

BIRD SIZE AND DENSITY: A REGIONAL APPROACH

Within groups of taxonomically related, ecologically similar organisms, large individuals demand more resources than small ones but also tend to occur at lower densities (Brown and Maurer 1987; Damuth 1987). The inverse relationship between weight (W) and density (d) for several zoological groups (Damuth 1981; Peters 1983; Peters and Wassenberg 1983; Peters and Raelson 1984; Robinson and Redford 1986) is well fitted to the equation $d = aW^b$ ($\log d = \log a + b \log W$), where d and W are normally obtained from bibliographical reviews. This relationship is unsatisfactory for birds apart from raptors (order Falconiformes), although this result lacks a convincing explanation (Peters and Wassenberg 1983; Juanes 1986). It may reflect the biological characteristics of birds (Juanes 1986) or the effect of variables such as predation, competition, and population structure, which are difficult to quantify (Peters and Raelson 1984).

Other aspects that have not been sufficiently studied may also play an important role. The first is the uneven quality of density estimates (Juanes 1986; Damuth 1987). Different census methods give distinct approaches to population sizes or densities, and, similarly, a method may vary in efficiency when applied to different bird species (for an extensive review, see Tellería 1986). Consequently, densities obtained from published material may represent different approaches to the species' true densities.

A second aspect refers to the uncertain meaning of the densities themselves (Damuth 1987). Robinson and Redford (1986) classed densities as "regional densities" (d_{reg}) when referring to the densities reached by species in a region that includes diverse types of habitats (e.g., study sites for raptors and large mammals) and "ecological densities" (d_i) when referring to densities achieved in a defined habitat. The latter is the more common approach in studies on communities of small vertebrates.

The third problem refers to the excessive conceptual simplification of the relationship between d and W . Because density is surely multiply determined, a more adequate relation would develop several complementary factors.

1. Species trophic behavior (T) is the only trait usually considered in these analyses. Different types of foods may be present in different abundances, and their qualities may impose different ecological and physiological limitations. Therefore, species trophic behavior may influence population density (Damuth 1987).

2. Regional population levels (P) of a species affect both d_i and d_{reg} . A species may, for example, have a lower density than expected because its numbers have been reduced in sectors outside the study region (e.g., wintering grounds of

birds). Atypical densities may also arise where marginal geographical areas are occupied by only small populations. At low population levels, resource pools may greatly exceed the energetic requirements of consumers, thus removing some size-dependent restrictions on bird densities.

3. Species habitat distribution (H) in the region is normally not considered because this complex variable cannot be evaluated from the bibliographical data. Conceptually, it is the density in optimal, marginal, and unsuitable habitats in the study area. This variable is especially important to d_i because this density varies with P , the regional population level (Fretwell 1972). For example, high densities in optimal habitats may result in the dispersion of the population over a range of poor habitats, where survival and/or reproductive success is diminished. As a result, the d_{reg} of a small, dispersed species in suboptimal habitats may be lower than that of a larger species confined to its optimal habitat.

The relationship $d = f(W)$ would thus be more properly expressed as $d_i = f(W, T, H, P)$ and $d_{\text{reg}} = f(W, T, P)$. An ideal study of the relationship between d and W should thus consider the type of density being analyzed (d_i or d_{reg}) and test the rest of the factors indicated above. This full analysis demands detailed knowledge of the patterns of distribution and abundance of each species, a knowledge that may only be achieved by means of carefully developed regional studies.

In this article, we investigate the relationship between d and W in the bird communities in northern Spain, an area that has been intensely studied ornithologically (Alvarez et al. 1984; Carrascal 1987). From the foregoing arguments, we can make two predictions about the relationships between d and W on the basis of regional studies.

1. The maximum ecological density (d_{max}) of each species is most likely to be the density that species achieves at its most optimum habitat in the area. Maximum ecological density is obtained from an analysis of d_i distribution in the study area. According to Fretwell's approach to animal distribution (see Fretwell and Lucas 1970; Fretwell 1972; Rosenzweig 1985), these habitats should be the first to be saturated when the regional population increases. At such sites, size-dependent restrictions on animal abundance are likely to be strong. The use of d_{max} in regressions therefore attenuates the distorting effects of H , or the high variability of ecological densities (d_i) with regional values of P , and of population levels (P) on $d = F(W)$. The correlation between d_{max} and W will thus be better than that obtained using an indiscriminate or random selection of ecological densities (d_i) of each species in any of the regions' habitats (see, e.g., Juanes 1986).

