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## Influence of body size on coexistence of bird species

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**Abstract** Theory suggests that body size is an important factor in determining interspecific competition and, ultimately, in structuring ecological communities. However, there is a lack of pragmatic studies linking body size and interspecific competition to patterns in ecological communities. The objective of the present study was to determine the effect of body size (mass) on competitive interactions between bird pairs and to investigate the influence of food guilds. Point-counts were carried out in nine sites every month from November 2002 to November 2003 in the Cuetzalan Region, Mexico, and we used presence/absence and abundance data for the analyses. To calculate the strength of competition we used the Angle Frequency Method to extract form factors from 20 pairwise interactions. A prototype competition interaction and random pairs were also constructed. We used clustering techniques (PCA) to calculate the dissimilarity scores (distances,  $D$ ) of each of the pairwise interactions to the prototype competition and random pairs and one-way ANOVA to test for differences between the means of the random and competitive pairs. The ratio in body mass ( $\ln BM$ ) for each of the interacting pairs was calculated, and the association between the  $\ln BM$  ratio and the strength of competition ( $D$ ) was tested using a Pearson product-moment correlation coefficient. To test for the influence of foraging guilds we used a univariate general linear model. Our results demonstrate a significant negative relationship between bird body mass ratio and competition strength – i.e. competition strength increased when the body masses of the birds became more similar. We did not find a significant influence of foraging guild on the relationship between body mass ratio and competition strength. On

the basis of these results, we suggest that high variation in body sizes amongst sympatric species promotes coexistence in communities.

**Keywords** Bird community · Body mass ratio · Foraging guilds · Interspecific competition · Phase portraits

### Introduction

Interspecific competition has long been recognised as a major ecological force shaping the community patterns (Ricklefs 1975; Giller 1984; Wiens 1989; Keddy 2001). The coexistence of species is determined to a great extent by the level of interspecific competition for limited resources (Bowers and Brown 1982). However, uncertainty still exists about the biological conditions under which interspecific competition has a greater or a lesser influence on the densities of the species populations and the community structure (Chesson and Huntley 1997; Gurevitch et al. 2000; Chase et al. 2002). The mechanisms and the strength of the interspecific competition have remained elusive. Body size is among one of the factors believed to have a major impact on the competitive strength of sympatric species in ecological communities. The role of significant differences in body size among coexisting species has been widely discussed (e.g. Wilson 1975; Brown and Maurer 1986; Gotelli and Ellison 2002; French and Smith 2005). Theory suggests that differences in body size follow a competitive gradient, where species can evade competition by differing in body size because species with dissimilar body masses have dissimilar energetic requirements and capacities in terms of food searching, harvesting or processing (Bowers and Brown 1982). Moreover, in two-species interactions, the effect of one competitor on the second is, in many cases, much greater than the reverse; a situation known as asymmetric competition (Persson 1985). A common example of asymmetric competition is where competing species differ in size, and the larger

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enjoys an advantage because of its increased feeding ability (Schoener 1983; Young 2004). However, despite the many years of discussion on the influence of body size on the strength of competition, the functional significance of body mass in community ecology remains unclear, and the relationship between coexistence and body mass differences among ecologically similar species is still an on-going debate.

The objective of the investigation reported here was to examine the effect of body mass differences on competitive interactions between species pairs of ecologically similar birds. Our hypothesis is that the competition strength between competing species will be negatively correlated to an increasing dissimilarity in body size, with the highest level of competition appearing between species with the lowest difference in body mass. An extension of this hypothesis is the presumption that species similar in morphology, physiology and behaviour will experience more intense competition (Brown and Wilson 1956; Hutchinson 1959; Grant 1972; Martin and Martin 2001). In particular, species that exploit the same food resource in a similar manner (i.e. same foraging strategy) will be expected to compete with each other, thereby separating the species ecologically at the niche level by a guild (Wiens 1989). A second objective of our study, therefore, was to determine whether species that share food resources exhibit stronger competition than species that differ in their resource use.

