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Limitations of ecomorphological analysis in explaining macrohabitat segregation in a songbird guild¹

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Abstract: It is not uncommon for different species within a guild to be non-randomly segregated within a landscape through the occupation of different preferred macrohabitats. The explanation most amenable with ecological theory is that different guild members are adapted for exploiting the different opportunities offered by such macrohabitats. Morphological characters are possible adaptations reflecting habitat preferences. We investigated morphological traits in a guild of small foliage-gleaning, insectivorous birds breeding in central Ontario, Canada (4 families; 23 species). We measured 27 skeletal features and compared 2 types of differences: those between conspecific sexes (that by necessity occupy the same macrohabitat) and those between different guild members (that tend to occupy different macrohabitats). We predicted that if macrohabitat differences are reflected in different morphologies, the differences between conspecific sexes would be less than the differences between species, at least after correcting for size. We used (a) principal components analysis (PCA), (b) distance matrices derived from PCA scores, and (c) Mantel tests. Although conspecific male and female morphologies were correlated, nearest neighbours in morphological space were frequently non-conspecifics. Accordingly, because morphological differences between similar species that tend to occupy different macrohabitats are often smaller than morphological differences between conspecific sexes, our findings indicate that skeletal morphology provides no basis for explaining patterns of within-guild macrohabitat segregation.

Keywords: *Dendroica*, ecomorphology, habitat, habitat segregation, habitat specificity, macrohabitat, microhabitat, morphology, passerine birds, sexual size dimorphism.

Résumé : À l'intérieur des guildes, il n'est pas rare que les espèces ne soient pas distribuées de façon aléatoire dans le paysage mais qu'elles soient regroupées selon les préférences de macrohabitat. L'explication la plus conforme à la théorie écologique est que les différents membres d'une guildes sont adaptés à exploiter les différentes opportunités offertes par les macrohabitats. Les caractères morphologiques peuvent constituer des adaptations reflétant les préférences d'habitat. Nous avons étudié les traits morphologiques d'une guildes de petits oiseaux insectivores s'alimentant dans le feuillage et nichant dans le centre de l'Ontario, Canada (4 familles, 23 espèces). Nous avons mesuré 27 paramètres du squelette et comparé 2 types de différences : celle entre les sexes de la même espèce (qui occupent nécessairement le même macrohabitat) et celle entre les différents membres de la guildes (qui ont tendance à occuper des macrohabitats différents). Si les différences de macrohabitat se reflètent dans des morphologies différentes, nous avons prédit que les différences entre les sexes d'une même espèce seraient moindres que celles entre les espèces, du moins après avoir corrigé pour la taille. Nous avons utilisé (a) une analyse en composantes principales (ACP), (b) des matrices de distance dérivées des résultats de l'ACP et (c) des tests Mantel. Même si la morphologie des mâles et des femelles d'une même espèce était corrélée, les plus proches voisins en terme morphologique étaient fréquemment des individus d'espèces différentes. En conséquence, puisque les différences morphologiques entre des espèces similaires occupant des macrohabitats différents étaient souvent plus petites que celles entre les sexes d'une même espèce, nos résultats indiquent que la morphologie squelettique ne constitue pas une base pouvant expliquer les patrons d'occupation des macrohabitats à l'intérieur d'une guildes.

Mots-clés : *Dendroica*, dimorphisme sexuel de taille, écomorphologie, habitat, macrohabitat, microhabitat, morphologie, passereaux, ségrégation d'habitat, spécificité d'habitat.

Nomenclature: AOU, 1998.

Introduction

Most organisms exhibit habitat preferences when choosing a place to occupy. Habitat relations among members of a guild are of particular interest because such species by definition make their living in a similar manner and because habitat segregation among them is commonly observed. Such segregation is non-random; numerous studies of North American breeding bird communities have demonstrated highly non-random distributions of species based on habitat variables (Debinski & Brussard, 1994;

Welsh & Loughheed, 1996). These species-habitat relationships are especially emphasized among those species whose breeding and winter habitats are most dramatically different, the Neotropical migrants (Kirk & Hobson, 2001). Among breeding wood-warblers (Aves: Parulidae) for instance, it has long been known that segregation exists, and that such segregation can occur at different habitat scales (MacArthur, 1958; James, 1971).

What mediates this apparent segregation? Many research programs have been dedicated to evaluating the role of competition, with varying results (Connell, 1983; Schoener, 1983; Gurevitch *et al.*, 1992; Luiselli, 2006). Research programs in ecomorphology rely on the operational

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assumption that the morphologies of organisms are fine-tuned to their ecologies (Lack, 1971; Moreno & Carrascal, 1993), with the argument that morphology plays a role in community organization (Carrascal, Moreno & Mozetich, 1995), especially as it relates to resource-based niches (Forstmeier & Kessler, 2001). In avian ecomorphological studies that connect habitats and morphology, skeletal measurements are commonly employed (Leisler & Thaler, 1982; Keast & Saunders, 1991; Forstmeier, Bourski & Leisler, 2001).