2. Because d_{reg} attenuates the potential distorting effect of the high variability of randomly selected d_i values by weighting the regional significance of each habitat in species abundance, d_{reg} should correlate better with W . A similar result is also expected for d_{mean} ($d_{\text{mean}} = \sum d_i/n$, where n is the number of habitats occupied by the species). Estimates of d_{mean} have often been used in this type of analysis (see, e.g., Damuth 1981, 1987; Peters and Wassenberg 1983).

METHODS

An extensive study of the breeding bird communities in the habitats of northern Spain (Basque country) was carried out during the springs of 1985 and 1986.

Densities in different habitats (d_i) were estimated using the Finnish line-transect method (Järvinen and Väisänen 1977). Although this method does not completely remove differences in species detectability (Hildén 1981), it can adequately approximate the densities of small passerines and similar species (Järvinen and Väisänen 1981). Species such as birds of prey and large crows were eliminated from the analysis in order to study a homogeneous group from a methodological perspective. Attention was thus limited to 47 species weighing between 6 g (*Regulus ignicapillus*) and 160 g (*Picus viridis*). This range is much narrower than Peters and Wassenberg's (1983; 10–3,980 g) or Juanes's (1986; 3–4,500 g for all birds, 3.4–570 g for insectivorous birds) and may prevent the production of significant correlations (see Juanes 1986), but such restriction offers the advantage of a methodologically and biologically homogeneous group of birds, as recommended for such comparative studies (e.g., Clutton-Brock and Harvey 1984). The results are expressed as the number of birds per 10 ha without recommended transformations (e.g., one singing male = a pair; see Järvinen and Väisänen 1977), because such arbitrary changes would artificially increase the density estimates of the more detectable species.

Species densities (d_i) in the 10 most extensive habitats of the region were characterized (see Carrascal 1987 for details) and used to select d_{\max} and to calculate d_{mean} . The regional density (d_{reg}) was obtained using the mean surface area of each habitat in the region as a weighting factor. Species weight (W) was taken from Perrins (1987) as the mean weight of males and females. Because the spring diets (T) of the species were predominantly insects (Géroudet 1961–1972), they were taken to represent a single trophic group (insectivores). Species that are marginal in the study area according to the Basque regional bird atlas (Alvarez et al. 1984) were eliminated from the analysis to remove the negative effects of their low P values. Regressions of d_{\max} , d_{reg} , and d_{mean} on W for the 47 species were computed after the logarithmic transformation of each variable.

To assess the predictions about these regressions relative to those based on an indiscriminate collection of d_i 's, these correlations were compared with those obtained from regressions based on a random selection of densities for each of the 47 species in the 10 habitats. When the d_i of a species in a given habitat was 0 (missing value), it was not included in the corresponding calculation. The operation was repeated 499 times. The mean correlation of the 500 tests and their confidence intervals was taken to represent the relationship between d_i and W that would have been obtained if values of d_i had been selected in the manner we assume was used in the bibliographic reviews.

RESULTS

Figure 1 shows the relationship between d_i and W for all species and habitats. As Brown and Maurer (1987) have shown in studying North American avifauna, the representation of d_i and W on both X - and Y -axes of coordinates results in a "polygon" of points in which d_i varies greatly for any interval of W (similar-sized species). The upper profile of this polygon descends as W increases, corresponding to the maximum densities (d_{\max}) of each species; the lower profile is parallel to the X -axis (lower densities).