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## Methods

### Phase portraits

Species interactions form the foundation of community ecology. However, in a natural community it is often difficult to first identify the interactions between species (e.g. competition) and subsequently to quantify the strengths of these interactions. Several studies have recently reported methods that can differentiate among these different “signals”, thereby providing the means to both identify the interaction type and to quantify the interaction strength using time series. Seip (1997) developed and tested a method called the Key Factor Method, which he used for characterising species interactions from ecological data using time series, which were plotted in so-called phase portraits. This method extracts quantitative variables that characterise species interactions. An extension of the Key Factor Method, called the Angle Frequency Method, was developed slightly later and tested in modelling studies (Seip and Pleym 2000; Sandvik et al. 2002) and observational studies (Sandvik et al. 2003; Sandvik et al. 2004).

Both methods are developed from the traditional graphical analysis of species interactions in ecology (Lotka 1925; Volterra 1926; Rosenzweig and MacArthur 1963; MacArthur 1972). The Key Factor Method and the Angle Frequency Method show that species

interactions (i.e. prey-predation, competition, mutualism and facilitator-gainer) can all be distinguished by their biomass trajectories, where different types of ecological interactions will show unique patterns in phase portraits. This simple approach avoids past difficulties in which studies relied either on simplifying assumptions which are often violated in ecological synoptic data or on the need for extensive information about the community under study (Sandvik et al. 2004).

In an ideal competition interaction, an numerical increase in species *a* will cause a proportional decrease of species *b*. The corresponding phase portrait (i.e. where the biomass of both species are plotted on the *x* and *y* axis) will show a sequence of trajectories along a line through the centre point at a 135° angle to the *x* axis that is clearly distinctive from other interaction types (i.e. mutualism, prey-predator and facilitator-gainer) (Gilpin et al. 1982; Seip 1997).

Moreover, even though a diverse of theories predict the conditions in which species interactions ought to be strong (Sarnelle 1994; Thompson 1999), it has proven to be difficult to determine the actual strength in a truly quantitative approach. Despite these difficulties, the aforementioned methods have been shown to be successful in differentiating competition interactions and the strength of these interactions in natural communities.

### Bird species data set

The bird species data set used this study was a compilation of presence-absence and abundance data obtained from point-count censuses from the Cuetzalan Region (approx. 54,200 ha) in the north-eastern mountain range of Puebla, Mexico. The point-count censuses were conducted on a monthly basis over a 1-year period from November 2002 to November 2003. We used standard point count techniques for bird detection (Bibby et al. 1992), with  $\pm 10$  point counts, within nine different sites. A modified double-observer approach was used for visual and auditory avian detection (Parker 1991). We used a modified double-observer approach because in comparison to a single-observer point-counts the overall detection probabilities of the former had proven to be significantly higher (Nichols et al. 2000). Moreover, both observers together covered a range of 360°, which is clearly larger than the 180° of Nichols et al. (2000). Birds were observed over a fixed-radius of 25 m during a counting period (single count) of 10 min (Dawson et al. 1997; Viellard 2000). The use of a short, fixed radius enabled us to maintain a high detection probability, thereby eliminating the need to correct for a decrease in detection probability using distance sampling methods (Buckland et al. 2001). A distance of 100 m between point counts was used to avoid dependency between point count observations. From this species data set we calculated the average number of individuals in all points per location for each species for each of the

12 months; these calculations enabled us to analyse changes in time series.

