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THE SPECIES BODY-SIZE DISTRIBUTION IN IBERIAN ANTS IS PARAMETER INDEPENDENT

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ANT ASSEMBLAGES
BODY SIZE
IBERIAN PENINSULA
MACROECOLOGY
PARAMETER
SPATIAL SCALING

ABSTRACT. – Macroecology aims to reveal hidden patterns in species-level traits over large spatial scales. One important species characteristic is body size. The parameter used to characterize body size *distributions* (BSD) for *individual* data is the mean of any variable representing – or related to – size, including: body length, body mass, forewing length, wing span or cephalothorax length, depending on the animal group. An appreciable proportion (21%) of the species of Iberian ants with workers show varying degrees of different body size (due to polymorphism or by highly variable monomorphism). Taking into account this specific variation in all Iberian BSD, we have explored the effect of a) the range in body size for those variable species, or b) only the maximum attained body size. No effect was detected in either case indicating that the mean dry body mass for *individual* data in Iberian ants, polymorphic species included, is a robust and adequate means of measuring the macroecological patterns of BSD. The mean dry mass for Iberian ants is 0.72 ± 1.01 mg and the median dry mass 0.30 mg (n = 242). For functional studies of local communities it is probably wise to take into account the variable degree of polymorphism.

COMMUNAUTÉS DE FOURMIS
ÉCHELLE SPATIALE
MACROÉCOLOGIE
PARAMÈTRES
PÉNINSULE IBÉRIQUE
TAILLE CORPORELLE

RÉSUMÉ. – La macroécologie, l'étude de la répartition de l'espace physique et des ressources écologiques parmi les espèces, tente de démontrer des patterns dans certains traits spécifiques à des échelles spatiales assez larges. Un trait spécifique très important est la taille corporelle. Pour caractériser la *distribution* spécifique de la masse corporelle, le paramètre utilisé pour les données *individuelles* est la moyenne des variables représentant la taille (longueur du corps, masse, longueur de l'aile antérieure, envergure des ailes, longueur du céphalothorax, selon les différents groupes). Chez les espèces de Fourmis ibériques ayant des ouvrières, une proportion non négligeable (21%) montre un degré de polymorphisme. Ce fait est dû à la présence d'espèces polymorphes et d'espèces monomorphes qui présentent une forte variation. Pour contrôler l'importance de cette variation corporelle nous avons étudié l'influence sur la distribution spécifique de la masse corporelle (matière sèche), a) du rang de variation, et b) du maximum de la masse corporelle atteinte. Aucun effet n'a été détecté ce qui indique que la *moyenne* de la masse corporelle est un paramètre adéquate et robuste pour caractériser les patterns macroécologiques de la taille des Fourmis. La moyenne (± d.s.) des masses corporelles (matière sèche) des Fourmis ibériques est de 0.72 ± 1,01 mg et la médiane 0,30 mg (n = 242). Pour des études fonctionnelles à des échelles locales, il est probablement plus judicieux de tenir compte du polymorphisme.

INTRODUCTION

Macroecological patterns are expected to reveal unapparent properties of how species divide and share physical space and ecological resources (Brown & Maurer 1989, Rosenzweig 1995, Brown 1995). Species-level traits such as body size, geographic range, or abundance, are analysed over large spatial scales and plotted on bivariate plots, sometimes showing strikingly characteristic shapes that call for a biological explanation. Body size is one extremely informative characteristic of any given species (Peters 1983, Calder 1984). The species body-size distribution (BSD) of a given group of organisms at different scales has received considerable attention recently. In particular, BSD in local communities tends to be log-uniform (however, see Schoener & Janzen 1968 for an example of the reverse) and is said to turn to log-skewed at the continental scale. This has been shown both for mammals (Brown & Nicoletto 1991, Maurer *et al.* 1992, Blackburn & Gaston 1994a, also see Bakker & Kelt 2000) and birds (Maurer *et al.* 1992, Blackburn & Gaston 1994b). The parameter used to characterize body size *distributions* (BSD) for *individual* data is the mean of any variable representing – or related to – size (body length, body mass, forewing length, wing span, cephalothorax length, average for male and female, depending on the animal group) (Blake *et al.* 1994, Brown & Maurer 1989, Novotny & Kindlmann 1996, Bakker & Kelt 2000). For taxa with a variable adult body size, such as fish, it is not clear which summary statistics should be used (mean, maximum body size) or what its effect is, if any, on the BSD (Blackburn & Gaston 1994b); Brown (1995) observed that a certain measure of variation, such as standard deviation or range of extreme values might also be used.

