unrelated to resource use or mate choice and species recognition. For instance, neutral processes seem to have been important in the variation of bill length of Berthelot's Pipit *Anthus berthelotii* among Atlantic islands (Spurgin *et al.* 2014, Armstrong *et al.* 2018) and were the main drivers of geographical variation in plumage colour of the Eastern Yellow Robin *Eopsaltria australis* at the continental scale (Morales *et al.* 2017). These results emphasize the need to test this hypothesis in studies of phenotypic divergence before assuming that the patterns under study arise solely from selective pressures.

Snipes (*Gallinago* spp.) are shorebirds, with cryptic plumage and specialized long and flexible bills that they use to probe the soil. The 17 extant species of snipe (Gill & Donsker 2019) exhibit limited plumage differences across species, except in the tail (Tuck 1972), which is a striking component of their ground and aerial displays (Sutton 1981, Cramp & Simmons 1983, Glutz von Blotzheim *et al.*, 1986). In addition, with the exception of the Great Snipe *Gallinago gallinago*, which lacks

an aerial display, the rectrices are responsible for the species-specific instrumental sound that is audible during flight displays (van Casteren *et al.* 2010, Clark & Prum 2015). Other aspects of snipe communication are poorly known but include display of the underwing (Sutton 1981, Cramp & Simmons 1983, Glutz von Blotzheim *et al.* 1986).

This study investigates phenotypic divergence between the closely related Common Snipe *G. gallinago* and Wilson's Snipe *Gallinago delicata* (Fig. 1). The Common Snipe is sympatric with at least four other snipe species across its Palaearctic breeding range, whereas Wilson's Snipe is the only *Gallinago* species that regularly breeds in North America. Slight mitochondrial DNA (mtDNA) differentiation between them suggests ongoing or recent speciation (Zink *et al.* 1995, Baker *et al.* 2009, Kerr *et al.* 2009, Johnsen *et al.* 2010). Fossils of the Common Snipe from the Palaearctic are known from the Early Pleistocene (Mlíkovský 2002). In North America, remains that represent Common Snipe or Wilson's Snipe also are known from the Pleistocene (Bordkorb 1967, Stock & Harris 1992) and have been identified at Rancho La Brea (Stock & Harris 1992) and at a site in Tennessee (Parmalee & Klippel 1982).

Phenotypic variation between Common Snipe and Wilson's Snipe was analysed in traits that probably are of little communicative significance (e.g. body size), others that may be used in optical signalling (e.g. traits of body plumage) and others that are known or likely to be important in communication (e.g. number and size of rectrices), using museum specimens of skeletons and study skins. The null hypothesis of neutral evolution was tested to investigate whether selection could be responsible for the differences observed. If drift was the main process responsible for the divergence, phenotypic variation within species should be proportional to that between species (Lande 1976, 1980, Lofsvold 1988, Ackermann & Cheverud 2002, 2004). The phenotypic distances between species were then evaluated to infer whether social selection could be responsible for the observed patterns.

METHODS

Sampling

Skeletons of fully grown Common Snipe ($n = 163$) and Wilson's Snipe ($n = 141$), and study skins of adult (after the first post-breeding moult) Common Snipe ($n = 355$) and Wilson's Snipe ($n = 403$) in 23 collections (Fig. 1; Acknowledgements and Table S1) were measured. Data on sex and age were taken from specimen tags or collection catalogues. Additionally, age classes of study skins were determined based on patterns of wing coverts and rectrices (Czajkowski 2002, Pyle 2008). Specimens analysed for this study are listed in Table S1.

Data collection

To quantify phenotypic variation in skeleton morphology, 16 skeletal variables were measured (Fig. 2a; terminology follows Baumel & Witmer 1993): (1) *Cranium*, cranial length, from distal end of rostrum maxillare to prominentia cerebellaris; (2) *Premaxilla*, length of premaxilla, from distal end of rostrum maxillare to ginglymus craniofacialis (frontonasal suture); (3) *Sternal length*, length of sternum, from anteriormost point on spina externa to posteriormost point on margo caudalis; (4) *Keel length*, length of sternal keel, from anteriormost point on apex carinae to posteriormost point on margo caudalis; (5) *Keel depth*, depth of sternum, perpendicular to length of sternal keel (along pila carinae), from dorsalmost point on spina externa to margo ventralis; (6) *Coracoid*, maximal length of coracoid, processus acrocoracoideus to distal point of the facies articularis intercoiracoidea; (7) *Humerus*, maximal length of humerus, caput humeri to condylus ventralis; (8) *Radius*, maximal length of radius, cotyla humeralis to facies articularis radiocarpalis; (9) *Ulna*, maximal length of the ulna, olecranon to condylus ventralis; (10) *Carpometacarpus*, maximal length of carpometacarpus, from trochlea carpalis to facies articularis digitalis major; (11) *Phalanx 1*, maximal length of phalanx proximalis digit majoris (along pila cranialis phalangis); (12) *Ischial length*, maximal length of the ischium, from margo iliocranialis to processus terminalis ischii; (13) *Ischial depth*, ischial depth, corpus ischii to crista dorsolateralis; (14) *Femur*, maximal length of the femur, trochanter femoris to condylus lateralis; (15) *Tibiotarsus*, maximal length of the tibiotarsus, crista cnemialis cranialis to condylus lateralis; (16) *Tarsometatarsus*, maximal length of the tarsometatarsus, eminentia intercotylaris to trochlea metatarsi III. Lengths of cranium and premaxilla were used to estimate length of the braincase (*Braincase = Cranium −*
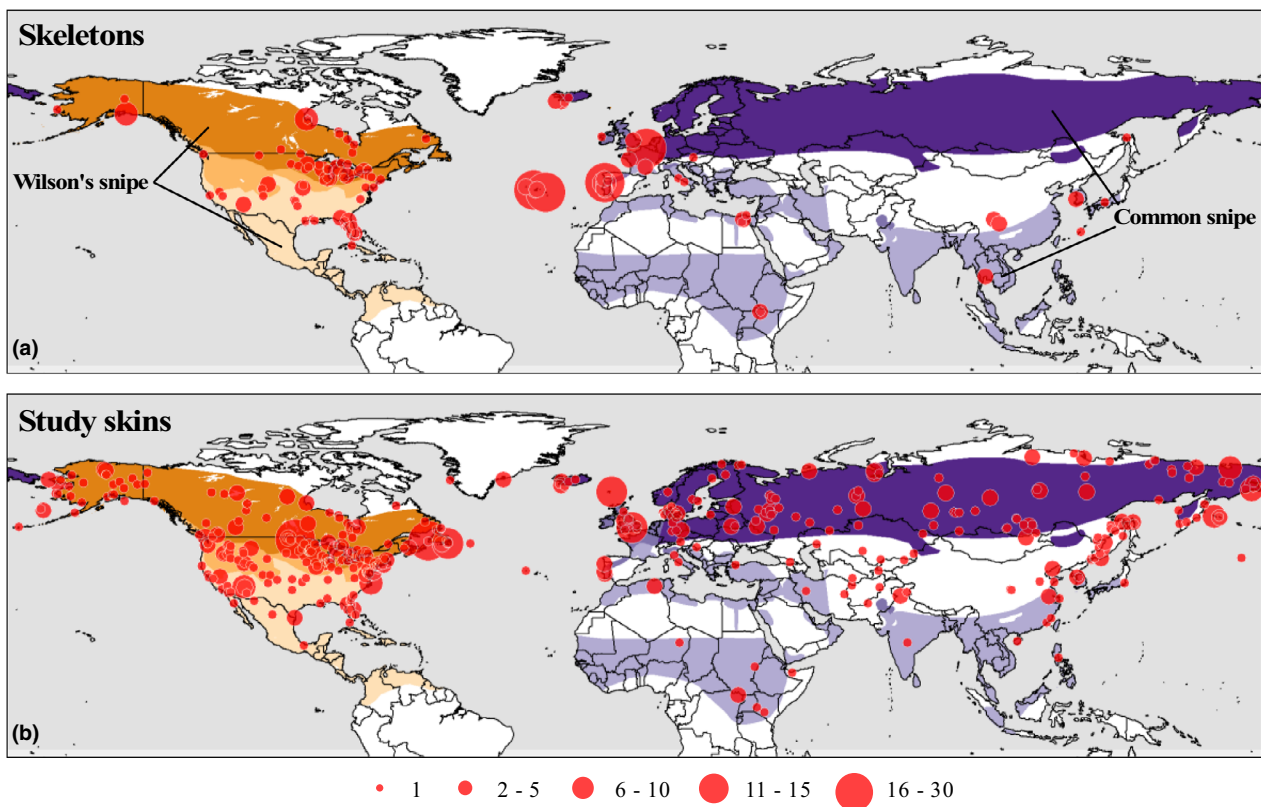
Figure 1. Geographical samples of (a) skeletons and (b) study skins of Common Snipe *Gallinago gallinago* and Wilson's Snipe *Gallinago delicata* analysed in this study. The area of the circles indicates relative sample size. The darker, intermediate and lighter shaded areas indicate, respectively, the breeding, year-round and wintering ranges of the Common Snipe (eastern hemisphere) and Wilson's Snipe (western hemisphere) (adapted from BirdLife International & NatureServe 2015).