### Selection of species and construction of the competition prototype

From the bird species data set ( $n=181$ ) we selected 20 competitive species pairs (C1, ..., Cn) and five non-competitive (S1, ..., Sn) (see Table 1). The most common species were selected, which in the majority of cases were those bird species that were resident birds; however, some migratory species were also selected. The competitive species pairs were selected on the basis of body mass similarity (ranging from 6.2 to 324 g), from which body mass ratios were calculated. Some species were included in more than one competitive species pair under the criterion that sufficient abundance data were available. In addition, similarity in foraging strategy was also used as a factor for the selection of the species pairs; as such, three types of

foraging strategy were determined: (1) diet specialists, with only one type of foraging strategy (e.g. insectivorous, granivorous); (2) opportunistic feeders, which have a facultative foraging strategy, thereby enabling them to shift to other food sources; (3) generalists, which accept a wider range of diet, i.e. omnivorous. For the non-competitive pairs, species were selected based on body mass but with unrelated foraging strategies. To compare and estimate the similarity of these observed pairs to a theoretically ideal competition interaction, we constructed a prototype case (COM) in which the assumptions underlying the expected patterns for competition were fulfilled – i.e. competing species replace each other consequently; an increase in the biomass of one species causes a proportional decrease in the biomass of the other species (Seip 1997). We also constructed a purely random interaction (STO) to identify stochasticity in the pairwise interactions. The random interaction was constructed using random numbers created by a random number generator with 10,000 permutations.

**Table 1** Bird species selected for the pair-wise comparisons together with their classification in terms of status, foraging strategy and body mass

Common name	Scientific name	Order	Family	Status <sup>a</sup>	Foraging strategy <sup>b</sup>	Body mass (g)
Red-billed Pigeon	<i>Columba flavirostris</i>	Columbiformes	Columbidae	R	G/F	324
White-tipped Dove	<i>Leptotila verreauxi</i>	Columbiformes	Columbidae	R	G/F	153
White-crowned Parrot	<i>Pionus senilis</i>	Psittaciformes	Psittacidae	R	F	212
Squirrel Cuckoo	<i>Piaya cayana</i>	Cuculiformes	Cuculidae	R	I	108
Wedge-tailed Sabrewing	<i>Campylopterus curvipennis</i>	Apodiformes	Trochilidae	R	N/I	6.2
White-bellied Emerald	<i>Amazilia candida</i>	Apodiformes	Trochilidae	R	N	3.8
Blue-crowned Motmot	<i>Momotus momota</i>	Coraciiformes	Momotidae	R	O	133
Golden-fronted Woodpecker	<i>Melanerpes aurifrons</i>	Piciformes	Picidae	R	I	80.9
Lineated Woodpecker	<i>Dryocopus lineatus</i>	Piciformes	Picidae	R	I	183.5
Dusky-capped Flycatcher	<i>Myiarchus tuberculifer</i>	Passeriformes	Tyrannidae	R	I/F	19.9
Great Kiskadee	<i>Pitangus sulphuratus</i>	Passeriformes	Tyrannidae	R	I/F	61
Social Flycatcher	<i>Myiozetetes similis</i>	Passeriformes	Tyrannidae	R	I/F	28
Sulphur-bellied Flycatcher	<i>Myiodynastes luteiventris</i>	Passeriformes	Tyrannidae	R	I	45.9
Masked Tityra	<i>Tityra semifasciata</i>	Passeriformes	Tyrannidae	R	F	79.3
Green Jay	<i>Cyanocorax yncas</i>	Passeriformes	Corvidae	R	O	157
Brown Jay	<i>Cyanocorax morio</i>	Passeriformes	Corvidae	R	O	235
Band-backed Wren	<i>Campylorhynchus zonatus</i>	Passeriformes	Troglodytidae	R	I	35.6
Spot-breasted Wren	<i>Thryothorus maculipectus</i>	Passeriformes	Troglodytidae	R	I	14.85
White-breasted Wood-Wren	<i>Henicorhina leucosticta</i>	Passeriformes	Troglodytidae	R	I	15.7
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	Passeriformes	Sylviidae	M	I	6
Clay-colored Robin	<i>Turdus grayi</i>	Passeriformes	Turdidae	R	I/F	73.8
White-throated Robin	<i>Turdus assimilis</i>	Passeriformes	Turdidae	R	I/F	67.5
Black-throated Green Warbler	<i>Dendroica virens</i>	Passeriformes	Parulidae	M	I	8.8
Wilson's Warbler	<i>Wilsonia pusilla</i>	Passeriformes	Parulidae	M	I	7.7
Golden-crowned Warbler	<i>Basileuterus culicivorus</i>	Passeriformes	Parulidae	R	I	10.5
Rufous-capped Warbler	<i>Basileuterus rufifrons</i>	Passeriformes	Parulidae	R	I	10.9
Yellow-throated Euphonia	<i>Euphonia hirundinacea</i>	Passeriformes	Thraupidae	R	G/F	14
Yellow-winged Tanager	<i>Thraupis abbas</i>	Passeriformes	Thraupidae	R	F	45
Green-backed Sparrow	<i>Arremonops rufivirgatus</i>	Passeriformes	Emberizidae	R	G	23.6
Dark-backed Goldfinch	<i>Carduelis psaltria</i>	Passeriformes	Fringillidae	R	G	9.5
Melodious Blackbird	<i>Dives dives</i>	Passeriformes	Icteridae	R	O	96.2
Great-tailed Grackle	<i>Quiscalus mexicanus</i>	Passeriformes	Icteridae	R	O	149
Altamira Oriole	<i>Icterus gularis</i>	Passeriformes	Icteridae	R	I/N	55.3
Black-headed Oriole	<i>Icterus graduacauda</i>	Passeriformes	Icteridae	R	I/N	42.2
Montezuma Oropendola	<i>Psarocolius montezuma</i>	Passeriformes	Icteridae	R	F	324