Ants are a very distinct group in the sense that body size may vary greatly because of polymorphism. This variation has considerable importance in the functioning of ant colonies given that ants of distinct sizes have different functional roles (Hölldobler & Wilson 1990). Therefore, when considering ants, the question of which variable to use when analysing body size distributions is not a trivial issue (nor is it, indeed, for the majority of organisms, in which different stages, from juvenile to adult, are functionally present within the field; however this aspect has not been considered as far as we know). In species of Iberian ants with workers, an appreciable proportion of the species (21%) show variation in body size (due to polymorphism or to highly variable monomorphism). In a recent analysis of Iberian ant sizes (Gómez & Espadaler 2000) the *mean* dry body mass for all species was used, without taking the degree of polymorphism into account. Here we explore the manner in which two distinct variables, specific body size *range* and specific *maximum* size influence the distribution of Iberian ant body sizes at different scales. We have found that mean body size is an adequate and robust parameter for central tendency in analyses of body size distributions even when polymorphic or highly variable monomorphic species are considered. We also explore the effect of body size range and specific maximum size on the relationship between body size and latitude (Cushman *et al.* 1993) as well as on the BSD, depending on spatial scale (local vs. peninsular) (Brown & Maurer 1989, Blackburn & Gaston 1997).

MATERIAL AND METHODS

Methodological consideration: In a previous study (Gómez & Espadaler 2000) a single formula (Kaspari 1999, Table V, all ants) for deriving biomass was used for the five subfamilies of ants found in Iberia. As four of the five subfamilies of Iberian ants have their own formula –the exception being the Leptanillinae, for which we used the general formula– we used those subfamily formulas to derive new body masses for each species. This consideration applies to all details that follows.

The data base: Using the mean size, the maximum size and taking into account the polymorphism we have generated three data sets of body size distribution for the updated (October 2001) list of 242 Iberian ant species with workers. Workerless parasitic species are not included. Polymorphism was categorized as follows: a) body size classes were stated using a width of 0.3 at a $\log_{10}$ scale (~ 2 mg dry mass); b) for monomorphic species, we used mean body mass, which pertained to a single class; c) for polymorphic species, we used two (minimum, maximum) or three (minimum, mean, maximum) body mass values, which fitted into one, two or three body mass classes, depending on the body mass range. In total, 191 species belonged to one size class, 40 species to two size classes and 11 species encompassed three size classes. Throughout this paper, dry body mass has been analysed, transformed as $\log_{10}$ dry body mass, but has been presented as non-transformed. Means are given ± S.D. Analyses were run under Statistica 5.01 (Statsoft, Inc.; Tulsa, OK) and consisted of pairwise comparisons of different BSD aspects generated when using the three data sets. Means were compared with ANOVA and post-hoc tests when needed, medians with a Kruskall-Wallis test and distributions with a Kolmogorov-Smirnov test. Regression analysis was used to test for a relationship between latitude and mean dry body mass. Bootstrappings were obtained with Simstat for Windows 2.0 (Provalis Research; Montreal, QC).