Because of a continuum of scales, habitat and its sub-categories microhabitat and macrohabitat are terms that have been employed with great ambiguity and imprecision (Morris, 1987; Jorgensen, 2004). One need only to sample current papers on passerine birds to witness the different scales to which they are applied (Tarvin & Garvin, 2002; Warkentin *et al.*, 2004; Smith & Wachob, 2006). The scale we focus on is the macrohabitat, in the sense employed by Morris (1987): distinguishable units whose minimum area corresponds to that within which an average individual performs all of its biological functions (home range) during a typical activity cycle. Because we focus on territorial passerines whose macrohabitat selections are strongly characterized by both structure and composition of vegetation (Lee & Rotenberry, 2005), the conception of macrohabitat that we employ is the composition and structure of the territory's vegetation. This is in contrast to the concept of microhabitat as employed by Paszkowski (1984), which consists of the parts of the macrohabitat (substrate types and height strata) that are disproportionately used.

While morphology is more likely to reflect characters of microhabitat than of macrohabitat, some concordance between morphology and macrohabitat is to be expected. This is only partly because microhabitat is found within macrohabitat. It is also because morphological differences are thought to mediate community structure (Carrascal, Moreno & Mozetich, 1995), and segregation within communities is most often documented along gradients of macrohabitat (James, 1971; Collins, James & Risser, 1982; Kirk & Hobson, 2001).

We asked whether there is a relationship between morphology and macrohabitat segregation within avian guilds. We investigated this question by considering a guild of breeding songbirds, the members of which exhibit different macrohabitat preferences within the breeding landscape. Central to our system of inquiry was the presence of sexual size dimorphism in our sample. Sexual dimorphism is almost universal among migratory songbirds (Dunning, 1984), a group that is commonly used in ecomorphology studies (Wiens, 1989). Yet despite its prevalence, sexual dimorphism is usually ignored in such studies.

Sexual dimorphism indicates that at least some of the selection pressures experienced by conspecific males and females are different. Among several hypotheses advanced to explain sexual dimorphism (Owens & Hartley, 1998; Massemin, Korpimäki & Wiehn, 2000; Blondel *et al.*, 2002), the prevalent ones involve sexual, as opposed to ecological, forces of selection (Payne, 1984; Dunn, Whittingham & Pitcher, 2001). For the majority of temperate-breeding, socially monogamous, migratory songbirds, males and

females are ecologically bound, occupying the same territory and, hence, the same macrohabitat. Accordingly, conspecific males and females, which exhibit some degree of morphological dissimilarity, face the same ecological conditions, during the breeding season at least. If morphology plays a role in the organization of breeding communities, in particular the segregation by macrohabitat within a guild, the expectation would be that differences among heterospecifics will exceed differences between conspecific opposite sexes, at least after correcting for size. If the contrary is the case, selective forces related to sexual dynamics prevail, and we would conclude that interspecific differences in skeletal morphology at this scale would not provide any explanatory power when considering patterns of within-guild macrohabitat use.

We studied territorial, foliage-gleaning, insectivorous, and mostly migratory passerine birds in a forested region of central Ontario. This guild was chosen as a study system because it has been used in several studies of niche partitioning and habitat preferences and it contained numerous similar congeneric species whose breeding macrohabitat preferences are well known. We monitored membership and spatial arrangements of guild members in the breeding landscape. We constructed a morphological data set for all guild members, treating the sexes separately. We made the general prediction that if variation in morphological traits were indeed associated with variation in macrohabitat, the closest pairs in a multivariate analysis of morphological space would be the conspecific sexes. More realistically, we predicted that because male migratory songbirds are almost invariably larger than females, the first component in multivariate analysis of morphological space, which usually reflects absolute size, would not produce conspecifics as closest neighbours. We predicted, however, that subsequent components, which deal with relative size or shape, would.

Methods

Fieldwork consisted of systematic bird surveys during the breeding seasons of 2002 and 2003 (May 30 to July 5), as well as a vegetation analysis of the survey transects. Survey routes were divided into 100-m lengths, and during repeated constant-effort surveys the presence of guild members was recorded, as were details of foraging behaviour. Not surprisingly, bird foraging and use of space were non-random with respect to woody plant species composition and structure, although these results will be reported elsewhere. Once the guild and the macrohabitat preference patterns of guild members were characterized, their morphologies were analyzed based on museum skeletons.