<sup>a</sup>M, Migratory; R, resident

<sup>b</sup>I, Insectivore; F, frugivore; N,nectarivore; G, granivore; O, omnivore

## Form factors

We used the Key Factor Method to characterise species pairwise interactions (Seip 1997). We first constructed phase portraits for each species pair, including the random interaction and the ideal competitive pairs, in which the average number of individuals for species  $x$  and  $y$  was plotted using the 12 synoptic samples. The phase portrait for the prototype competition interaction was plotted and the sequences of trajectories depicted as a line through the centre point at a  $135^\circ$  angle to the  $x$  axis (Gilpin et al. 1982; Seip 1997; Seip and Pleym 2000). Thereafter, we extracted 13 form factors from each of the phase portraits of pairwise interactions. The form factors express attributes that characterise each phase portrait for the competition (see Seip 1997).

To calculate dissimilarity scores (distances) for each of the pairwise interactions with the prototype competition and random pairs we used clustering techniques based on principal component analysis (PCA) (Jongman et al. 1987). We constructed a matrix ( $27 \times 13$ ) that contained the independent form-factor variables, i.e. 25 species pairs, one random interaction and one prototype competition interaction (rows), and 13 parameters (columns). The scaling was done by interspecies correlations, and the species scores were divided by standard deviations; data were not transformed and subsequently centred by species. The resulting scatter plot shows points representing the interacting pairs in a coordinate system formed by the principal axes defined by the PCA. We used the scores of the first and second axis to calculate distance scores ( $D$ ) from the interacting pairs to the prototype competition interaction. We used the Pythagorean Theorem to calculate the distance between each of the interacting pairs ( $x, y$ ) and the reference competition point from their coordinates on the first and second principal component axis. These distance scores ( $D$ ) were used as the dependent variable for hypothesis testing. To test if there were significant differences between the means of the random and potentially competitive pairs, we used a one-way ANOVA procedure, with  $D$  as the dependent variable and the random/non-random pair interactions as the independent factor.

We next calculated the ratio of the ln body mass (lnBM) for each of the interacting pairs (Table 2). Body masses of the bird species were taken from Dunning (1993). We subsequently calculated the association between the lnBM ratio and the strength of competition ( $D$ ) using a Pearson product-moment correlation coefficient (SPSS ver.12; SPSS, Chicago, Ill.). A univariate general linear model (GLM with Type III sums of squares) was then used for regression analysis, where the lnBM ratios were used as the covariate and the distance scores  $D$  as the dependent variable. We included two fixed factors to categorise the species pairs. The first fixed factor contained three groups, classifying the different foraging guilds into specialist-generalist classes; the second fixed factor was used to distinguish the classes for random/non-random pair interactions.