RESULTS

Peninsular body-size distribution

The frequency distribution of dry masses spans more than three orders of magnitude: the biggest worker ant (*Messor barbarus*, dry mass 16.98 mg) is >4000 times heavier than the smallest ant (*Leptanilla charonea*, dry mass 0.0038 mg). When using the updated data base of 242 ant species – workerless species not considered-and the specific formulas for each subfamily (Table I) neither the mean dry body mass (ANOVA; $F_{1,482} = 0.14$; $p = 0.70$) nor the median (Mann-Whitney test; $z = 0.14$; $p = 0.88$) were different from those obtained using the general formula for all Formicidae. Nor was the distribution different (Kolmogorov-Smirnov test; max. dif. 0.049; $p > 0.1$) when using the specific or general for-

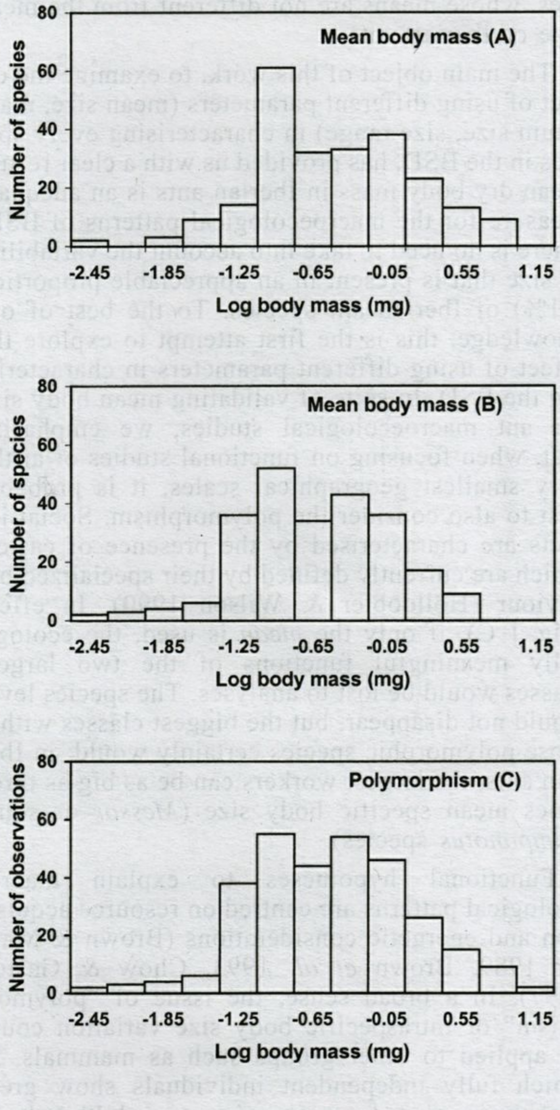

Fig. 1. – Frequency distribution (BSD) of $\log_{10}$ dry body mass of workers of Iberian ant species (n = 242) using different parameters. A: mean, using a single formula to estimate body mass from head length (Kaspari 1999; Table V, All ants). B: mean, using a specific formula for each subfamily (Kaspari1999, Table V but for Formicinae in which we used the formula: *dry mass = 0.4101(head length) 2.6814* (deduced from Espadaler & Gómez 2001). C: using the degree of size variation for polymorphic species (see text); two new bigger classes appear. D: using the upper limit (maximum) of body size.

mula. The body mass of the five subfamilies of Iberian ants was strongly divergent between subfamilies (Table I). We compared each subfamily using two kinds of formulae and the interaction term in ANOVA; no statistical difference ($F_{4,473} = 0.94$; $p = 0.43$) in the mean body mass was detected, neither when the dry body mass was estimated with the formula for each subfamily, nor when it was estimated with a general formula for the family Formicidae. In spite of the absence of statistical differences, in the work that follows we used the BSD generated with the specific subfamily formulas because, even if the difference is minimal, it is still more correct.

Formal tests of normality (Lilliefors & Shapiro-Wilks' W test) were conducted on the three BSD (using the mean, the maximum or polymorphism). Lilliefors test rejected normality in the BSD when using maximum size ($p < 0.01$) and the Shapiro-Wilks' test rejected normality in the BSD using the mean ($p < 0.01$) and the maximum size ($p < 0.02$). Neither test rejected normality in the BSD using polymorphism ($p < 0.15$ and $p < 0.06$).