Limiting analysis to a guild is necessary because guild members are more likely to be similar morphologically, either through phylogeny or convergence, and are more likely to interact in the use of a resource. Limiting the guild is a somewhat arbitrary exercise because foraging traits among birds represent a continuous variable, but it is a necessary exercise in order to generate a coherent but substantially complete representation of the guild. We chose all those species that were under 20 g that largely feed by gleaning insects from foliage ("small foliage-gleaning insectivores"), resulting in the following: vireos (Vireonidae:

Vireo), kinglets (Regulidae: *Regulus*), black-capped chickadee (Paridae: *Poecile atricapilla*), and most wood-warblers (Parulidae) (Table I). Black-capped chickadees and black-and-white warblers (*Mniotilta varia*) frequently foraged from branches and twigs as well as foliage, but both were included. We did not include wood-warbler species of the genus *Seiurus*, which fed largely on the ground. Scarlet tanagers (*Piranga olivacea*) gleaned foliage and were present in modest numbers, but they are about 70% larger than the otherwise largest species in the guild and so were not included. Nor were red-breasted nuthatches (*Sitta canadensis*) included, a species that sometimes fed from evergreen foliage.

We obtained skeletons from the Royal Ontario Museum in Toronto. For each specimen, one of us (Mills) measured 27 skeletal measurements (skull length, skull width, culmen length, premaxilla length, premaxilla width, premaxilla depth, nares length, inter-orbital distance, mandible length, mandible width, mandible depth, coracoid length, scapula length, sternum length, sternum depth, keel length, humerus length, ulna length, radius length, carpometacarpus length, synsacrum length, synsacrum width, femur length, femur width, tibiotarsus length, tarsometatarsus length, and hallux length). These are diagrammed in Robins and Schnell (1971).

We applied the term *morphotype* to guild members identified by species and sex, so for 23 species there were 46 morphotypes. With a few exceptions, the 5 skeletons randomly selected for each morphotype were from adult specimens collected in southeastern Canada or the northeastern United States. When the geographic preference

could not be met, we used more distant birds, but this was infrequent. Similarly, when adults were unavailable, which was also infrequent, we used one or more birds collected in the autumn of their first year. We determined that the impact of age on size was negligible by comparing 5 individuals of each sex and each age (adult and hatch-year) for red-eyed vireo and black-throated blue warbler; immatures were less than 0.8% smaller than adults in linear measurements.

For each sex of each species we obtained all 27 measurements, with 4 exceptions. In 2 of those exceptions (female Cape May warbler and female pine warbler), we had 5 specimens but several bones were missing from 1 or 2 skeletons. In 2 other exceptions (female northern parula and male golden-winged warbler), we had only 3 specimens, also with several bones missing from 1 or 2 skeletons. Principal components analysis (PCA) frequently placed male and female northern parulas, and also male and female golden-winged warblers, close together in morphological space, suggesting that the partial data sets for those species did not distort results. We derived mean sizes for each of the 27 measures for each sex of each species.

The comparisons we focus on are those between males and females of the same species. Since they obviously share phylogenies, the data sets were not corrected for evolutionary history. In fact, if males and females of a phylogenetically uncorrected data set are not the closest morphological pairs, it is all the more reason to conclude that morphological variation does not primarily prescribe macrohabitat specificity.

Many data sets used for ecomorphological multivariate analysis are standardized by dividing morphological measures by size, such the cube root of mass (Leisler & Winkler, 1991). Mass, however, is an inherently unreliable measure of size (Rising & Somers, 1989). Furthermore, ratios are frequently not normally distributed (Atchley, Gaskins & Anderson, 1976) and such standardizing leads to constraints in the covariance or correlation structure that can profoundly affect ordination analysis (Jackson, 1997), leading to spurious relationships (Jackson & Somers, 1991). Finally, size may be the most important variant in ecomorphological space.

Instead, we used PCA and did not divide by size. In fact, we considered size by analyzing the first component (which reflects absolute size), and we considered size-independent morphological variation by analyzing components beyond the first component. This eliminated problems associated with using mass corrections and ratios, and it preserved size as ecomorphologically relevant.

Our units of measurement (mm) did not vary, and the standard deviations of our variables did not vary greatly (within one order of magnitude in all but the case of femur width). Consequently, in order to maximize the retention of size and shape information in our data, we used a covariance matrix comprising the means of the 27 morphological measurements. For all analyses, we used the Biplot and Singular Value Decomposition Macro add-in for Microsoft Excel (Lipkovich & Smith, 2002).

We analyzed different subsets of the whole data set that reflected different amounts of taxonomic complexity:

TABLE I. Small foliage-gleaning insectivorous species found at the study site. Numbers in the first column correspond to numbers on the biplots of Figure 2.