**Table 2** Body mass ratios for the selected competitive and non-competitive species pairs, and their codes

Selected species pairs	Body mass ratio	PCA code
<b>Competitive</b>		
<i>Columba flavirostris</i> – <i>Leptotila verreauxi</i>	0.750	C8
<i>Campylopterus curvipennis</i> – <i>Amazilia candida</i>	0.490	C1
<i>Melanerpes aurifrons</i> – <i>Campylorhynchus zonatus</i>	0.821	C9
<i>Myiozetetes similis</i> – <i>Myiarchus tuberculifer</i>	0.341	C5
<i>Myiodynastes luteiventris</i> – <i>Campylorhynchus zonatus</i>	0.254	C14
<i>Tityra semifasciata</i> – <i>Thraupis abbas</i>	0.567	C18
<i>Cyanocorax morio</i> – <i>Cyanocorax yncas</i>	0.403	C7
<i>Henicorhina leucosticta</i> – <i>Thryothorus maculipectus</i>	0.056	C15
<i>Turdus grayi</i> – <i>Turdus assimilis</i>	0.089	C16
<i>Turdus grayi</i> – <i>Pitangus sulphuratus</i>	0.190	C11
<i>Basileuterus culicivorus</i> – <i>Dendroica virens</i>	0.177	C20
<i>Basileuterus rufifrons</i> – <i>Basileuterus culicivorus</i>	0.037	C4
<i>Basileuterus rufifrons</i> – <i>Wilsonia pusilla</i>	0.348	C19
<i>Euphonia hirundinacea</i> – <i>Poliophtila caerulea</i>	0.847	C17
<i>Arremonops rufivirgatus</i> – <i>Carduelis psaltria</i>	0.910	C3
<i>Quiscalus mexicanus</i> – <i>Momotus momota</i>	0.114	C13
<i>Quiscalus mexicanus</i> – <i>Dives dives</i>	0.438	C12
<i>Icterus gularis</i> – <i>Icterus graduacauda</i>	0.270	C6
<i>Psarocolius montezuma</i> – <i>Pionus senilis</i>	0.424	C2
<i>Dryocopus lineatus</i> – <i>Piaya cayana</i>	0.530	C10
<b>Non-competitive</b>		
<i>Pionus senilis</i> – <i>Cyanocorax morio</i>	0.103	S1
<i>Melanerpes aurifrons</i> – <i>Tityra semifasciata</i>	0.020	S2
<i>Dryocopus lineatus</i> – <i>Cyanocorax yncas</i>	0.171	S3
<i>Dendroica virens</i> – <i>Carduelis psaltria</i>	0.077	S4
<i>Thraupis abbas</i> – <i>Icterus graduacauda</i>	0.064	S5

## Results

### Competition dissimilarity scores

The PCA scores for the assumed competitive and random interactions were dissimilar, forming distinct clusters that are signals of competition or stochasticity for the different species pairs (Fig. 1). The first principal component axis explained 50% of the variability in the data, and the second axis explained 43%, a total of 93% for the two axes.

