Weight-Density Relationships between and Within Bird Communities: Implications of Niche Space and Vegetation Structure

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NOTES AND COMMENTS

WEIGHT-DENSITY RELATIONSHIPS BETWEEN AND WITHIN BIRD COMMUNITIES: IMPLICATIONS OF NICHE SPACE AND VEGETATION STRUCTURE

The population density of a species in a given area is limited by the number of individuals that the area can support, equivalent to the amount of energy available to the population divided by the energetic requirements per individual of each species (Damuth 1981; see nevertheless Wiens 1989 and references therein for a critique to this equilibrium-based view and for other factors limiting population density apart from energy limitations). Energetic requirements scale positively with body weight, while population density usually scales negatively (but see Cotgreave and Harvey 1992 and Griffiths 1992 for examples of this nonubiquitous pattern). Some studies have attempted to evaluate this capacity rule (Brown 1981) by examining the inverse relationship between density (D) and body weight (W) in several animal groups using the equation $D = aW^b$, where a and b are constants (Damuth 1981, 1987; Peters 1983; Peters and Wassenberg 1983; Peters and Raelson 1984; Brown and Maurer 1986; Robinson and Redford 1986). This relationship, however, has proven difficult to analyze in small birds (e.g., Passeriformes: Juanes 1986; but see Carrascal and Tellería 1991). This difficulty may be due to problems in methodology used to evaluate D as well as to the influence of other biological variables (e.g., competition, predation, population structure, zoogeographical limits, phylogenetic relatedness; Juanes 1986; Robinson and Redford 1986; Damuth 1987; Carrascal and Tellería 1991; Nee et al. 1991; Cotgrave and Harvey 1992). These variables are difficult to quantify (Peters and Raelson 1984) yet may be important in the determination of resource allocation among species (allocation rules; Brown 1981). Alternatively, it is possible that difficulties in showing expected relationships between D and W in birds could be due to some biological features of birds not usually considered. Pagel et al. (1991) have pointed out metabolic rate and ability to survive environmental fluctuations as two possible ecological features, and they believe that the best way for understanding density and body size relationships is focusing on the biological characteristics of given species.

Flight and the radiation and adaptation to contrasting conditions have permitted birds to exploit food in a variety of sites using a variety of methods (foraging methods, habitats, and feeding substrates). This wide use of habitats entails some

body weight restrictions: small birds have adaptations for foraging on slender and pliable substrates, like twigs and foliage, that require higher maneuverability (Croxall 1977; Norberg 1977; Alatalo 1982; Winkler and Leisler 1985; Carrascal et al. 1990; Gustafsson 1988 at the intraspecific level). Body weight could thus figure importantly in an allocation rule restricting use of some arboreal substrates, through its allometric effects on morphological shape and biomechanical functions (Peters 1983). Therefore, bird assemblages that exploit the firmest (e.g., ground, trunk, thick branches) substrates should contain heavier species than assemblages that exploit twigs and foliage. Analysis of all assemblages belonging to a community should show that the greater the significance of slender and pliable substrates (e.g., foliage), the lower the average weight of member species. This trend is opposite to the postulated size increase of species weights along successional series (Odum 1969; but see Smith and MacMahon 1981; Glowacinski and Weiner 1983).

These differences in mean body weight of bird species belonging to different assemblages, resulting from ecomorphological constraints, merit a detailed analysis to clarify the energetic implications of the relationships between W and D. Some authors have suggested that energy use of ecologically and taxonomically similar populations is independent of body size (Damuth 1981, 1987; Carrascal and Tellería 1991), while others support the view that energy use should be higher in larger (Brown and Maurer 1986, 1989; Maurer and Brown 1988; Du Toit and Owen-Smith 1989; Pagel et al. 1991) or smaller species (Harvey and Lawton 1986). This controversy may be due to ignorance of the range of variation of body weight in the species under study (a problem of size scale). In effect, if b is a function of the mean body weight of bird species in assemblages, does this result in differences in energy allocation related to bird size among assemblages? If so, the understanding of variation of b within bird communities requires knowledge of habitat structure and the ecological niches of each species (e.g., a previous autecological study of the species).