Premaxilla; here and below, variable names are italicized and in capitals). Measurements were made with a digital calliper to ±0.1 mm. In a few cases, broken bones were reassembled with the help of modelling clay for measurement. Distorted bones (e.g. due to healed injuries) were not measured. Left-side measurements were used when possible for consistency, although right-side measurements were used if left-hand elements were damaged or missing.

Phenotypic variation in morphology was also quantified from four external body size-related variables (hereafter 'external variables') measured on study skins: *Bill*, length of the bill from its tip to the dorsal swelling at its posterior end, on the midline; *Tarsus*, length of the tarsus from the back of the intertarsal joint to the distal front edge of the last complete scale before the toes diverge; *Tail*, length of the tail, from the insertion of the central pair of rectrices to the tip of the longest

(central) rectrix; and *Wing*, length of flattened wing, from the carpal joint to the tip of the longest primary (Eck *et al.* 2011). *Bill* and *Tarsus* were measured with digital callipers to ±0.1 mm. *Tail* and *Wing* were measured with a ruler to ±1 mm. Additionally, to assess variation in wing morphology, the distances between the tips of the longest primary and all other primaries were measured along the flattened wing with digital callipers to ±0.1 mm. Primary lengths (*P1–P10*) were then calculated by subtracting those distances from *Wing* (Evered 1990).

To evaluate phenotypic variation in plumage, five non-primary plumage variables were quantified (hereafter 'plumage variables'): *White in the secondaries*, mean value of the depth of the white portion on the tip of each secondary feather (on the right wing), measured along the shaft in the inner web of the feather with a digital calliper to ±0.1 mm (Fig. 2b); *Outer rectrix vane length,*

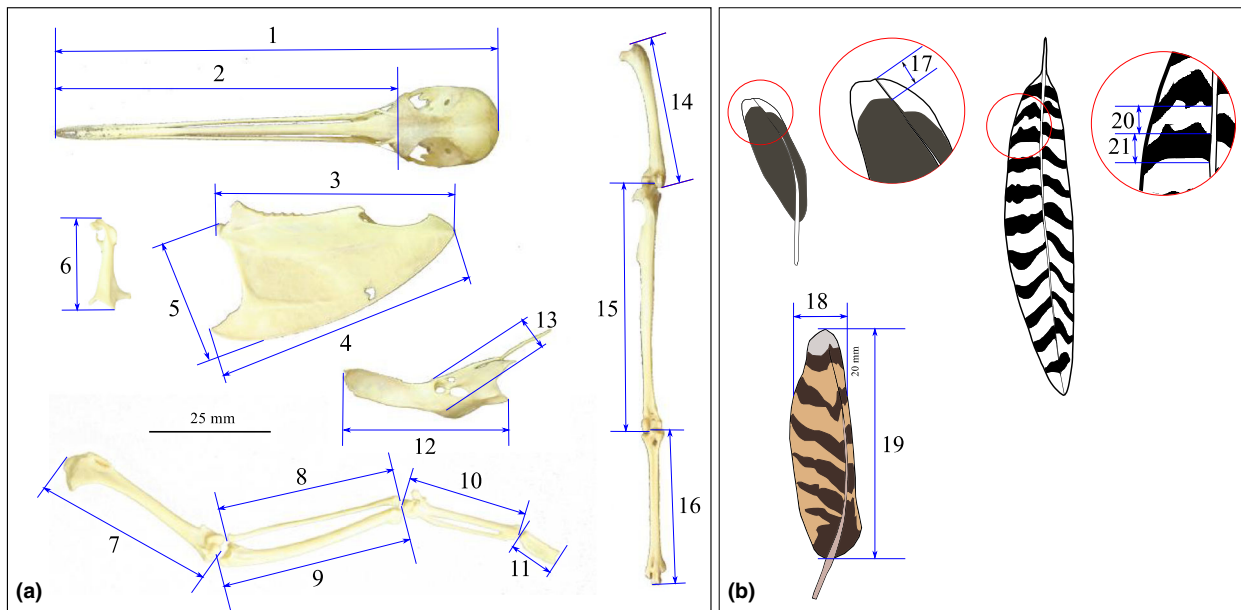**Figure 2.** (a) Variables measured on skeletons (see text for descriptions): (1) *Cranium*, (2) *Premaxilla*, (3) *Sternal length*, (4) *Keel length*, (5) *Keel depth*, (6) *Coracoid*, (7) *Humerus*, (8) *Radius*, (9) *Ulna*, (10) *Carpometacarpus*, (11) *Phalanx 1*, (12) *Ischial length*, (13) *Ischial depth*, (14) *Femur*, (15) *Tibiotarsus* and (16) *Tarsometatarsus*. (b) Variables measured on plumage: (17) *White in the secondaries*, (18) *Outer rectrix vane width* and (19) *Outer rectrix vane length*; (20, 21) projection of white and dark markings along the axillary's shaft, respectively, used to calculate the variable *White in the axillaries*.

length of the vane of the outermost rectrix (preferably the left) measured with a ruler to ±1 mm; *Outer rectrix vane width*, width of the vane of the outermost rectrix (preferably the left) measured with a ruler to ±0.5 mm at 20 mm from its distal tip (Fig. 2b); *Number of rectrices*, the number of rectrices on specimens with at least one half of the rectrices present (any signs of moulting or missing rectrices were recorded; when rectrices were missing on one side, the total number of rectrices was inferred assuming tail symmetry); and *White in the axillaries*, proportion of white on the axillaries, dividing the sum of the extent of white by the sum of white and dark markings, the projection of each dark and white marking on the longest axillary measured with a digital calliper to ±0.1 mm (Fig. 2b).