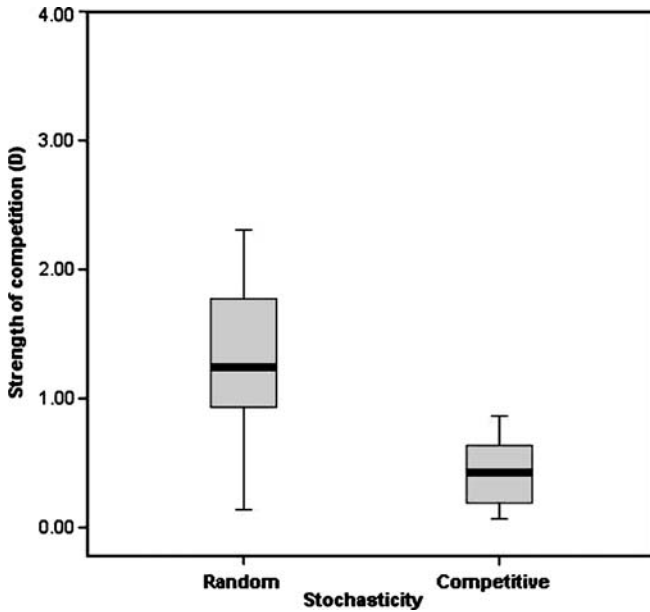
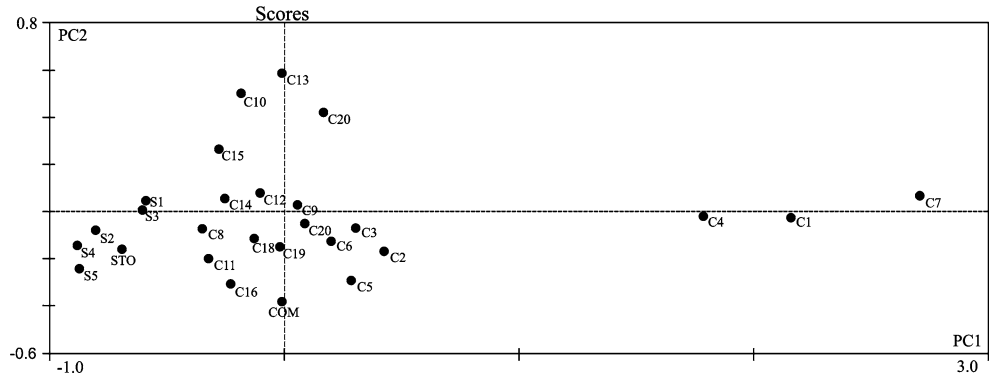
The analysis of variance showed that the  $D$  scores of the random and competitive groups were significantly different ( $F_{1, 26} = 7.226$ ,  $P = 0.015$ ) (Fig. 2), with a higher  $D$  score (i.e. a larger distance from the competition reference point) for random pairs than for potentially competing pairs.

### Effects of body mass on species competition

We found a significant negative correlation between the body mass ratio and the strength of competition ( $D$ ) ( $r = 0.536139$ ,  $P = 0.02$ ,  $R^2 = 0.446$ ) (Fig. 3). Note that in Fig. 3 the  $y$  axis ranges from strong to weak competition, beginning at the origin (0).



**Fig. 1** The score plot shows the first principal component in the  $x$ -axis, which explains 50% of the variance, and the second principal component in the  $y$ -axis, which explains 43% of the variance. It shows the position of the prototype interaction for competition ( $COM$ ), the stochastic interaction ( $STO$ ), the interacting pairs ( $C1, \dots, Cn$ ) and the random pairs ( $S1, \dots, Sn$ )

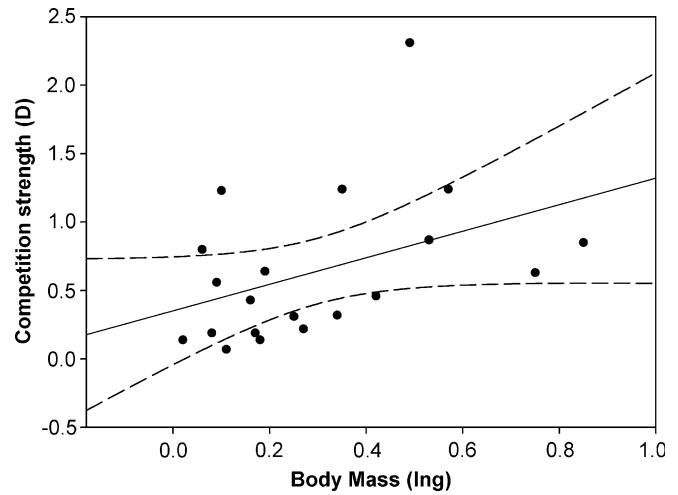


**Fig. 2** Significant differences in the mean  $D$  scores of the two random and competitive groups ( $F_{1, 26} = 7.226, P = 0.015$ )

In addition, the foraging guild included as a fixed factor in the model did not show a significant effect of foraging guild on competition strength ( $D$ ) ( $P = 0.421$ ).