In this note, we develop two different analyses that compare bird communities on two distinct spatial scales. The first approach incorporates information on foraging behavior to analyze body weight–density relationships within different assemblages (according to substrate use). This is a large-scale comparison that emphasizes similarities among forest bird communities in widely different forest habitats across two continents; species from different habitats and continents are assigned to the same set of foraging assemblages. The second analysis compares communities of birds in the same geographical region, analyzing the allometric relationship of population density for all species in the same community. The results are compared across a systematically varying environmental gradient (foliage volume).

METHODS

To analyze the relationship between mean body weight of assemblages and rate of density change with bird size, we reviewed studies on bird use of space

during the breeding season in five woodland communities of North America (Holmes et al. 1979, 1986; Sabo 1980; Rosenberg et al. 1982; Landres and MacMahon 1983) and in two of Europe (Carrascal et al. 1987). We have not considered studies dealing with a very limited guild ($\leq$ 5 species; few species and thus low degrees of freedom), those in which species' weights were not available, or those with a very incomplete description of substrate use by species. Species densities within assemblages exploiting ground, trunks, branches, and foliage in each forest were obtained by weighting species density by the percentage of foraging observations recorded on each substrate. As some authors grouped branches according to their diameter (e.g., < 1 cm, 1–10 cm, > 10 cm), in this study twigs (< 1-cm diameter) were grouped with foliage (deciduous leaves or needles), and thick branches (> 10 cm diameter) with trunks.

The second analysis, focused at the community level, was performed on data on passerine density and vegetation structure of 17 habitats in northern Spain (43°N, 3°W) differing in foliage height diversity and volume (data from Carrascal 1987). A principal components analysis of 16 structural and floristic variables provided a first principal component related to structural complexity (vegetation layer diversity and foliage density; Carrascal 1987). This structural component was highly correlated ($P < .001$) with tree height and density. Therefore, we use the product of tree height and tree density to work with a simple and easily interpretable measurement of foliage volume. For each of the 17 bird communities, we calculated the slope (b) of the log-log regression model of species density on bird weight (number of species ranged between five and 22). Body weight of species was taken from Perrins (1987) as the mean weight of males and females, or as the average value of body weight range.

In both within- and between-community-level analyses, species heavier than 350 g were excluded as they are usually censused inaccurately by methods employed to record small passerine abundance (Tellería 1986). Birds were censused by means of the line transect method using belts of 25 m at each side of the transect. Minimum area censused for each of the 17 habitats in northern Spain was 40 ha. Densities refer to breeding period when the considered species are mainly insectivorous and territorial. Therefore, our analyses have been performed with a methodologically and biologically homogeneous group.

Finally, the validity of the allometric relationship between body weight and density has been tested by removing the effect of phylogeny (i.e., species share similar attributes because of recent common ancestry, so they do not constitute independent points for statistical analysis; Felsenstein 1985). We have analyzed the correlation between body weight and maximum ecological density of 40 terrestrial passerine species censused in 17 habitats of northern Spain (see Carrascal and Tellería 1991 for justification of the selection of maximum ecological densities [D_{max}] at a between-habitat level). For analysis, we have applied the independent contrasts method of Felsenstein (1985). The phylogeny used as the basis for this analysis was obtained from Sibley and Ahlquist (1990; a study of molecular systematics using DNA-DNA hybridization), because this is the only systematic analysis of whole birds providing phylogenetic topology for many genera. These

40 passerine species were grouped (average of body weight and maximum density) into 28 genera because of lack of phylogenetic data at the species level. We have used a punctuational model of evolution (FL1P method in Martins and Garland 1991), as Sibley and Ahlquist (1990) did not analyze and provide delta values of DNA-DNA hybridization for some genera in our sample (*Cettia, Pyrrhocorax, Oenanthe, Pyrrhula*, and *Serinus;* inclusion of these genera in the phylogenetic tree was easy considering Sibley and Ahlquist's [1990] comments on each family). The FL1P method for analyzing independent contrasts has proved to be a proper comparative approach in terms of both power and statistical estimation (Martins and Garland 1991). To test whether the branch lengths being used yield adequate standardization of contrasts when using Felsenstein's (1985) method, we plotted absolute values of standardized independent contrast for the foliage-volume index and maximum ecological density, plus their standard deviations (independent contrasts and their standard deviations computed with CMSINGLE program by Martins and Garland 1990; Garland et al. 1992). For none of these two traits being analyzed did the bivariate scatterplots indicate any significant trend ($P > .1$). Thus, branch lengths in figure 3 adequately standardized the independent contrasts. We developed analyses using programs by Martins and Garland (1990). Therefore, our phylogenetic analysis of the correlated evolution of body weight and density can be considered conservative because of the reduction of original sample size (species-specific values).