Variable to characterize body size and local assemblages

Although to the naked eye, certain differences can be seen in the BSD depending on the variable used (mean, polymorphism, maximum; Fig. 1, Table I), there are no statistical differences between the *means* of BSD based on mean body size or on polymorphism (ANOVA, $F_{2,785} = 2.76$; $p = 0.063$), between the *medians* of BSD (Kruskal-Wallis test; $H_{2,788} = 4.6$; $p = 0.09$) or between all *distributions* of BSD (Kolmogorov-Smirnov tests; $p > 0.1$ for all possible pairs of comparisons). A separate comparison of the BSD mean and median for local inventories at the smallest scale (< 10 km^2) and for different localities also failed to show any differences, whether the mean dry body mass or polymorphism were used (Kruskal-Wallis and Kolmogorov-Smirnov tests; $p>0.1$). These latter results are not presented here.

Local assemblages on Iberian ants

We applied a bootstrapping procedure to test if the local assemblages were a random sub-sample of the entire Iberian BSD or were different in a systematic way, as is usually assumed (Brown & Nicoletto 1991, Gaston & Blackburn 1996, but see Bakker & Kelt 2000). We drew 1000 random sub-samples from the entire Iberian BSD, with the same number of species for a given locality. The proportion of those simulations that were less than the observed median was taken as an indication of the failure to reject the null hypothesis of no difference between the two assemblages: in no case was

Table I. – Top, Dry body mass (mg) of Iberian ants according to subfamily. Different superscripts indicate statistical differences by a post-hoc Tukey's test (unequal n) following ANOVA (F4, 237 = 34.4; $p < 001$). N = species number. Mean dry mass calculated from raw data: 0.72 ± 1.01 mg; median dry mass: 0.30 mg ($n = 242$). The mean corresponds to *Myrmica wesmaeli*; the median to *Goniomma blanci*. Bottom, dry body mass of Iberian ants using different parameters (mean, maximum, polymorphism) for *individual* data (=species). For the mean and maximum n is the number of species without considering the presence and degree of polymorphism; when polymorphism is considered (see text) some species contribute more than one value to the distribution pushing the data up to 304 values (not species).

Subfamily	Mean ± s.d.	N
Ponerinae	$0.32 \pm 0.26^{a,b}$	10
Myrmicinae	0.49 ± 0.86^{a}	131
Dolichoderinae	0.17 ± 0.08^{a}	10
Formicinae	1.22 ± 1.16^{b}	86
Leptanillinae	0.008 ± 0.003^{c}	5

	Mean ± S.D.	Median	n
Mean	0.72 ± 1.01	0.30	242
Maximum	1.23 ± 2.41	0.34	242
Polymorphism	1.22 ± 2.22	0.43	304

a difference detected, as had already been obtained in Gómez & Espadaler (2000).

Latitudinal trend

This trend was also absent. The mean dry body mass of local samples was not greater at higher latitudes within the Iberian Peninsula (mean dry body mass = –1.09 + 0.07 latitude; $r^2 = 0.058$; $F = 0.49$; $p = 0.5$).

DISCUSSION

We maintain the same general conclusions as in a previous paper (Gómez & Espadaler 2000): 1) In Iberian ants, the relative body size of the most diverse genus (*Leptothorax*) is 29.2%, well within the range found by Dial & Marzluff (1988), indicating that there is a much higher number of smaller species than of larger ones; 2) Particular subsets of species at the local scale are not different in their BSD from random samples taken from the entire Iberian ant fauna, and do not show a growing log-uniformity at smaller scales. 3) Latitude has no bearing on the mean size of local samples, whose means are not different from the mean size of Iberian ants.