Common Name	Scientific Name
PARULIDAE	
1 Yellow warbler	<i>Dendroica petechia</i>
2 Chestnut-sided warbler	<i>Dendroica pensylvanica</i>
3 Black-throated blue warbler	<i>Dendroica caerulescens</i>
4 Black-throated green warbler	<i>Dendroica virens</i>
5 Cape May warbler	<i>Dendroica tigrina</i>
6 Pine warbler	<i>Dendroica pinus</i>
7 Yellow-rumped warbler	<i>Dendroica coronata</i>
8 Blackburnian warbler	<i>Dendroica fusca</i>
9 Magnolia warbler	<i>Dendroica magnolia</i>
10 Nashville warbler	<i>Vermivora ruficapilla</i>
11 Golden-winged warbler	<i>Vermivora chrysoptera</i>
12 Northern parula	<i>Parula americana</i>
13 Black-and-white warbler	<i>Mniotilta varia</i>
14 American redstart	<i>Setophaga ruticilla</i>
15 Mourning warbler	<i>Oporornis philadelphia</i>
16 Common yellowthroat	<i>Geothlypis trichas</i>
17 Canada warbler	<i>Wilsonia canadensis</i>
18 Wilson's warbler	<i>Wilsonia pusilla</i>
VIREONIDAE	
19 Red-eyed vireo	<i>Vireo olivaceus</i>
20 Blue-headed vireo	<i>Vireo solitarius</i>
REGULIDAE	
21 Ruby-crowned kinglet	<i>Regulus calendula</i>
22 Golden-crowned kinglet	<i>Regulus satrapa</i>
PARIDAE	
23 Black-capped chickadee	<i>Poecile atricapilla</i>

the *Dendroica* wood-warblers ($n = 9$ species), the non-*Dendroica* wood-warblers ($n = 9$ species), all wood-warblers ($n = 18$ species), and the whole guild ($n = 23$ species). We ran independent PCAs on each.

Using PCA, we chose to interpret the first 4 components from each subset analysis, as these explained in excess of 90% of variation in all cases. We analyzed the data in 4 stages. First, we considered components independently (1 dimension) to assess whether conspecific males and females were morphological neighbours in each component.

For the second and third stages, we collectively analyzed the components generated by the PCAs by using the PopTools macro add-in for Microsoft Excel (Hood, 2004) in order to produce 8 Euclidean distance matrices, 2 for each of the 4 different taxonomic groupings. We considered 3 principal components in each case. The first set of 4 analyses used components 1 through 3, which, by virtue of component 1, were strongly influenced by absolute size (“size-dependent analyses”). The second set of 4 analyses used components 2 through 4, which, by elimination of the first component, tended to eliminate the influence of absolute size (“size-independent analyses”). The fourth component never accounted for more than 4% of variation explained by the first 4 components, although it accounted for 11% to 16% of variation when the first component was eliminated. In all cases, we weighted the components according to the proportion of variance explained.

In the second stage, we subjected the distance matrices to Mantel tests (PopTools; 999 iterations) to assess correlation between conspecific sexes. We used binary matrices of 0s and 1s as null models, in which the conspecific differences were set to 0 and all others were set to 1. We conducted such analyses on all 8 data sets.

Using the 8 distance matrices independently, in the third stage we assessed the closeness of conspecific males and females in morphological space. For each morphotype, we determined the number of morphotypes that occupied a closer position in Euclidean space than the conspecific opposite sex, which we refer to as the number of intervening morphotypes.

The fourth stage involved consideration of separate body regions for the whole guild ($n = 23$ species) once differences in the occupation of morphological space between conspecific opposite sexes were demonstrated. We considered independently the measurements for beak and skull (anterior: $n = 11$), chest area and wing (mid-body: $n = 9$), and posterior body and leg (posterior: $n = 7$). We subjected each body region to PCA, and for each morphotype we determined the number of other morphotypes closer than the conspecific opposite sex in morphological space.

Results

MALES ARE INVARIABLY LARGER

In each of the 4 data subsets (*Dendroica*, non-*Dendroica* wood-warblers, all wood-warblers, and the whole guild), the first PCA component explained most of the variation (Table II: mean 70.6%; see Appendix I for eigenvector coefficients for the whole guild). Further, in

all 4 cases, all scores had the same sign, indicating that the first component is largely one that ordinales absolute size (Rising & Somers, 1989). For each species in all 4 data subset analyses, male first component scores exceeded those of the conspecific female. This is consistent with known mass differences that show male songbirds are usually heavier than their female conspecifics; published differences for 20 of the 23 species in our guild indicate males average 4.6% heavier than females (SE = 0.6%) (Dunning, 1984; Poole & Gill, 1992–2002).

CONSPECIFIC OPPOSITE SEXES ARE COMMONLY NOT NEIGHBOURS IN SINGLE MORPHOLOGICAL DIMENSIONS

When each component was considered independently, conspecific sexes were most commonly not closest neighbours, even among members of the genus *Dendroica*. Regardless of which of the 4 data subsets and which of the 4 principal components were considered, the mean number of morphotypes between the conspecific sexes was significantly different from zero (probability range: $P < 0.049$ to 0.0001). The average number of intervening morphotypes between conspecific sexes ranged from 1.1 (2nd component of breeding *Dendroica*) to 8.8 (4th component of whole guild) (Figure 1).