RESULTS AND DISCUSSION

Mean body weight of assemblages decreased as thinness and pliability of foraging substrates increased (fig. 1A). The relationship between D and W within each assemblage, as shown by slopes from allometric equations (b), gave an inverse association with thinness of foraging substrates (sample sizes for regressions ranged between five and 17, with an average of 10 species per assemblage; fig. 1B). Slope b was positively correlated with mean weight (weighted by density) of birds in each assemblage (log-log correlation: $r = 0.51$, $n = 28$; this correlation should be considered as a tentative one because of nonindependence between b and W). That is, the lower the body weight of birds in assemblages, the more negative the slope of the allometric regression of D on W. These results support the view that bird assemblages show varying relationships between density and species' body weight within the niche space of communities. The W-D relationships, as measured by b, suggest that larger species are able to gain resources in proportion to their size, whereas smaller species have more equitable resource allocations and so show the expected D-W associations.

Analysis at the community level provided similar results (fig. 2). Average weight (weighted by density of each species) of bird communities decreased with increasing foliage-volume index (log-log regression: $r = -0.704$, $P = .002$, $n = 17$; fig. 2A). This trend, opposed to that postulated by Odum (1969), shows the problem of generalization in bird community analyses without considering the specific characteristics of environments and species (e.g., niche space) under study (see also Smith and MacMahon 1981; review in Wiens 1989). Slopes of the
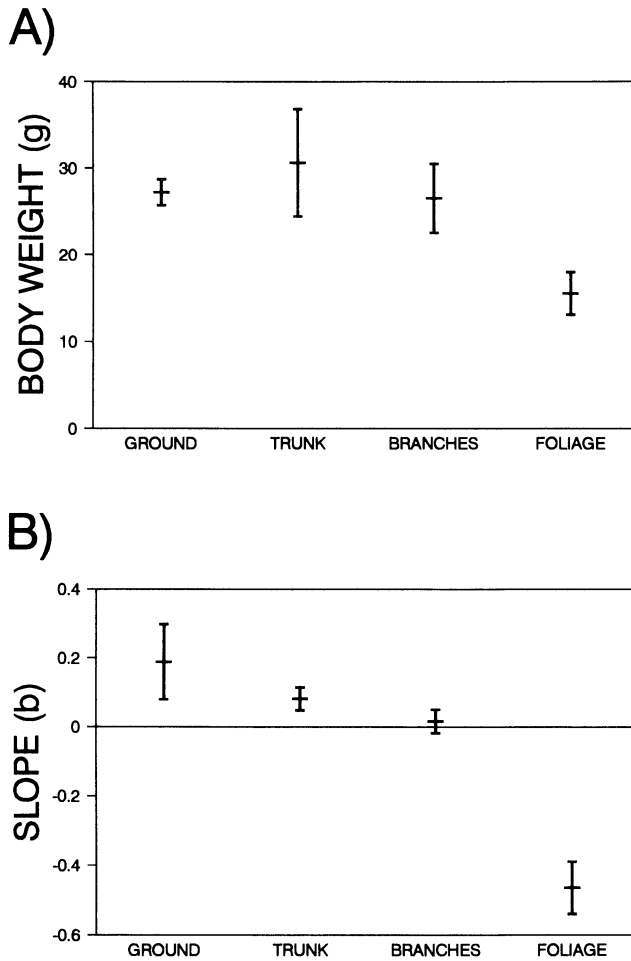
Fig. 1.—Mean body weights (A) and slopes of the allometric regressions (B) of density on body weight in bird species foraging on different substrates in seven bird communities. Sample sizes of regressions ranged between five and 17. Intervals represent mean ± 1 SE ($n = 7$ in all cases).

allometric regressions of D on W (b) were inversely and significantly correlated with the foliage-volume index (log-log model: $r = -0.761$, $P = .0004$, $n = 17$; fig. 2B) and directly associated with average weight of bird communities (log-log model: $r = 0.613$, $n = 17$; significance not provided because of partial dependence between b and W).