Measurement repeatability

The first author made all measurements. Subsamples of 30 skeletons and 30 study skins of Common Snipe and Wilson's Snipe were measured three times, in random order, to quantify measurement error (ME). The R package ICC (Wolak *et al.* 2012) was used to estimate repeatability expressed as the intraclass correlation coefficient (ICC) and percentage of measurement error (% ME) computed as $(1 - \text{ICC}) \times 100$ (Table S2).

Statistical analyses

All variables were ln-transformed before analyses. Patterns of phenotypic variation in skeletal, external, wing and plumage traits were investigated through principal components analyses (PCAs) and included 15 skeletal variables, the four external variables, the lengths of the 10 primaries and five plumage variables, respectively. PCAs (non-rotated) based on correlation matrices were performed using the 'princomp' function of the R stats package (version 3.6.1; R Core Team 2019). The Kaiser criterion (Kaiser 1960) and the scree test (Cattell 1966) were used to decide the number of components to retain. Differences between species on these components were tested with non-parametric analyses of variance, with 1000 permutations, including sex, species and their interaction as independent variables in the R package lmPerm (Wheeler & Torchiano 2016).

To test whether selection could be responsible for phenotypic differences between species, in skeletons, skins, wings and plumage, the beta-test of Ackermann and Cheverud (2002), which assumes that genetic drift is the only process responsible for differences between species, was used to attempt to reject the null hypothesis of neutral evolution (Lande 1976, 1979). Accordingly, if phenotypic disparity between Common Snipe and Wilson's Snipe results from neutral evolutionary processes, the between-species variance (B) should be proportional to the within-species variance (W; Ackermann & Cheverud 2002). R code in Mutumi *et al.* (2017) was used to determine B and W for each partition. First, the residuals variance–covariance (VCV) matrices of non-parametric multivariate analyses of variance, with 1000 permutations, including sex and species as independent variables, were computed to remove variation explained by differences between sexes and species (Mutumi *et al.* 2017). PCAs were performed with each residual VCV matrix, and the eigenvalues were extracted to represent W (Cornuault *et al.* 2015, Mutumi *et al.* 2017). The last PC of each PCA was not considered due to low explained variance (Table S3). The matrices of the eigenvectors were multiplied by the respective matrices of the trait means for each species, and the variances associated with each column of the new matrices were calculated to represent B (Mutumi *et al.* 2017). Finally, the proportionality between B and W was evaluated by regressing $\ln(B)$ over $\ln(W)$; slopes of 1 indicate that drift was the diversifying source, whereas significant deviations from this value suggest that this process was probably not responsible for the observed pattern (Ackermann & Cheverud 2002).

Phenotypic distances between the Common Snipe and Wilson's Snipe were determined with a non-parametric distance measure, Δp (Safran *et al.* 2012). Distances were measured in terms of the percentiles at which the median of each population lies on a joint cumulative distribution function. In comparison with other metrics, Δp is relatively insensitive to unequal variances and sample sizes among populations (Safran *et al.* 2012).

All analyses were performed in R 3.6.1 (R Core Team 2019) or MATLAB R2017b (The Math-Works, Inc., Natick, MA, USA) and results were considered to be significant at $P < 0.05$. Šidák's

correction (Šidák 1967) was computed to adjust *P*-values for multiple comparisons.

RESULTS

Phenotypic variation

The first two axes of the PCA of the skeletal variables accounted for 51 and 11% of the variance, respectively (Table 1). All 15 traits loaded positively and significantly on PC1 ($r_s = 0.32$–0.89; all $P < 0.001$; Table 1), which mainly represented variation in body size. The birds with relatively larger bodies had higher scores on PC1. Traits with the greatest contribution to PC2 were *Keel length*, *Sternum* and *Keel depth* ($r_s = 0.78$, 0.71 and 0.42, respectively; all $P < 0.001$; Table 1), indicating that PC2 primarily represented variation in sternal size. Birds with a relatively larger sternum had higher PC2 scores. Results of a non-parametric analysis of variance (ANOVA) showed that sex but not species or sex–species interaction had a significant effect on PC1 scores (Table 2), indicating that females had larger skeletons than males in both species (Fig. 3a). Both species and sex, but not species–sex interaction (Table 2), had significant effects on PC2 scores. The Common Snipe had a larger sternum compared with Wilson's Snipe, and males had a larger sternum than females in both species (Table 3).

The first two axes of the PCA using the four external variables accounted for 48 and 25% of the variance, respectively (Table 1). The four variables had significant positive loadings on PC1 ($r_s = 0.48$–0.80; all $P < 0.001$; Table 1), which mostly represented variation in body size. Again, larger birds had higher PC1 scores. PC2 was mostly affected by *Tail* and *Tarsus* ($r_s = -0.79$ and 0.51, respectively; $P < 0.001$; Table 1). The loadings for *Wing* and *Bill* ($r_s = -0.27$ and 0.25, respectively, $P < 0.001$; Table 1) were substantially lower. Birds with relatively shorter tails and longer tarsi had higher PC2 scores. A non-parametric ANOVA of PC1 scores (Table 2) indicated that Common Snipe were larger than Wilson's Snipe and females were larger than males (Fig. 3b); the species–sex interaction had no significant effect on PC1 scores. Species and sex, but not the species–sex interaction, had a significant effect on PC2 scores (Table 2). The Common Snipe had a proportionally longer tail but a shorter tarsus compared with Wilson's Snipe (Fig. 3b,

Table 1. Component loadings (correlations), eigenvalues and percentage of the variance explained by the first two components from principal components analyses (PCAs) on ln-transformed skeletal and external variables, primary lengths and plumage variables of Common Snipe *Gallinago gallinago* and Wilson's Snipe *Gallinago delicata*. Correlations that were significant at $\alpha = 0.05$ are shown in bold type.

	PC1	PC2
Skeletal variables		
Premaxilla	**0.586*****	0.140
Braincase	**0.319*****	**0.313*****
Sternum	**0.621*****	**0.705*****
Keel length	**0.479*****	**0.776*****
Keel depth	**0.634*****	**0.417*****
Coracoid	**0.747*****	−0.126
Humerus	**0.886*****	**−0.185***
Radius	**0.879*****	**−0.179***
Carpometacarpus	**0.870*****	−0.119
Phalanx 1	**0.684*****	**−0.168***
Ischial length	**0.737*****	−0.100
Ischial depth	**0.516*****	−0.100
Femur	**0.847*****	**−0.236****
Tibiotarsus	**0.835*****	**−0.195***
Tarsometatarsus	**0.811*****	**−0.165***
Eigenvalue	7.684	1.656
% variance	51.224	11.0
External variables		
Bill	**0.799*****	**0.247*****
Tarsus	**0.734*****	**0.509*****
Tail	**0.479*****	**−0.787*****
Wing	**0.723*****	**−0.268*****
Eigenvalue	1.930	1.012
% variance	48.259	25.288
Primary lengths		
P10	**0.914*****	**0.329*****
P9	**0.943*****	**0.293*****
P8	**0.961*****	**0.220*****
P7	**0.962*****	**0.177****
P6	**0.971*****	0.071
P5	**0.976*****	−0.040
P4	**0.964*****	**−0.142***
P3	**0.950*****	**−0.243*****
P2	**0.928*****	**−0.321*****
P1	**0.876*****	**−0.369*****
Eigenvalue	8.928	0.599
% variance	89.284	5.991
Plumage variables		
Outer rectrix vane length	**0.771*****	**0.431*****
Outer rectrix vane width	**0.880*****	−0.029
White in the secondaries	**0.903*****	0.037
White in the axillaries	**0.875*****	0.115
Number of rectrices	**−0.754*****	**0.586*****
Eigenvalue	3.518	0.544
% variance	70.355	10.887

The first components (PC1) of PCAs for skeletal and external variables were interpreted as axes of multivariate body size, and the second components (PC2) as body shape. Both components of the PCA on primary lengths explained variations in wing size (PC1) and pointedness (PC2). Most variation in plumage variables was explained by the first components (PC1). Asterisks indicate the significance of each correlation. Primaries are numbered from body toward the wing tip. *P < 0.05. **P < 0.01. ***P < 0.001.