TABLE II. Distribution of variation (and cumulative variation) given in percentages among the first 4 PCA components for each data subset. The first component is primarily a measure of absolute size.

Data subset	Component			
	1	2	3	4
<i>Dendroica</i> warblers ($n = 9$)	71.0	14.7	5.8	2.6
		(85.7)	(91.5)	(94.1)
Non- <i>Dendroica</i> warblers ($n = 9$)	68.1	18.6	5.8	3.4
		(86.7)	(92.5)	(95.9)
Wood-warblers ($n = 18$)	62.7	20.2	6.6	3.6
		(82.9)	(89.5)	(93.1)
Whole guild ($n = 23$)	80.5	7.9	5.2	1.8
		(88.4)	(93.6)	(95.4)
Means	70.6	15.4	5.9	2.9
		(85.9)	(91.8)	(94.6)

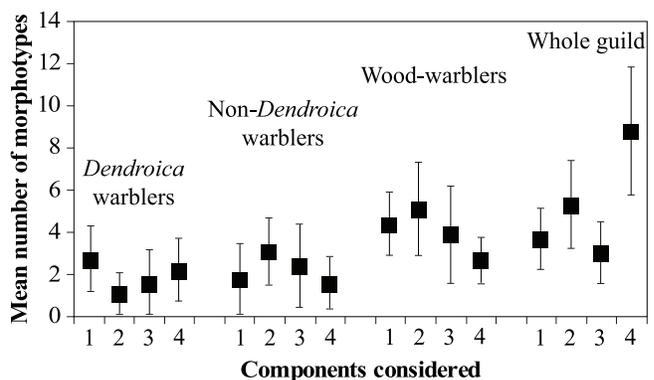


FIGURE 1. The mean number of morphotypes between conspecific opposite sexes for each component. Bars show 95% confidence limits for the estimate of means. Probabilities that the means are not zero range from 0.049 to < 0.0001 .

CONSPECIFIC OPPOSITE SEXES ARE NONETHELESS CORRELATED

The size-dependent 3-dimensional space generated from the first 3 components accounted for most variation (mean 91.8%; Table II), whereas the size-independent 3-dimensional space generated from components 2 through 4 accounted for substantially less (mean 24.0%, although they accounted for 83.7% of all variation after the first component; Table II). For each morphotype, Euclidean distance matrices generated from component scores allowed multi-dimensional comparisons of the distance to the conspecific opposite sex against the distances to all other morphotypes. Mantel tests on both the size-dependent and size-independent distance matrices demonstrated that conspecific opposite sexes are morphologically correlated ($P < 0.001$ for each data subset).

CONSPECIFIC OPPOSITE SEXES ARE COMMONLY NOT THE CLOSEST PAIRS IN MORPHOLOGICAL SPACE

While morphotypes other than the conspecific opposite sex are frequently closer in single morphological dimensions, intraspecific correlations from Mantel tests suggest that when multiple morphological dimensions are considered together, conspecific opposite sexes may be nearest neighbours. Furthermore, multidimensional considerations may be more ecologically realistic. However, when multiple components were analyzed simultaneously for both the size-dependent and size-independent distance matrices, the nearest neighbour was still frequently not the conspecific opposite sex (Table III and Figure 2). In all cases, the mean number of closer morphotypes was significantly different from zero (range: $P < 0.04$ to 0.0001), although in 2 cases the mean number of closer morphotypes was very small: 0.44 in the size-independent analysis of breeding *Dendroica* and 0.89 in the size-dependent analysis of breeding non-*Dendroica* wood-warblers. In the former, 13 of 18 morphotypes had the conspecific opposite sex as the closest neighbour, and in the latter, the figure was 12 of 18.

Notwithstanding the considerable potential of phylogeny to separate morphotypes, especially in size-independent cases, the interspersed morphotypes in morphological space was substantial, even at levels above that of genus. In the wood-warbler analysis ($n = 18$; 9 *Dendroica* species and 9 species of 7 other genera), the mean number of morphotypes closer than the conspecific opposite sex was 3.28 in both size-dependent and size-independent analyses, with 61% and 57%, respectively, being the number of closer morphotypes related at the family, rather than the genus, level. In the whole guild (4 families), there was substantial interspersed in the size-dependent analysis at least within the wood-warblers (see Figure 3a for the first 2 components). There was even more interspersed in the size-independent level: only 3 of 23 species showed morphologies substantially different from the rest, regardless of sex (see Figure 3b for the first 2 components). The 3 species were black-capped chickadee, common yellowthroat, and mourning warbler, none of which had congeners in the data set. The other 20 species, representing 3 families and 8 genera, were highly interspersed morphologically once absolute size was removed.

TABLE III. Mean numbers of morphotypes closer than the conspecific opposite sex for each data subset. Half of the analyses use the first 3 components, preserving the influence of absolute size, and half use components 2 through 4, largely eliminating the influence of absolute size.