Nee et al. (1991) recently showed that phylogenetic relatedness might be an important indicator of the shape of the relationship between body size and abundance. Correlation coefficients between body weight and maximum ecological density in the 17 habitats of northern Spain was -0.457; when compared with an empirical null distribution (500 simulations of the evolution of D_{max} and W
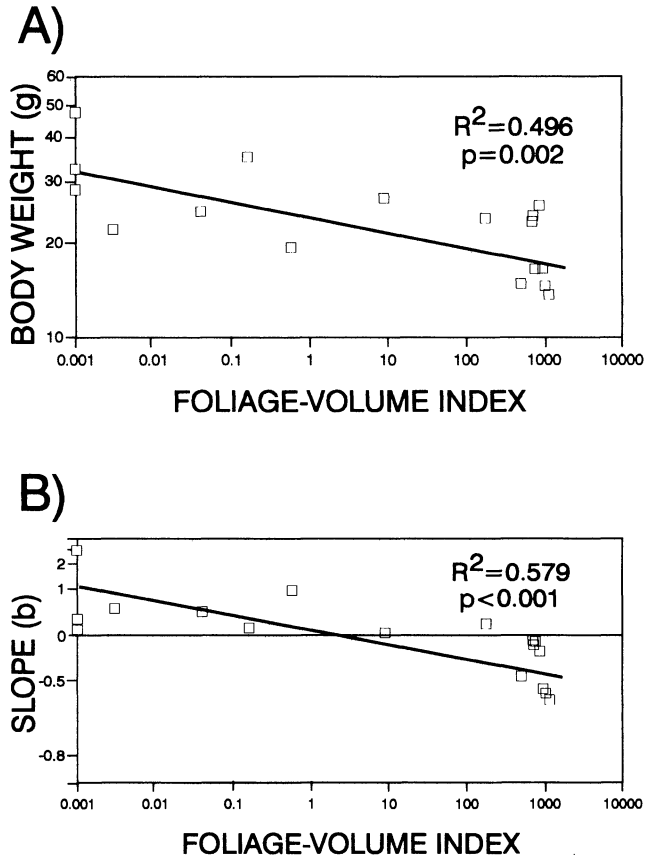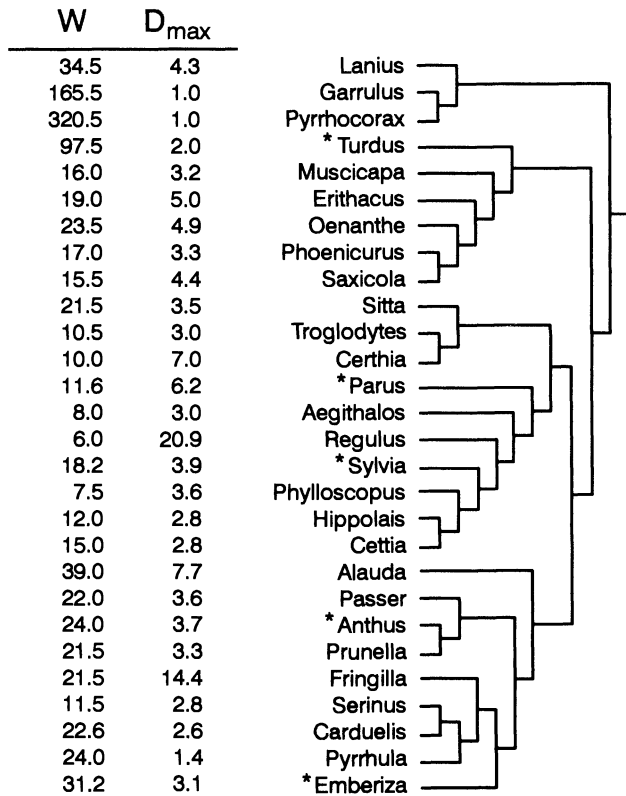
A)

