

The relationship between distribution and abundance in a dung-beetle community (Col., Scarabaeoidea)

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Abstract

The relationship between species' local abundance and distribution over a range of spatial scales was analysed in the case of a community of Iberian dung beetles. On a local scale, abundance and distribution are correlated, as statistics would lead one to expect (the larger the population of a species, the more frequently they occur in dung pats and samples). Nevertheless, this correlation is not observed in the data derived from annual sampling, due to presence of species characterized by high population growth rates and narrow seasonal occurrences. The supposition (BROWN, 1984) that broad-niche species should also be locally abundant is not corroborated; species were found that were well-distributed locally, but without large local populations.

On a regional scale, the results are in agreement with the model proposed by BROWN & MAURER (1987); locally abundant species tend to be well-distributed, although there is considerable variation in this correlation. On a geographical scale the results are as would be expected, although there are exceptions, possibly due to historical factors.

Keywords: Local abundance, distribution, dung-beetles, Iberian peninsula, Scarabaeoidea.

Résumé

La relation entre l'abondance locale des espèces et leur distribution le long d'échelles spatiales a été analysée pour une communauté de bousiers ibériques. A une échelle locale, l'abondance et la distribution sont corrélées, comme les statistiques tendraient à le faire penser (plus la population d'une espèce est grande, plus on la trouve fréquemment dans les bouses et les échantillons). Néanmoins, cette corrélation ne s'observe pas dans les données provenant de l'échantillonnage annuel, en raison de la présence d'espèces caractérisées par de forts taux de croissance populationnelle et des occurrences saisonnières restreintes. L'hypothèse (BROWN, 1984) selon laquelle les espèces à large niche devraient également être abondantes localement n'est pas corroborée ; on a trouvé des espèces bien distribuées localement, mais sans grandes populations locales.

A l'échelle régionale, les résultats sont en accord avec le modèle proposé par BROWN et MAURER (1987) ; les espèces localement abondantes ont tendance à être bien distribuées, bien qu'il y ait une variation considérable dans cette corrélation. A l'échelle géographique, les résultats sont tels qu'on pouvait s'y attendre, bien qu'il y ait des exceptions, probablement dues à des facteurs historiques.

INTRODUCTION

One of the questions of current interest that links ecology and biogeography is the well-documented relationship between species' local abundance and distribution. Some studies have indicated that distribution and abundance are positively correlated (McNAUGHTON & WOLF, 1970; HANSKI, 1982; BOCK & RICKLEFS, 1983; BROWN, 1984; BOCK, 1987; GOTELLI & SIMBERLOFF, 1987; GASTON & LAWTON, 1988*a*, *b* and 1990), although there are differences of opinion about the causes of such a relation.

Two alternative but complementary models have been developed in an attempt to explain this relation: one is the so-called "niche model" (BROWN, 1984) and the other which could be called the "rescue effect hypothesis" (HANSKI, 1991*a*). From the "niche-model" comes the assertion that both distribution and local abundance are the consequence of the ecological specialization of species (BROWN, *op. cit.*). Specialist species with narrow niches will occur as small local populations and in restricted areas of distribution, whereas unspecialized species, with their broad niches, will occur as large local populations and in wide-spread areas of distribution.

The positive distribution-abundance relationship may also be generated by a metapopulation dynamic mechanism, which is not based on differences in the ecological capacity of species. Metapopulations can be defined as ensembles of interacting populations with an expected time of extinction (HANSKI & GILPIN, 1991). If the emigrants from surrounding populations sites reduce the probability of local extinction ("the rescue effect"; BROWN & KODRIC-BROWN, 1977); and if the rate of immigration per patch is proportional to the fraction of suitable habitat patches occupied, then the rescue effect inevitably generates a positive correlation between distribution and abundance (HANSKI, 1982 and 1991*b*). This correlation comes about as a consequence of the simple variation in the local rates of immigration and extinction in systems of local populations or metapopulations.

This paper is not meant to investigate the validity of these two alternative models, but rather provides data bearing on the relation between local abundance and distribution over a range of spatial scales. The relation between distribution and local abundance is investigated in the case of dung beetles (*Scarabaeoidea sensu* BALTHASAR, 1963), a group of systematically homogeneous organisms adapted to the same microhabitat.

METHODS

The data used in this work come from a sampling carried out in high-altitude pastures of the Central Massif of Gredos, the roughest and highest part of all the Iberian Central System (Spain). Six different samplings were carried out in 1984 on the dates of September 22 to 24, and October 28 to 30; and in 1985 on the dates of May 1 to 3, June 11 to 13, July 22 to 24, August 21 to 23. In each of these six samplings, three 1.5 kg artificially constructed cow-dung pats were left in five different areas (a total of 15 dung-pats) for a two-day period. Each dung-pat is considered a sampling unit, while each dung-pat triplet is taken to be a sample (6 months x 5 zones = 30 samples; and 30 x 3 = 90 sampling units). The sampling sites are located on a north-south oriented line running from the settlement of "Hoyos del Espino" to "Candeleda": at altitudes of 1,500 and 1,740 m on the northern slope (U.T.M. 30TUK123640 and U.T.M. 30TUK102611); 1,500 and 1,720 m on the southern slope (U.T.M. 30TUK096553 and U.T.M. 30TUK096563); and 2,000 m in the pass "Puerto de Candeleda" (U.T.M. 30TUK093578). The three dung pats in each zone were separated 10 m (local scale) one from

the other, while the five samples sites were at an average separation of 2.5 km (regional scale). The maximum distance between sites was 10 km.