The main object of this work, to examine the effect of using different parameters (mean size, maximum size, size range) in characterising every species in the BSD, has provided us with a clear result: mean dry body mass in Iberian ants is an adequate measure for the macroecological patterns of BSD. There is no need to take into account the variability of size that is present in an appreciable proportion (21%) of Iberian ant species. To the best of our knowledge, this is the first attempt to explore the effect of using different parameters in characterising the BSD. In spite of validating mean body size for ant macroecological studies, we emphasize that, when focusing on functional studies or at the very smallest geographical scales, it is probably best to also consider the polymorphism. Social insects are characterised by the presence of castes, which are currently defined by their specialized behaviour (Hölldobler & Wilson 1990). In effect (Fig. 1 C), if only the *mean* is used, the ecologically meaningful functions of the two largest classes would be lost to analyses. The species level would not disappear, but the biggest classes within those polymorphic species certainly would: in Iberian ants, the largest workers can be as big as three times mean specific body size (*Messor* or some *Camponotus* species).

Functional hypotheses to explain macroecological patterns are centred on resource acquisition and energetic considerations (Brown & Maurer 1989, Brown *et al.* 1993, Chow & Gaston 1997). In a broad sense, the issue of "polymorphism" or intraspecific body size variation could be applied to other groups such as mammals, in which fully independent individuals show great change in size from weaning to adulthood, or heterometabolous insects in which from birth, each individual insect has a fully functional significance. Juveniles of a given species A might perfectly well be the functional equivalents of adults in a (smaller) species B. We are not aware of any attempt to consider and analyse this question.

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REFERENCES

Bakker VJ, Kelt DA 2000. Scale-dependent patterns of body size distributions of Neotropical mammals. *Ecology* 81: 3530-3547.

Blackburn TM, Gaston KJ 1994a. The distribution of body sizes of the world's bird species. *Oikos* 70: 127-130.

Blackburn TM, Gaston KJ 1994b. Animal body size distributions: patterns, mechanisms and implications. *Trends Ecol Evol* 9: 471-474.

Blackburn TM, Gaston KJ 1997. A critical assessment of the form of the interspecific relationship between abundance and body size in animals. *J Anim Ecol* 66: 233-249.

Blake S, Foster GN, Eyre MD, Luff ML 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia* 38: 502-512.

Brown JH 1995. Macroecology. The University of Chicago Press.

Brown JH, Marquet PA, Taper ML 1993. Evolution of body size: consequences of an energetic definition of fitness. *Am Nat* 142: 573-584.

Brown JH, Maurer BA 1989. Macroecology: the division of food and space among species on continents. *Science* 243: 1145-1150.

Brown JH, Nicoletto PF 1991. Spatial scaling of species compositions: body masses of North American land mammals. *Am Nat* 138: 1478-1512.

Calder WA 1984. Size, function and life history. Harvard University Press.

Chow SL, Gaston KJ 1997. The species-body size distribution: energy, fitness and optimality. *Funct Ecol* 11: 365-375.

Cushman JH, Lawton JH, Manly BFJ 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* 95: 30-37.

Dial KP, Marzluff JM 1988. Are the smallest organisms the most diverse? *Ecology* 69: 1620-1624.

Gaston KJ, Blackburn TM 1996. Range size-body size relationships: evidence of scale dependence. *Oikos* 75: 479-485.

Gómez C, Espadaler X 2000. Species body-size distribution and spatial scale in Iberian ants. *Vie Milieu* 50: 289-295.

Hölldobler B, Wilson EO 1990. The ants. Springer Verlag.

Kaspari M, Weiser MD 1999. The size-grain hypothesis and interspecific scaling in ants. *Funct Ecol* 13: 530-538.

Maurer BA, Brown JH, Rusler RD 1992. The micro and macro in body size evolution. *Evolution* 46: 939-953.

Novotny V, Kindlmann P 1996. Distribution of body sizes in arthropod taxa and communities. *Oikos* 75: 75-82.

Peters RH 1983. The ecological implications of body size. Cambridge University Press.

Rosenzweig ML 1995. Species diversity in space and time. Cambridge University Press.

Schoener TW, Janzen DH 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. *Am Nat* 102: 207-224.

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