Table 3). Females had a relatively shorter tail and a longer tarsus than males (Fig. 3b, Table 3).

In the PCA on primary lengths, the first two axes explained 89 and 6% of the variance, respectively (Table 1). The 10 primaries had significant positive loadings on PC1 ($r_s = 0.88$–0.98; all $P < 0.001$; Table 1), which represented variation in wing size: birds with larger wings had higher PC1 scores. The four distal primaries (*P7–P10*) were positively correlated with PC2 ($r_s = 0.18$–0.33; all $P < 0.01$; Table 1), whereas the four proximal primaries (*P1–P4*) had significant negative loadings ($r_s = -0.37$ to -0.31; all $P < 0.05$; Table 1). Loadings increased outwards (Table 1), denoting variation in wing pointedness. Non-parametric ANOVA of PC1 and PC2 scores (Table 2) showed that females had larger wings with a less pointed wingtip (Fig. 3c). Neither species nor species–sex interaction had significant effects on PC1 or PC2 scores (Table 2).

The first two axes of the PCA with the five plumage variables explained 70 and 11% of the variance, respectively (Table 1). The five variables were highly correlated with PC1, but whereas the correlations of the white in the secondaries, white in the axillaries, length of the outer rectrices and width of the outer rectrices were positive ($r_s = 0.77$–0.90; all $P < 0.001$; Table 1), correlation with the number of rectrices was negative ($r_s = -0.75$; $P < 0.001$; Table 1). Birds with few rectrices, but with larger outermost rectrices, and more white in the secondaries and axillaries, had higher PC1 scores. Only the number of rectrices and the length of the outermost rectrices correlated significantly with PC2 ($r_s = 0.59$ and 0.43, respectively; all $P < 0.001$; Table 1). Birds with more rectrices and relatively longer outermost rectrices had higher loadings on PC2. The non-parametric ANOVA of PC1 scores revealed a significant effect of sex and species, but not their interaction (Table 2); however, the effects were disparate, as the *F*-value for species was 67 times greater than the *F*-value for sex. The Common Snipe had more white in the axillaries, broader white edges of the secondaries, and broader and longer vanes of the outer rectrices, but fewer rectrices (Fig. 3d, Table 3). Only sex had a significant effect on PC2 scores (Table 2), suggesting that PC2 is primarily related to sexual dimorphism in the variation of signalling characters. Males of both species had relatively more rectrices, and the outermost ones were relatively longer.

Table 2. Results of permutational two-way crossed designs ANOVA with TAXON and SEX as factors and computed principal components as variables. *P*-values and differences that were significant at α = 0.05 are shown in bold type.

Skeletal variables	df	PC1 ('*body size*') SS	F	P	diff.	PC2 ('*sternal size*') SS	F	P	diff.
TAXON	1	1.0	0.24	0.624	**−0.58**	81.0	37.01	**<0.001**	**1.49**
SEX	1	1623.0	32.82	**<0.001**	**−6.57**	10.0	4.59	**0.033**	**0.51**
SEX × TAXON	1	17.0	0.35	0.557		0.3	0.15	0.699	
Residuals	146	7220.0				319.4			

External variables	df	PC1 ('*body size*') SS	F	P	diff.	PC2 ('*body shape*') SS	F	P	diff.
TAXON	1	59.80	17.96	**<0.001**	**1.89**	8.95	10.34	**<0.001**	**−0.41**
SEX	1	88.20	26.49	**<0.001**	**−1.05**	15.07	17.42	**<0.001**	**−0.52**
SEX × TAXON	1	12.70	3.83	0.051		0.14	0.16	0.687	
Residuals	291	968.60				251.67			

Primary lengths	df	PC1 ('*wing size*') SS	F	P	diff.	PC2 ('*wing pointedness*') SS	F	P	diff.
TAXON	1	55.00	0.72	0.397	1.17	0.44	1.33	0.250	0.10
SEX	1	899.00	11.85	**<0.001**	**−4.43**	5.90	17.77	**<0.001**	**0.34**
SEX × TAXON	1	23.00	0.30	0.584		0.01	0.04	0.839	
Residuals	227	17 234.00				75.36			

Plumage variables	df	PC1 SS	F	P	diff.	PC2 SS	F	P	diff.
TAXON	1	1282.70	1422.21	**<0.001**	**5.59**	0.60	1.21	0.271	−0.10
SEX	1	20.00	22.14	**<0.001**	**0.67**	4.81	9.68	**0.002**	**0.29**
SEX × TAXON	1	0.10	0.10	0.753		0.44	0.89	0.347	
Residuals	220	198.40				109.34			

The Common Snipe *Gallinago gallinago* and Wilson's Snipe *Gallinago delicata* differ on skeletal and external body-size-related and non-primary plumage variables. Apart from one sternal variable, differences in body size were only manifest externally, and wing size and pointedness did not differ. Sexes differ on size and shape of the body and the wing, and on non-primary plumage variables. df, degrees of freedom; *F*: pseudo-*F*-values; *P*: *P*-value after 1000 permutations; SS, explained sum of squares; diff., differences (Tukey HSD) males − females and Common Snipe − Wilson's Snipe.

Selection

The regression slopes of between- vs. within-species phenotypic variance differed significantly from 1 for skeletal variables (Fig. 4a), primary lengths (Fig. 4c) and plumage variables (Fig. 4d) but not for external variables (Fig. 4b). In the last, the small number of data points might explain the lack of significance. However, for the other three, after adjusting for multiple comparisons, the null hypothesis could not be rejected at α = 0.05.