The species might be scarce due to their being located on the periphery of their niche or on the periphery of their area of distribution. These objections have been rejected sometimes by different authors (BOCK & RICKLEFS, 1983; BOCK, 1987). I do not exclude that sometimes, for a particular species, the estimated abundances are lesser than the real populations, but generally the estimates of abundance reveal the real populations of dung beetles in the sampling area.

RESULTS

There is a statistically non-significant positive correlation ($r=0.195$, $df=48$) between the local abundance of each species and the number of dung pats in which they are found (fig. 1a). Excluding the four most abundant species, there is a strong positive correlation ($r=0.713$, $P<0.001$, $df=44$), as in the case of the linear regression between both variables ($Y=0.047 X+8.338$; $t=6.916$, $P<0.001$). The relation between abundance and the number of samples in which each species occurs is similar (fig. 1b). Neither in this case is the correlation statistically significant when all the captured species are considered ($r=0.167$, $df=48$), but it becomes so when the four most abundant species are excluded ($r=0.637$, $P<0.001$, $df=44$; linear regression: $Y=0.017 X+4.963$; $t=5.488$, $P<0.001$).

There is a positive correlation between the abundance of captured species and the number of dung pats in which these occurred in each one of six sampling periods (fig. 2). During the summer both the number of species and the size of populations in these communities are very small. Perhaps for this reason no species was found to occur in more than 50% of the dung pats in this season. Interestingly enough, however, the abundance of species captured in more than 80% of dung pats was very unequal. Species such as *Aphodius bonvouloiri* HAROLD, 1860; *A. affinis* PANZER, 1823; *A. sphacelatus* (PANZER, 1798) and *A. contaminatus* HERBST, 1873 have high population growth rates and are of brief seasonal occurrence in the sampling zone (LOBO, 1992). On the other hand, species such as *Geotrupes ibericus* BARAUD, 1958; *Onthophagus similis* (SCRIBA, 1790), *Euoniticellus fulvus* (GOEZE, 1777) and *Aphodius fimetarius* (LINNAEUS, 1758) have a broader phenology, but generally do not form large populations.

These two groups of species are clearly defined in figure 1. These groups also occur if we examine the relation between abundance and number of dung pats in which each species appears in the samples from each sampling site (fig. 3). Data derived from species with high population growth rates and of brief seasonal occurrence skew the total data set, so that the relation is a statistically non-significant positive correlation.

If we examine the relation between the average abundance and the number of sites in which the species were captured in each sample period (fig. 4), we can see that species captured in less than four sites are represented by 10 individuals or fewer per dung pat, and that regionally well-distributed species generally are represented by one individual or more per dung pat. All of the captured species represented by 10 individuals or more per dung pat occurred in four or all sites (five), whatever the sampling month. It is remarkable that species with very unequal population densities may be found regionally well-distributed. It might seem self-evident that a species with a small population should inhabit few sites, but there