Data subset	Number of species	Mean (95% CI)	Probability Mean = 0
COMPONENTS 1, 2, 3			
<i>Dendroica</i> warblers	9	2.4 (1.1–3.7)	< 0.0001
Non- <i>Dendroica</i> warblers	9	0.9 (0.1–1.7)	0.04
Wood-warblers	18	3.3 (2.0–4.5)	< 0.0001
Whole guild	23	3.0 (1.8–4.2)	< 0.0001
COMPONENTS 2, 3, 4			
<i>Dendroica</i> warblers	9	0.4 (0.1–0.8)	0.03
Non- <i>Dendroica</i> warblers	9	2.3 (1.4–3.2)	< 0.0001
Wood-warblers	18	3.3 (2.0–4.6)	< 0.0001
Whole guild	23	3.9 (2.1–5.7)	< 0.0001

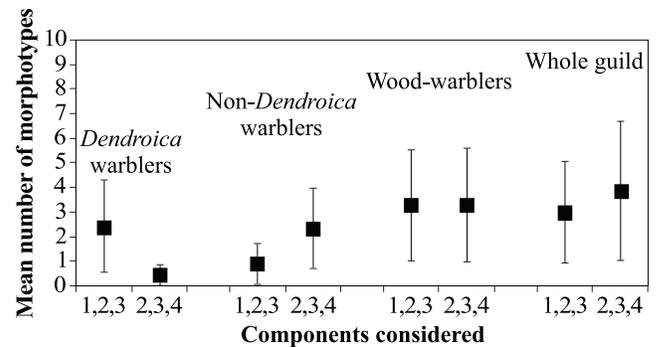


FIGURE 2. The mean number of morphotypes between conspecific opposite sexes for both the size-dependent analyses (components 1, 2, and 3) and the size-independent analyses (components 2, 3, and 4). Bars show 95% confidence limits for the estimate of means. Probabilities that the means are not zero range from 0.04 to < 0.0001.

PRINCIPAL COMPONENTS ANALYSIS OF THE DECONSTRUCTED BIRD

The morphological data set for the 23-species guild was divided into 3 separate matrices, one for beak and skull (“anterior”), one for chest and wing (“mid-body”), and one for synsacrum and leg (“posterior”). Again, the eigenvector coefficients of the first component from each correlation-based PCA all had the same sign, confirming that the first component is an indication of absolute size for each part of the body.

In each body region analysis, most variation was explained by this size component. For the mid-body, the first component explained all but 5.7% of variation, whereas the residual variation was considerably more for the anterior (13.3%) and the posterior (21.2%) regions. In other words, size better separated morphotypes in the mid-body data set than it did in the anterior and posterior body region data sets. Consideration of the number of morphotypes between conspecific opposite sexes indicated that males and females are more morphologically different in the mid-body region than fore or aft. The mean number of intervening morphotypes for the mid-body was 5.6, whereas for the anterior and posterior the figures were 2.3 and 1.7, respectively. Evidently, intersexual differences are as much about shape as size.