Phenotypic distance

Despite some significant differences between species on skeletal and external variables, the phenotypic distance analyses (Δp) indicated that the largest species differences occurred in plumage variables (Fig. 5a). Furthermore, with the exception of PC2 for skeletal variables (i.e. *sternal size*), Δp for PC1 of plumage variables was greater than for any of the other principal components computed (Fig. 5a). For each sex, Δp was similar across
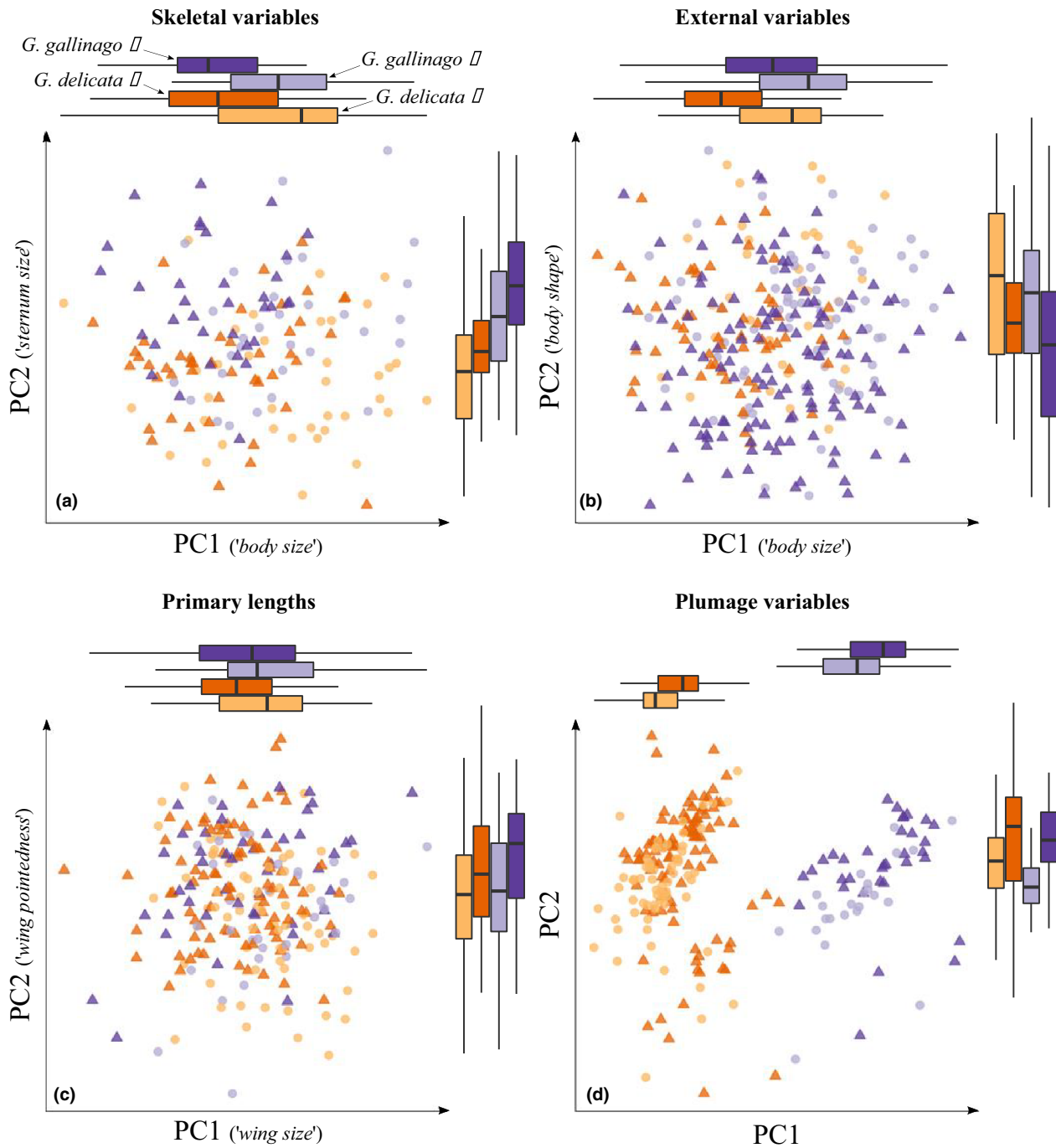
Figure 3. Scatter plots of the scores for the first two principal components (PCs) of variation in (a) skeletal variables, (b) external variables, (c) primary lengths and (d) plumage variables. Triangles indicate males; circles indicate females. The Common Snipe *Gallinago gallinago* and Wilson's Snipe *Gallinago delicata* are similar in size and shape of body and wing, but differ in plumage variables. Boxplots of the PCs scores for each species and sex are presented along the respective axis. The middle line indicates the median (50% quantile), whereas the lower and upper hinges correspond to 25 and 75% quantiles, respectively. The whiskers indicate the largest/smallest value within 1.5 times the interquartile range above the 75% quantile and below the 25% quantile, respectively.

Table 3. Descriptive statistics of traits measured on skeletons and study skins (in mm) of Common Snipe *Gallinago gallinago* and Wilson's Snipe *G. delicata*.

	Common Snipe			Wilson's Snipe		
	Males	Females	SSD	Males	Females	SSD
Skeletal variables						
Cranium	93.9 ± 3.51 (64) 82.5–104.6	96.0 ± 3.68 (67) 86.6–104.5	−2.19	92.1 ± 3.23 (63) 85.4–101.1	94.8 ± 2.98 (53) 86.5–99.9	−2.85
Premaxilla	73.5 ± 3.39 (65) 63.9–84.3	75.7 ± 3.58 (67) 65.9–83.8	−2.91	71.9 ± 3.02 (63) 65.1–79.8	74.7 ± 2.85 (54) 66.4–79.9	−3.75
Braincase*	20.5 ± 0.66 (64) 18.6–22.5	20.4 ± 0.72 (65) 17.7–22.6	0.49	20.4 ± 0.57 (61) 19.1–21.6	20.3 ± 0.55 (53) 18.9–21.5	0.49
Sternum	47.8 ± 1.27 (73) 45.2–50.9	48.6 ± 1.74 (74) 45.4–52.8	−1.65	46.8 ± 1.32 (66) 44.5–50.3	47.4 ± 1.56 (59) 43.9–51.4	−1.27
Keel length	50.9 ± 1.62 (72) 47.2–54.3	51.3 ± 2.14 (76) 47.6–57.0	−0.78	49.4 ± 1.43 (67) 46.2–52.2	49.6 ± 1.68 (59) 46.3–53.8	−0.40
Keel depth	25.6 ± 0.84 (67) 23.8–27.2	26.1 ± 0.85 (64) 24.5–28.0	−1.92	25.0 ± 0.89 (63) 22.8–27.6	25.6 ± 0.88 (60) 23.8–27.8	−2.34
Coracoid	19.5 ± 0.50 (74) 18.4–20.8	19.8 ± 0.54 (83) 18.4–21.0	−1.52	19.5 ± 0.51 (70) 18.0–20.6	19.8 ± 0.61 (63) 18.3–21.3	−1.52
Humerus	36.8 ± 0.94 (74) 34.8–38.7	37.9 ± 0.90 (81) 35.5–39.7	−2.90	37.2 ± 0.87 (68) 35.4–39.2	38.0 ± 1.04 (62) 35.1–40.1	−2.11
Radius	37.1 ± 0.92 (73) 35.1–38.9	38.0 ± 0.99 (76) 35.9–41.0	−2.37	37.1 ± 1.04 (69) 34.8–40.2	37.9 ± 1.20 (61) 34.7–40.5	−2.11
Ulna	39.7 ± 0.94 (69) 37.4–41.8	40.6 ± 1.05 (72) 37.4–43.2	−2.22	39.6 ± 1.04 (67) 37.5–42.5	40.4 ± 1.21 (57) 37.2–43.2	−1.98
Carpometacarpus	25.5 ± 0.61 (68) 23.8–26.6	26.1 ± 0.75 (76) 24.5–27.7	−2.30	25.3 ± 0.74 (70) 24.1–27.7	25.8 ± 0.80 (63) 23.9–27.4	−1.94
Phalanx 1	10.5 ± 0.39 (68) 9.4–11.3	10.6 ± 0.41 (80) 9.4–11.4	−0.94	10.3 ± 0.34 (69) 9.5–11.1	10.5 ± 0.47 (59) 9.6–11.4	−1.90
Ischial length	34.4 ± 1.03 (72) 32.4–37.4	35.4 ± 1.16 (79) 32.8–38.5	−2.82	34.7 ± 1.12 (71) 32.1–36.8	35.5 ± 1.23 (63) 32.1–37.6	−2.25
Ischial depth	7.0 ± 0.31 (73) 6.3–7.7	7.2 ± 0.37 (79) 6.5–8.1	−2.78	7.0 ± 0.39 (71) 6.1–8.0	7.1 ± 0.35 (63) 6.3–8.0	−1.41
Femur	31.2 ± 1.00 (78) 28.8–33.2	32.4 ± 1.06 (78) 29.8–35.6	−3.70	31.7 ± 0.84 (69) 29.9–33.8	32.5 ± 0.91 (61) 29.8–34.5	−2.46
Tibiotarsus	55.5 ± 1.70 (68) 49.0–57.3	54.8 ± 1.55 (71) 52.0–59.6	1.28	53.9 ± 1.70 (66) 51.2–57.9	54.8 ± 1.90 (58) 48.9–58.5	−1.64
Tarsometatarsus	33.0 ± 1.33 (74) 29.6–36.2	33.8 ± 1.12 (83) 31.1–36.5	−2.37	32.5 ± 1.14 (69) 30.1–35.8	33.3 ± 1.40 (64) 28.6–36.0	−2.40
External variables						
Bill	64.7 ± 3.64 (169) 57.0–75.9	66.9 ± 3.44 (100) 60.0–76.4	−3.29	62.4 ± 2.80 (130) 56.1–69.6	64.8 ± 3.31 (95) 57.1–73.1	−3.70
Tarsus	32.2 ± 1.44 (175) 28.5–35.8	32.8 ± 1.37 (104) 29.7–36.4	−1.83	31.9 ± 1.04 (129) 29.4–34.7	32.7 ± 1.36 (97) 30.0–36.3	−2.45
Tail	56.6 ± 2.92 (154) 49.0–62.0	55.42 ± 2.63 (95) 48.0–61.0	2.13	53.3 ± 2.52 (82) 47.0–58.0	53.2 ± 2.82 (52) 46.0–58.0	0.19
Wing	131.4 ± 4.06 (156) 122.0–140.0	131.9 ± 3.75 (86) 123.0–140.0	−0.38	131.4 ± 3.19 (109) 122.0–138.0	132.4 ± 3.35 (79) 125.0–141.0	−0.76
Plumage variables						
Outer rectrix vane length	53.9 ± 2.77 (175) 45.0–60.0	50.0 ± 2.92 (106) 42.0–59.0	7.80	46.7 ± 2.78 (195) 40.0–55.0	44.2 ± 2.59 (145) 37.0–52.0	5.66
Outer rectrix vane width	11.9 ± 1.16 (171) 9.0–15.5	11.7 ± 1.12 (100) 8.5–14.0	1.71	8.3 ± 0.64 (195) 6.5–10.0	8.4 ± 0.68 (145) 6.5–10.5	−1.19
White in the secondaries	4.1 ± 1.11 (182) 1.3–7.2	3.6 ± 0.82 (113) 1.6–5.7	13.89	1.3 ± 0.38 (206) 0.4–2.4	1.2 ± 0.34 (154) 0.4–2.3	8.33