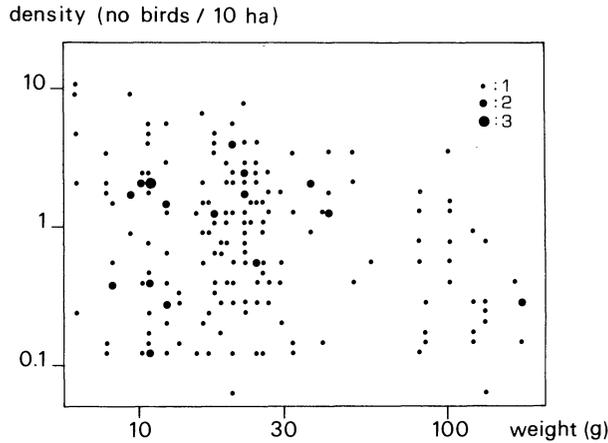


FIG. 1.—The relationship between ecological densities and average body weight for all bird species and habitats. Large spots indicate two or three species with the same density and body weight.

The mean r of the correlations between randomly selected d_i and W for each species (null model) in this polygon is -0.217 ($df = 19$). The corresponding confidence intervals are from -0.332 to -0.102 at 1% and from -0.305 to -0.129 at 5%. Table 1 provides the results using the regression analyses of W on d_{\max} , d_{reg} , and d_{mean} for the 47 species (fig. 2). In every case, the correlation is negative and the value of r exceeds that from the null model. The use of d_{\max} thus improves the relationships between d and W . The explained variation (25.14%) is substantially greater than that (9%) obtained by Juanes (1986) for North American insectivorous birds. A similar trend occurs with d_{mean} and d_{reg} (table 1), thus confirming prediction 2.

DISCUSSION

The results of this study demonstrate a negative relationship between d and W in small insectivorous birds and thus confirm the validity of the model proposed by Mohr (1940) and Damuth (1981). The formulation of the relationship, however, demands methodological improvements to be developed in the estimation of densities. It is important to consider the variability of densities due to the uneven distribution of the species among habitats and their different regional demographic levels.

The poor results of previous studies on passerines may be due to the disregard for these precautions as well as an inadequate selection of the material being analyzed. Although Peters and Wassenberg (1983) used d_{mean} , they centered their analysis on the results provided by Emlen (1972) on a wintering bird community in Texas, an excessively atypical sample. Juanes (1986), on the other hand, used broad information on breeding bird communities in North America, but his analysis used d_i without any consideration of habitat selection or demographic levels.

TABLE 1
REGRESSIONS OF DENSITY VERSUS BODY WEIGHT

	log a		b		R^2	P
d_{\max}	1.16	(.22)	-.62	(.15)	25.27	<.001
d_{mean}	.71	(.18)	-.50	(.13)	26.04	<.001
d_{reg}	.60	(.40)	-.87	(.28)	17.58	.003

NOTE.—Results of regression analyses of body weight (g) on maximum densities (d_{\max}), average densities (d_{mean}), and regional densities (d_{reg}), all of which are expressed as the number of birds/10 ha, are as follows: log a = intercept; b = slope; R^2 = coefficient of determination. Numbers given in parentheses are SEs; $n = 47$.

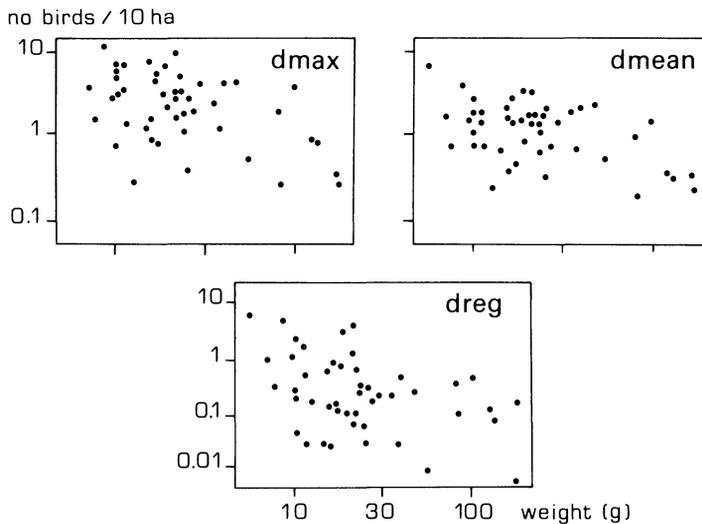


FIG. 2.—Relationships between maximum densities (d_{\max}), mean densities (d_{mean}), regional densities (d_{reg}), and body weight.