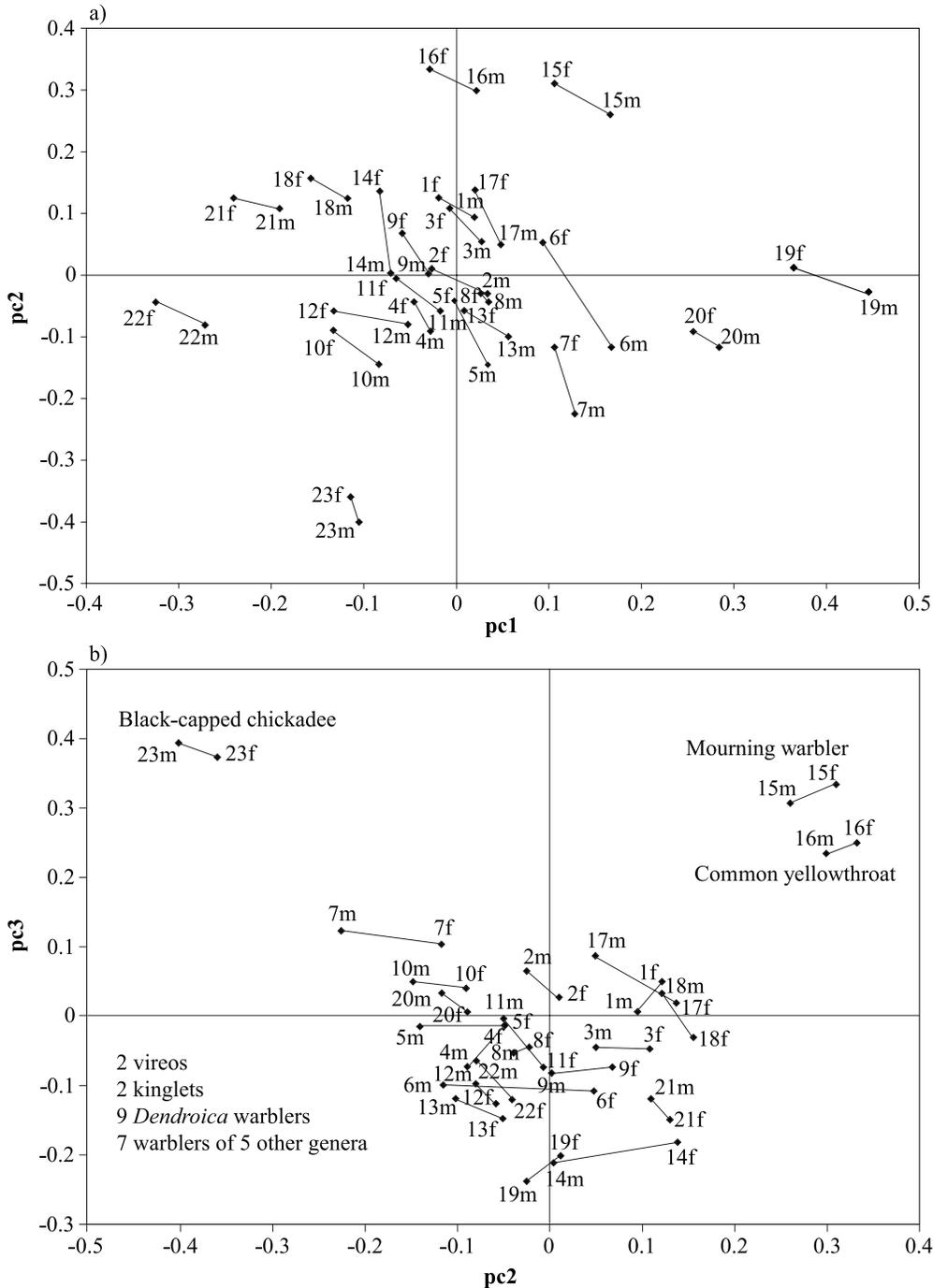


FIGURE 3. PCA biplots for the 23-species guild (m = male, f = female). Each species is designated with the number given in Table I. Lines join conspecific sexes. The biplot in (a) is generated from the first 2 components, accounting for 80.5% and 7.9%, respectively of variation. The first component is primarily one of size, and accordingly this biplot strongly reflects size differences along the horizontal axis, with the smaller kinglets at one end and the larger vireos at the other. The biplot in (b) is generated from the second and third components, which account for 7.9% and 5.2% of variation, respectively. These 2 components together explain 67% of shape variation but only 13.1% of total variation when absolute size (the first component) is also considered. Three labelled species are distinctly different in shape from the rest, regardless of sex; the other 20 species (40 morphotypes) are highly clustered.

Discussion

Analysis of morphological data assembled for members of this foliage-gleaning insectivorous guild indicates that there are correlations among morphological traits for conspecific opposite sexes. Such results are not unexpected for

the phylogenetically diverse data subsets of non-*Dendroica* wood-warblers (7 genera), all wood-warblers (8 genera), and the whole guild (4 families), but even within *Dendroica*, in which phylogenetic history is confounded by a basal polytomy (Lovette & Bermingham, 1999), correlation is high. However, notwithstanding that conspecific males and

females occupy the same macrohabitat during breeding, analysis also indicates that conspecific males and females are commonly not nearest neighbours in morphological space. This is not merely true within the *Dendroica* genus only; despite the power of phylogenetic influences, nearest neighbours are frequently not even congeneric in this guild.

Certainly, there is some connection between a species' preferred habitats and its gross morphology (Wiens, 1989). However, when the focus is on the similar species of a guild and their finer details of morphology, our findings indicate that we should not expect analysis of skeletal morphology to suggest any functional explanation of patterns of macrohabitat segregation among them. Other researchers have concluded there are linkages between specific habitat and small morphological differences in birds (Bairlein, 1980; Leisler & Winkler, 1985; 1991; Keast & Saunders, 1991; Marchetti, Price & Richman, 1995; Forstmeier, Bourski & Leisler, 2001). While such linkages may occur in some cases, our analysis suggests caution should be exercised in drawing such conclusions without direct functional evidence. If conspecific differences related to sexual dynamics can be greater than interspecific differences, with the former being accommodated by shared habitat, clearly differences at this morphological scale can be unrelated to matters of macrohabitat.