(continued)

Table 3. *(continued)*

	Common Snipe			Wilson's Snipe		
	Males	Females	SSD	Males	Females	SSD
White in the axillaries	0.7 ± 0.14 (39) 0.6–1.0	0.7 ± 0.17 (27) 0.4–1.0	0.00	0.4 ± 0.06 (105) 0.3–0.6	0.4 ± 0.06 (74) 0.2–0.6	0.00
No. of rectrices						
12	(9)	(5)		(5)	(1)	
14	(192)	(108)		(30)	(21)	
16	(4)	(2)		(182)	(132)	
18	–	–		(3)	(1)	

Cell entries are mean ± se (*n*), and the range. SSD (sexual size dimorphism) = 100((male/female) − 1).   *Derived trait, *Braincase* = *Cranium* − *Premaxilla*.

these axes except for PC1 of external variables (i.e. *body size*). The difference for (external) body size between Common Snipe and Wilson's Snipe was larger among males. On the other hand, for both species, differences between males and females were more prominent on skeletal and external variables than on four of the five plumage variables (Fig. 5b). The exception was the length of the outermost rectrix, which was the most sexually dimorphic plumage variable.

DISCUSSION

Selection usually is suggested as responsible for phenotypic differences between allopatric populations; however, they also might diverge through neutral evolutionary processes such as drift (Mayr 1954, Lande 1976, 1980). The beta-test results suggest that drift alone cannot explain differences in skeleton, wing or plumage between the Common Snipe and Wilson's Snipe, and thus selection was probably responsible for the divergence. However, the null hypothesis could not be rejected after adjusting the level of significance for multiple comparisons. This hypothesis is difficult to reject when few taxa are compared, and a significant result in any single test probably indicates selection (Ackermann & Cheverud 2004).

The Common Snipe has a larger sternum than Wilson's Snipe, but otherwise the species do not differ in skeletal size. Sternal size is related to volume of the pectoral muscles (Piersma *et al.* 1984), which are responsible for powered flight and nutrient storage (Lindström & Piersma 1993, Lindström *et al.* 2000). Migratory species of passerines have larger sterna than their sedentary congeneric relatives, and sternal size within migratory *Sylvia* species is correlated with migration distance (Calmaestra & Moreno 1998, 2000). The distances between centroids of the breeding and wintering ranges of the Common Snipe (*c.* 5600 km) and Wilson's Snipe (*c.* 3000 km) suggest an almost two-fold higher total migration distance in the Common Snipe, which can explain its relatively larger sternum. However, because both Common Snipe and Wilson's Snipe also perform aerial displays, it is difficult to provide a qualified interpretation for the difference we found. A comparative study of skeletons of sedentary and migratory snipes would help in better understanding this pattern.