B)

FIG 2.—Regressions of weighted averages of body weights (A) and slopes of allometric relationships (B) of W on D on a foliage-volume index (tree height × tree density per 0.2 ha) in 17 bird communities.

along the known phylogeny in fig. 3) the observed correlation was significant at $P = .011$ (one-tailed t-test). This result points out that phylogenetic relatedness alone cannot explain the consistent patterns of change of b within and between communities. Therefore, the provocative result found on a wide geographical scale by Nee et al. (1991) must be corroborated on lower scales (as between habitats or within communities in which relationships between birds and resources are tighter) to attain generality and to avoid scale problems (Wiens 1989).

Our results allow us to evaluate whether population energy use ($D \times E$, where E is the energy use per individual) of ecologically and taxonomically similar species is independent of body weight. This question is usually approached by comparing the values of coefficients (b and b') of the allometric equations $D = aW^b$ and $E = cW^{b'}$ (Damuth 1981). If b is negative, as it usually is, $|b| = |b'|$ means that population energy use is independent of body size; population energy

W	D_{max}	
34.5	4.3	Lanius
165.5	1.0	Garrulus
320.5	1.0	Pyrrhocorax
97.5	2.0	*Turdus
16.0	3.2	Muscicapa
19.0	5.0	Erithacus
23.5	4.9	Oenanthe
17.0	3.3	Phoenicurus
15.5	4.4	Saxicola
21.5	3.5	Sitta
10.5	3.0	Troglodytes
10.0	7.0	Certhia
11.6	6.2	*Parus
8.0	3.0	Aegithalos
6.0	20.9	Regulus
18.2	3.9	*Sylvia
7.5	3.6	Phylloscopus
12.0	2.8	Hippolais
15.0	2.8	Cettia
39.0	7.7	Alauda
22.0	3.6	Passer
24.0	3.7	*Anthus
21.5	3.3	Prunella
21.5	14.4	Fringilla
11.5	2.8	Serinus
22.6	2.6	Carduelis
24.0	1.4	Pyrrhula
31.2	3.1	*Emberiza

Felsenstein method of standardized
contrasts: r=-0.457 p=0.011

F$_{IG}$. 3.—Hypothesized phylogenetic relationships among the 28 genera of bird passerines in northern Spain. Genera with *asterisks* represent averages of two or more species. W, body weight in g; D_{max}, maximum ecological density. The *lower part* of the figure illustrates pairwise correlation between W and D_{max} using the Felsenstein method of standardized contrasts assuming a punctuational model of change.

use should be lower in larger species when $|b| > |b'|$ and higher when $|b| < |b'|$ or when b is positive. The average daily energy use of free-living birds scales allometrically as approximately $W^{0.67}$ in all birds as a whole and $W^{0.75}$ in passerines (Nagy 1987). Using this approach, the positive correlations found between b and mean body weight within and between communities show that larger species should use a disproportionately larger proportion of energy in several "heavy" substrata (ground and trunk) and open habitats (grasslands, shrublands). This pattern is less pronounced in assemblages exploiting foliage or in habitats with a high foliage volume, in which smaller bird species predominate because of ecomorphological constraints (low body mass for hovering, hanging, and

pouncing among foliage). This general pattern supports the view of Brown and
Maurer (1986) and Pagel et al. (1991) on the dominant use of energy by larger
species, and it also shows how the relative importance of different-sized birds in
a given community (and the energy allocation between different-sized species) is
related to habitat structure. The results provided by this note illuminate the previ-
ously contrasting patterns obtained about resource extraction by species within
communities (see, e.g., Damuth 1981 vs. Brown and Maurer 1986). The confusing
patterns of the D-W relationships that are so frequently observed in birds could
at least partly result from the use of bird densities obtained from habitats that,
because of their different structure, provide different niche opportunities to spe-
cies of different sizes. Therefore, a more autecological approach ought to be
employed in the analysis of allometric relationships linking body weight to
density.

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