The conclusions that we have drawn in rejecting a breeding landscape ecological explanation for small morphological differences among similar species are independent of the decision to preferentially consider either size-dependent or size-independent analyses. It is sometimes contended that absolute size differences among species in the data set should be eliminated by employing ratios prior to analysis (Leisler & Winkler, 1991). Not only does such correction lead to problems in analysis, but also absolute size differences may be ecologically important (Polo & Carrascal, 1999). Size certainly dominated our ordinations, showing up without exception as the first component and accounting in all cases for most of the variation. In the data sets here it accounted for 62.7% of variation at a minimum (wood-warbler data set). And, as with other components, for the first component there was substantial interspersing of morphotypes, especially within the wood-warbler family. Our data also showed that dividing by weight would in fact distort the comparison of shapes, because conspecific males and females are not simply scaled versions of each other but instead differ disproportionately in the pectoral region. Nonetheless, both the size-dependent and the size-independent analyses indicated that within the guild, conspecific sexes are commonly not the closest neighbours in morphological space.

Among different morphological variables, bone characteristics are a common choice in ecomorphological studies because they are more reliable than more transitory structures. We acknowledge that they are not the only contributors to size and shape, however, and that even a comprehensive set of measurements like that used here does not capture all skeletal information. With birds, feather characteristics contribute to morphology (Winkler & Leisler, 1992), but age and wear make them unreliable in delineating small differences (Francis & Wood, 1989; Rising & Somers,

1989). Muscle and fat also contribute to morphology and have been used in ecomorphology studies (Moreno & Carrascal, 1993; Moreno, Barbosa & Carrascal, 1997), but they too vary with time, particularly with season or migratory status (Hipkiss, 2002). Furthermore, in some cases external morphology may not be what is determinative. In terns, for instance, Hulsman (1981) found that oesophagus length was more closely related to prey size than bill length, and Carothers (1982) found that tongue structure was a better predictor than bill morphology in Hawaiian honeycreeper feeding patterns. Analysis of non-skeletal morphological traits of the guild we studied might reveal greater interspecific differences than those suggested by our data set.

If the very modest morphological differences between similar species within a guild are not accounted for by breeding macrohabitat differences, why then do these similar species tend to segregate by macrohabitat given their similar morphologies? Perhaps some or all of the morphological differences result from drift, from environmental factors unrelated to macrohabitat (James, 1983; Swennen, De Bruijn & Duiven, 1983), from selective forces elsewhere, or from acute selection during relatively rare periods of stress or scarcity (Boag & Grant, 1984; Grant, 1986). Alternatively, the breeding macrohabitat specificity might reflect behavioural more than morphological adaptations for resource exploitation. Breeding-habitat specificity may even be a trait prescribed by mate choice dynamics (Mills, 2005), especially in the face of arguments that breeding season food resources may not be limiting (Lack, 1965; Schoener, 1965; Lozano & Lemon, 1998), meaning that selection for macrohabitat partitioning could be weak.

Although the sexual differences we have documented in size and shape must be accommodated by the ecology of the respective species, they are likely to have been engineered by sexual selection. The fact that one breeding macrohabitat can accommodate 2 conspecific but modestly different morphotypes should alert researchers that interspecific morphological differences at the scale seen between conspecific sexes are unlikely to be helpful in informing us about within-guild breeding macrohabitat differences among different species.

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APPENDIX I. Eigenvector coefficients of the principal components analysis for the whole guild ($n = 23$ species). The first through fourth components represent 80%, 8%, 5%, and 2%, respectively, of the total variance.

Measurement	Component 1	Component 2	Component 3	Component 4
Skull length	0.367	0.278	-0.172	0.265
Skull width	0.126	-0.103	0.172	0.343
Bill length	0.205	0.295	-0.393	0.023
Premaxilla length	0.111	0.188	-0.265	-0.109
Premaxilla width	0.101	-0.003	0.005	0.149
Premaxilla depth	0.045	-0.033	0.066	0.114
Nares length	0.071	0.148	-0.210	-0.096
Intra-orbital distance	0.066	0.021	-0.003	0.073
Mandible length	0.331	0.249	-0.317	0.136
Mandible depth	0.029	-0.050	0.060	0.097
Mandible width	0.157	-0.146	0.182	0.424
Coracoid length	0.223	-0.103	0.127	0.079
Scapula length	0.261	-0.078	0.152	-0.061
Sternum length	0.236	-0.142	0.122	-0.108
Sternum depth	0.101	-0.045	0.029	-0.126
Keel length	0.275	-0.230	0.063	-0.297
Humerus length	0.246	-0.139	0.132	0.122
Radius length	0.256	-0.300	-0.198	-0.223
Ulna length	0.290	-0.313	-0.188	-0.248
Carpometacarpus length	0.159	-0.188	-0.063	-0.132
Synsacrum length	0.194	-0.040	0.128	0.094
Synsacrum width	0.119	-0.072	0.109	0.035
Femur length	0.198	0.219	0.250	0.150
Femur width	0.014	-0.002	0.011	0.004
Tibiotarsus length	0.205	0.384	0.463	-0.332
Tarsometatarsus length	0.080	0.379	0.265	-0.308
Hallux length	0.064	0.023	0.004	0.189