The species did not differ in wing size or pointedness, traits that are usually related to flight distance (Fernandez & Lank 2007, Milá *et al.* 2008, Baldwin *et al.* 2010, Forschler & Bairlein 2011, Minias *et al.* 2015), relative fuel load (Burns 2003) and manoeuvrability (Hedenström & Møller 1992, Burns & Ydenberg 2002). This was an unexpected finding in light of the difference observed in sternal size between the species. Differences in wing morphology may develop rapidly in response to selective pressures (Lank *et al.* 2017, Anderson *et al.* 2019) and may occur between conspecific populations. For instance, during autumn migration of Common Snipe in central Poland, Minias *et al.* (2013) observed that first-year late migrants had longer and more rounded wings than those migrating early in the season, probably due to differences in their origin. However, a comparative study between migratory and sedentary Common Snipe found no differences in wing shape, suggesting a possible influence of display behaviour, and
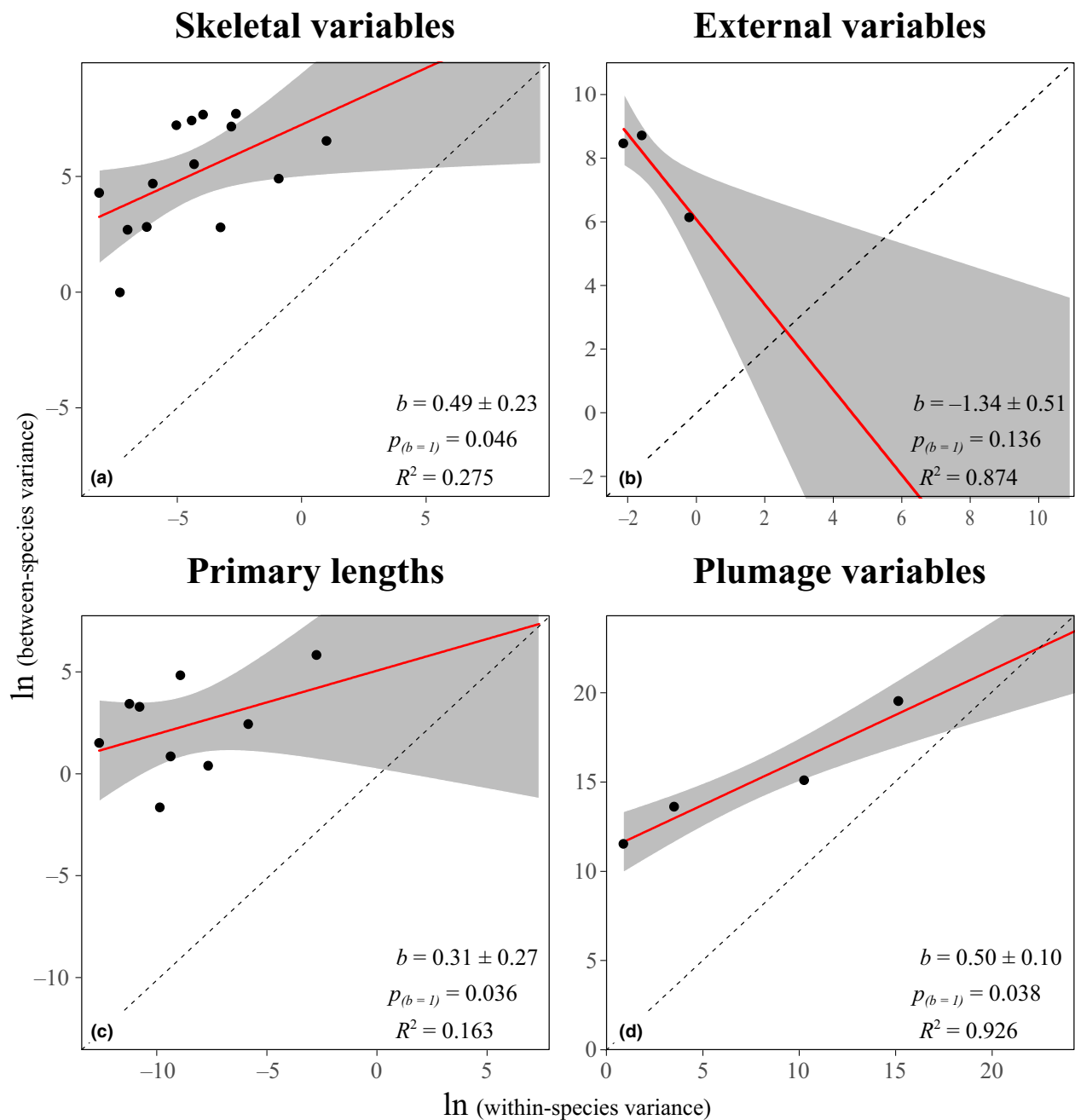
Skeletal variables

$b = 0.49 \pm 0.23$

$p_{(b=1)} = 0.046$

$R^2 = 0.275$

(a)

External variables

$b = -1.34 \pm 0.51$

$p_{(b=1)} = 0.136$

$R^2 = 0.874$

(b)

Primary lengths

$b = 0.31 \pm 0.27$

$p_{(b=1)} = 0.036$

$R^2 = 0.163$

(c)

Plumage variables

$b = 0.50 \pm 0.10$

$p_{(b=1)} = 0.038$

$R^2 = 0.926$

(d)

ln (between-species variance)

ln (within-species variance)

Figure 4. Regression of between-species and within-species variance on (a) skeletal variables, (b) external variables, (c) primary lengths and (d) plumage variables of the Common Snipe *Gallinago gallinago* and Wilson's Snipe *Gallinago delicata*.

thus social selection, on this trait (Rodrigues *et al.* 2018).

Species differences in skeleton and external measurements are small compared with those in plumage traits, suggesting that the latter diverged more rapidly. The Common Snipe has fewer rectrices, longer and wider outermost rectrices, more extensive white on tips of the secondary feathers, and more white in the axillaries. Both species expose these parts of their body in various ground
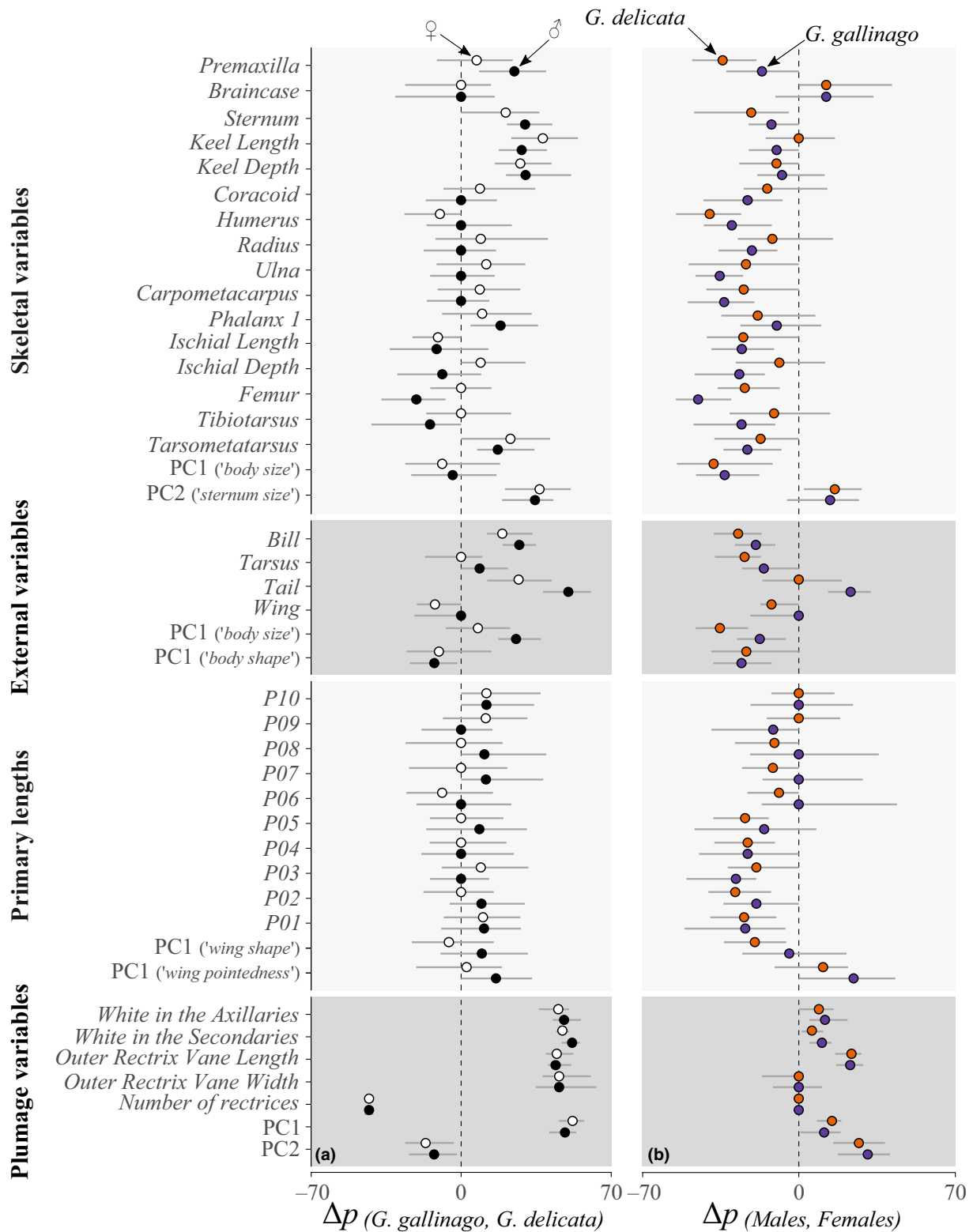
Figure 5. Summary of phenotypic distances between (a) Common Snipe *Gallinago gallinago* and Wilson's Snipe *Gallinago delicata*, and (b) males and females (*Δp*; Safran *et al.* 2012) for each variable and multivariate axis. Horizontal lines correspond to 95% confidence intervals (estimated by bootstrapping). Primaries are numbered from body toward the wing tip. The species differ more in plumage variables than in most skeletal and external variables.

and aerial displays, and also use the rectrices to produce instrumental sounds in aerial displays (Tuck 1972, Sutton 1981, Cramp & Simmons 1983, Glutz von Blotzheim *et al.* 1986), so social selection potentially played a role in their evolutionary differentiation.