If d_{\max} is not selected or the variability of d_i is not reduced by calculating d_{mean} or d_{reg} , an adequate and significant correlation between d_i and W is unlikely. It is thus not fortuitous that the only birds showing a clear relationship between W and d are the Falconiformes, the densities of which are usually obtained regionally (Fuller and Mosher 1981) or are calculated as the inverse of home-range size (Newton 1979).

This study thus illustrates the high predictive value of weight as a determinant of density in birds, even when working with limited size intervals. We believe that further studies should be focused to analyze and improve the predictive value of $d = f(W)$ for small intervals of W . While not wishing to ignore the importance of the originality of previous studies, it seems likely that there is a negative relationship between d and W when using size intervals that oscillate, for example, between 10 g and 3.2 kg (Damuth 1981) or between 10 g and 2 kg (Peters and

Wassenberg 1983), bearing in mind the spatial projection of the trophic requirements of such differently sized species (Nagy 1987).

These results confirm the extremely low densities and biomass of birds in relation to other animal groups (Peters and Wassenberg 1983; Juanes 1986). If, according to the methodological approach of previous studies, we predict densities and biomass at the mean body size of the studied avifauna (34.5 g), we obtain 1.630, 0.875, and 0.182 birds/10 ha for d_{\max} , d_{mean} , and d_{reg} , respectively (and 56.24, 30.19, and 6.29 g/10 ha). These values are lower than the predicted d_{mean} and biomass obtained for mammals (21 individuals/10 ha, 7,800 g/10 ha), vertebrate poikilotherms (960 and 14,000), or invertebrates ($25 \cdot 10^7$ and 93,000) in Peters and Wassenberg's (1983) study. Not even the predicted d_{\max} for the smallest bird species (*Regulus ignicapillus*; 6 g) reaches such high values (4.8 birds/10 ha). This low density may be partly explained by the low efficiency of the line-transect method used to census bird communities. According to several methodological studies (see review in Tellería 1986), true densities may be 1.1–2.5 times the calculated values depending on the behavior of the species. But even if we multiply the d_{\max} for this smallest species by 2.5, it does not approach the d_{mean} values calculated by Peters and Wassenberg (1983) for other animal groups.

This low density and biomass in birds may reflect some specific characteristics of this group. Birds have the highest per-gram turnover of energy, a characteristic that reduces the amount of energy that they can effectively store over daily or annual cycles and limits their options for energy allocation relative to those of other vertebrates (Pough 1980; Paladino 1989). This low efficiency in energy storage and their constant high level of activity (birds do not hibernate, as some mammals and all the ectothermic animals do) may produce periodic "bottle-necks" for bird populations occupying regions with periodic food shortages, thus accentuating their relatively low density and biomass (Wiens 1974, 1989).

These results may also be used to comment on some energetic implications of the relationships between d and W . Damuth (1981, 1987) suggested that the energy use of ecologically and taxonomically similar populations is independent of body size, whereas other researchers have suggested that energy use (E) should be higher in larger species (Brown and Maurer 1987) or smaller species (Peters 1983). The methodological approach to this problem is to compare the absolute values of the coefficients (b and b') of the allometric equations $d = aW^b$ and $E = cW^{b'}$. If $|b| = |b'|$, the energy use should be independent of the body size, whereas the energy use should be higher or lower in large species if $|b| < |b'|$ or $|b| > |b'|$. As Nagy (1987) showed, the average daily energy use of a free-living individual scales allometrically as approximately $W^{0.67}$ in all birds and $W^{0.75}$ in passerines. Brown and Maurer (1987) obtained a b/b' relationship of $-0.30/0.67$ in birds and concluded that large birds use more energy than small ones ($b = -0.31$ for insectivorous birds; Juanes 1986). Our b values for insectivorous birds in the spring (table 1) are higher and approach Damuth's values. The similarity between the absolute values of our coefficients in table 1 and those derived from energetic allometric equations (see above) seems to indicate that the amount of energy used by these small insectivorous birds is independent of their body size ($|b| = |b'|$; see Damuth 1987 for a similar result).