## Discussion

We have demonstrated a significant negative relationship between bird body mass and the competition strength: the larger the difference in body mass between species pairs, the lower the competition strength. Although this is not direct proof that the coexistence of species in communities is structured by differences in body mass, evidence of size-related resource division supports the conclusion that different size classes in the community may promote coexistence (Hutchinson 1959; Bowers and Brown 1982; Grant 1986; Ernest 2005). Theory suggests that a reduction in niche overlap associated with asymmetric competition can facilitate evolutionary divergence by subjecting species to selection



**Fig. 3** Positive correlation between the body mass ratio, i.e.  $|\ln BM_{species1} - \ln BM_{species2}|$ , and the strength of competition ( $D$ ) ( $r = 0.536, P = 0.02, R^2 = 0.446$ ). Here, the  $y$  axis ranges from a strong to weak competition, beginning at the origin (0)

pressures that are different from those prevailing when competition is symmetric (Rummel and Roughgarden 1985; Taper and Case 1992; Law et al. 1997). This relationship may also result from restrictions imposed by size-dependent metabolic rates, biotic interactions and energy availability to different size classes (Knouft 2002). Previous results have suggested that body size-mediated competition may be important for structuring energy use (Ernst 2005) and that energy is unequally available across body sizes. Therefore, body sizes with the greatest access to resources would be favoured, resulting in aggregations of species around specific masses (Holling 1992). Moreover, Brown and Bowers (1984) found that species of similar size (body mass) coexist less frequently in local communities, suggesting that their co-occurrence is precluded by interspecific competition. Our results indicate that similarity in body size (i.e. a low body mass difference) increases competition and, thereby, would promote character displacement. However, no data are available on resource availability; therefore, it remains unclear whether the coexistence of species with relative similar body sizes is

supported by an unequal access to resources. In addition, morphological differences (i.e. beak size and structure) in similar-sized bird species that occupy the same habitat might promote coexistence through feeding niche differentiation (Baldwin 1953; Grant 1966, 1968, 1999; Freed et al. 1987; Conant 1988). In our results, the influence of phylogenetic relatedness in interacting couples did not show a clear pattern as it is presented in the PCA. Species pairs – those with higher competition strengths clustered closely to the prototype competition pair – do not necessarily belong to the same taxonomic order and/or family, with the majority of competitive pairs being phylogenetically unrelated. Some species pairs with lower competition strengths were closely related, belonging to the same genus or family. However, there is a need for further analyses that incorporate the impact of phylogenetic relatedness on competition.

In accordance with our results, it has been suggested that body mass – not diet specialisation – is the main factor influencing the dominance patterns of competitive species (French and Smith 2005). In our results we did not find a significant influence of guild type in the relationship between body mass and competition strength. Alternative explanations are based on the theory of speciation and radiation, where genetically variable traits in morphological differences (e.g. beak size) may result in a greater specialisation in obtaining some particular food, thereby avoiding competition (Grant 2001). It has also been suggested that allometric scaling partly determines coexistence through competition, thereby structuring species assemblages, especially between closely related species of similar size in the same guild (Brown and Bowers 1984).

Our results indicate that the body mass-competition strength relationship may be a valuable, robust and powerful tool to identify patterns of community structure. However, further exploration of the body mass-competition relationship in which different temporal and spatial scales as well as different taxa are taken into consideration should produce deeper insights into the forces shaping community structure and species coexistence. Experiments aimed at measuring the competition intensity should also be performed to corroborate the existing gradient in competition intensity (i.e. from diffuse competition to monopolistic competition) in natural communities.

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