Most Common Snipe and Wilson's Snipe specimens examined had 14 and 16 rectrices, respectively, but the number varied substantially (Common Snipe, 12–16; Wilson's Snipe, 12–18). These findings agree with previous information (Tuck 1972, Cramp & Simmons 1983, Glutz von Blotzheim *et al.* 1986) except that we noted no specimens of Common Snipe with 18 rectrices. The number of rectrices varies substantially across snipe species (Seebohm 1888, Tuck 1972). Seebohm (1888) mused that interspecific variation in the number of rectrices would eventually be explained by sexual selection. At least in the Latham's Snipe *Gallinago hardwickii*, the number differs between sexes (Ura *et al.* 2005). In the Common Snipe and Wilson's Snipe, males seemed to have relatively more rectrices compared with females in multivariate analysis but the number of rectrices alone did not differ between sexes (Table 3).

The vanes of the outer rectrices were wider and longer in the Common Snipe than in the Wilson's Snipe, in agreement with other accounts (Tuck 1972), probably contributing to differences in drumming sounds between the species (Carr-Lewty 1943, Thönen 1969, Byrd & Gibson 1978, Miller 1996, Arkhipov 2009, van Casteren *et al.* 2010, Clark & Prum 2015). These feathers have evolved morphological modifications to cope with the demands of sound production during aerial displays (Bahr 1907, van Casteren *et al.* 2010, Clark & Prum 2015). In the Common Snipe, the angle between the barbs and the rachis is reduced in the outermost rectrices, when compared with other non-sound-producing rectrices, or with the outermost rectrices of the Eurasian Woodcock *Scolopax rusticola*. Additionally, the morphology of the barbules in the hind vane varies with distance from the rachis (van Casteren *et al.* 2010). A recent study found an inverse correlation between the structural quality (evaluated by mass–length residuals) and the brightness of the outer rectrices in the Common Snipe, suggesting that the mechanical properties of these feathers might benefit from melanization and that both social selection and natural selection might have influenced evolution

of melanin-based coloration of these feathers (Minias *et al.* 2018).

The larger white markings at the tips of the secondaries and the higher proportion of white in the axillaries of the Common Snipe resemble some differences between other scolopacids of the Palaearctic and Nearctic (Prater *et al.* 1977). Because scolopacids expose these traits during displays (Miller 1984), they probably have a function in communication, so social selection is likely to have played a role in the evolution of clear taxon-specific signalling. Natural selection, in addition to social selection, might promote differences in social traits between allopatric populations by shaping them according to the physical properties of their habitats (Boncoraglio & Saino 2007, Tobias *et al.* 2010) or as a by-product of adaptive divergence (Servedio *et al.* 2011, Wilkins *et al.* 2013). For instance, ambient light can affect the evolution of colour and optical communication in fish (Fuller 2002, Seehausen *et al.* 2008), reptiles (Leal & Fleishman 2002) and birds (Marchetti 1993, Bloch 2015, but see Anciães & Prum 2008). However, differences in plumage between the Common Snipe and Wilson's Snipe are subtle and would only be detected over short distances, when environmental effects would be minimal.

All analyses revealed sexual differences between the Common Snipe and Wilson's Snipe. Females have larger bodies and wings than males, but their sterna are relatively smaller, the wings are less pointed, and the rectrices are shorter. Many studies support a role of sexual selection in the evolution of SSD in birds (Székely *et al.* 2000, 2004, Drovetski *et al.* 2006). However, for the Common Snipe, in which only females incubate the eggs (Tuck 1972, Green *et al.* 1990, Green 1991), the less pointed wingtips in females were interpreted to be a result of natural selection acting on more efficient take-off performance and predator escape (Minias *et al.* 2013). This hypothesis is supported by the results of a study in *Calidris* sandpipers (Burns & Ydenberg 2002), but Tuck's (1972) anecdotal records on Wilson's Snipe and systematic observations on the Great Snipe (Höglund *et al.* 1992) suggest snipes rely on their cryptic plumage, freezing, hiding or ignoring potential predators rather than by flying away. Alternatively, the smaller bodies and wings of males could increase agility in aerial displays (Székely *et al.* 2000, 2004). The more pointed wings, besides influencing the wingtip vortices (Lockwood *et al.*

1998), may increase flight speed, due to their higher loading (Rayner 1988), thus improving aerial display performance. The drumming sound of the Common Snipe is audible when air speed is between 12 and 42 m/s, during the diving part of the drumming flight (Carr-Lewty 1943, Reddig 1978, Sutton 1981, van Casteren *et al.* 2010). Tuck (1972) commented that females are unable to produce a drumming sound because they cannot dive at the necessary speed and angle for the outer rectrices to vibrate. This difference in behaviour can also explain the sexual differences found in the relative size of the sternum and shape of the wingtip. Other contributing factors to the observed sexual size dimorphism could include diet, habits, habitat use and migration between males and females (Green *et al.* 1990, Green 1991, Devort 1997, McCloskey & Thompson 2000, McCloskey *et al.* 2009, Cline & Haig 2011).

In summary, we observed stronger differences between Common Snipe and Wilson's Snipe in plumage characters, which probably have important signalling functions, than in traits related to resource use. These findings suggest that traits under social selection diverged more rapidly than those under natural selection in the two species, in agreement with differing rates and strengths of social and natural selection (Panhuis *et al.* 2001, Kingsolver & Pfennig 2007, Safran *et al.* 2013). However, tests of the null hypothesis yielded borderline results, so adding other species of snipe and more traits (including acoustic data), or replicating this study, might strengthen this conclusion.

AUTHOR CONTRIBUTIONS

Tiago M Rodrigues: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (equal);

Methodology (equal); Writing-original draft (lead); Writing-review & editing (equal). **Edward H. Miller:** Formal analysis (supporting); Methodology (equal); Supervision (supporting); Writing-review & editing (equal). **Sergei V. Drovetski:** Conceptualization (equal); Funding acquisition (supporting); Methodology (equal); Supervision (supporting); Writing-review & editing (supporting). **Robert Zink:** Funding acquisition (supporting); Methodology (equal); Writing-review & editing (supporting). **Jon Fjeldsa:** Funding acquisition (supporting); Writing-review & editing (supporting). **David Afonso Gonçalves:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (equal); Supervision (lead); Writing-review & editing (supporting).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad at https://doi.org/10.5061/dryad.02v6wwq0s (Rodrigues *et al.* 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of collections and specimens analysed for this study.

Table S2. Most measurements were highly repeatable.

Table S3. Little variance explained by the last principal components (PC) of principal components analyses (PCA) on residuals' variance–covariance matrices. PC scores of analyses of traits measured on skeletons and study skins of Common Snipe *Gallinago gallinago* and Wilson's Snipe *G. delicata*.