ACKNOWLEDGMENTS

J. Damuth, J. Díaz, and two anonymous reviewers considerably improved an earlier version of this note. This study was partially supported by project PB86-0006-C02-01 (Dirección General de Investigación Científica y Técnica; Spanish Ministry of Education and Science).

LITERATURE CITED

- Alvarez, J., A. Bea, J. M. Faus, E. Castien, and I. Mendiola. 1984. Atlas de los Vertebrados Continentales de Alava, Vizcaya y Guipúzcoa. Gobierno Vasco, Bilbao.
- Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *American Naturalist* 130:1–17.
- Carrascal, L. M. 1987. Relaciones entre la avifauna y estructura de la vegetación en el País Vasco atlántico. Ph.D. diss. Universidad Complutense, Madrid.
- Clutton-Brock, T. H., and P. H. Harvey. 1984. Approaches to investigating adaptation. Pages 7–29 in J. R. Krebs and N. B. Davies, eds. *Behavioural adaptation: an evolutionary approach*. Blackwell Scientific, Oxford.
- Damuth, J. 1981. Population density and body size in mammals. *Nature* 290:669–670.
- . 1987. Interspecific allometry of population density in mammal and other animals: the independence of body mass and population energy-use. *Biological Journal of the Linnean Society* 31:193–246.
- Emlen, J. T. 1972. Size and structure of a wintering avian community in southern Texas. *Ecology* 53:317–329.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, N.J.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- Fuller, M. R., and J. A. Mosher. 1981. Methods of detecting and counting raptors: a review. *Studies in Avian Biology* 6:235–246.
- Géroutet, P. 1961–1972. Les Passereaux I, II, and III. Delachaux & Niestlé, Neuchâtel.
- Hildén, O. 1981. Sources of error involved in the Finnish line transect method. *Studies in Avian Biology* 6:152–159.
- Järvinen, O., and R. A. Väisänen. 1977. Line transect method: a standard for field-work. *Polish Ecological Studies* 3:7–17.
- . 1981. Methodology for censusing land bird faunas in large regions. *Studies in Avian Biology* 6:146–151.
- Juanes, F. 1986. Population density and body size in birds. *American Naturalist* 128:921–929.
- Mohr, C. D. 1940. Comparative populations of game, fur and other animals. *American Midland Naturalist* 24:581–584.
- Nagy, K. E. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57:111–128.
- Newton, I. 1979. *Population ecology of raptors*. Poyser, Berkhamsted.
- Paladino, F. V. 1989. Constraints of bioenergetics on avian population dynamics. *Physiological Zoology* 62:410–428.
- Perrins, C. 1987. *Aves de España y de Europa*. Omega, Barcelona.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, New York.
- Peters, R. H., and J. V. Raelson. 1984. Relation between individual size and mammalian population density. *American Naturalist* 124:498–517.
- Peters, R. H., and K. Wassenberg. 1983. The effect of body size on animal abundance. *Oecologia (Berlin)* 60:89–96.
- Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* 115:92–112.

- Robinson, J. G., and K. H. Redford. 1986. Body size, diet, and population density of Neotropical forest mammals. *American Naturalist* 128:665–680.
- Rosenzweig, M. L. 1985. Some theoretical aspects of habitat selection. Pages 517–540 in M. L. Cody, ed. *Habitat selection in birds*. Academic Press, Orlando, Fla.
- Tellería, J. L. 1986. *Manual para el censo de los vertebrados terrestres*. Raices, Madrid.
- Weins, J. A. 1974. Climatic instability and the “ecological saturation” of bird communities in North American grasslands. *Condor* 76:385–400.
- . 1989. *The ecology of bird communities*. Cambridge University Press, Cambridge.

L. M. CARRASCAL

DEPARTMENT OF EVOLUTIONARY ECOLOGY
MUSEO NACIONAL DE CIENCIAS NATURALES
c/JOSÉ GUTIÉRREZ ABASCAL 2
28006 MADRID, SPAIN

J. L. TELLERÍA

DEPARTMENT OF ANIMAL BIOLOGY (ZOOLOGY)
UNIVERSIDAD COMPLUTENSE
FACULTAD DE BIOLOGÍA
28040 MADRID, SPAIN

Submitted July 24, 1989; Revised August 30, 1990; Accepted September 19, 1990