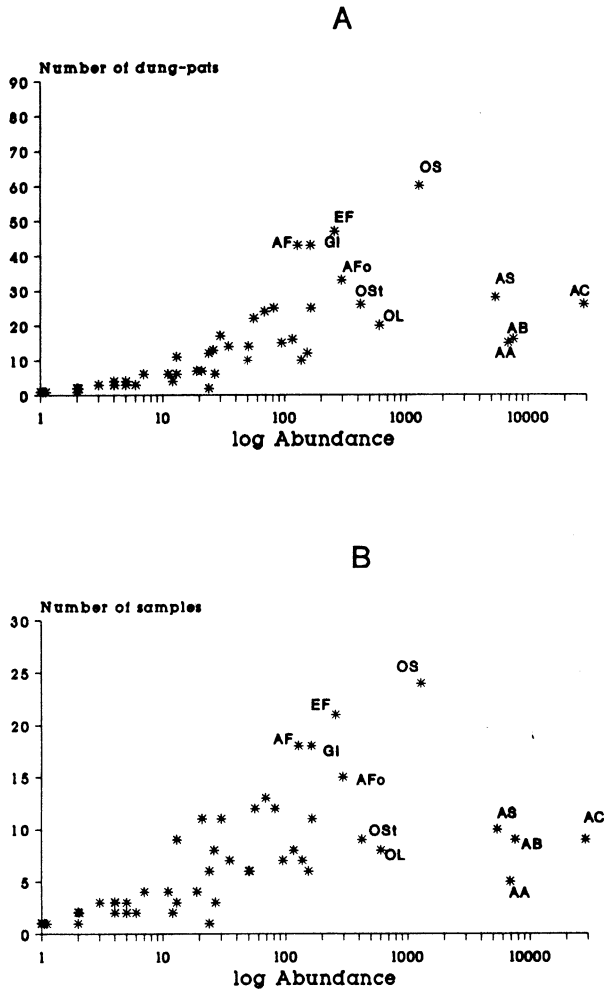


FIG. 1. – Relation between the logarithm of abundance of each species and the number of dung pats (A, sample units) or samples (B) in which they were found. OS = *Onthophagus similis* (SCRIBA, 1790); OSt = *O. stylocerus* GRAELLS, 1851; OL = *O. lemur* (FABRICIUS, 1781); OV = *O. vacca* (LINNAEUS, 1767); *O. taurus* (SCHREBER, 1759); EF = *Euoniticellus fulvus* (GOEZE, 1777); AF = *Aphodius fimetarius* (LINNAEUS, 1758); Afo = *A. foetidus* (HERBST, 1783); AS = *A. sphacelatus* (PANZER, 1798); AA = *A. affinis* PANZER, 1823; AC = *A. contaminatus* HERBST, 1873; AB = *A. bonvouloiri* HAROLD, 1860; GI = *Geotrupes ibericus* BARAUD, 1958.

are species represented by fewer than one individual per dung pat that occur in all the zones, and other spatially restricted species represented by 10 individuals per dung pat.

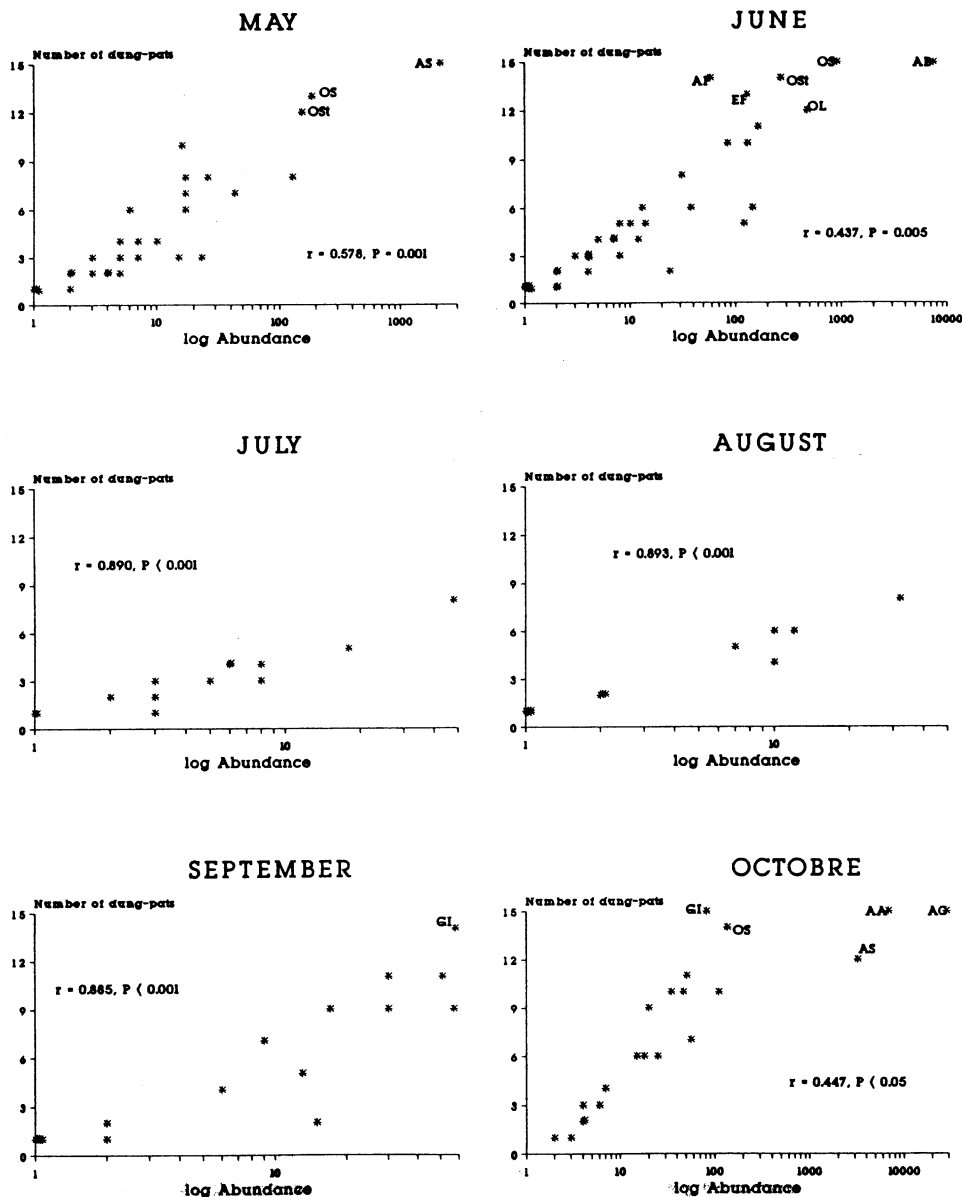


FIG. 2. — Relation between the logarithm of abundance of each species and the number of dung pats in which they were found for any one of six sampling periods. Abbreviations as in figure 1.

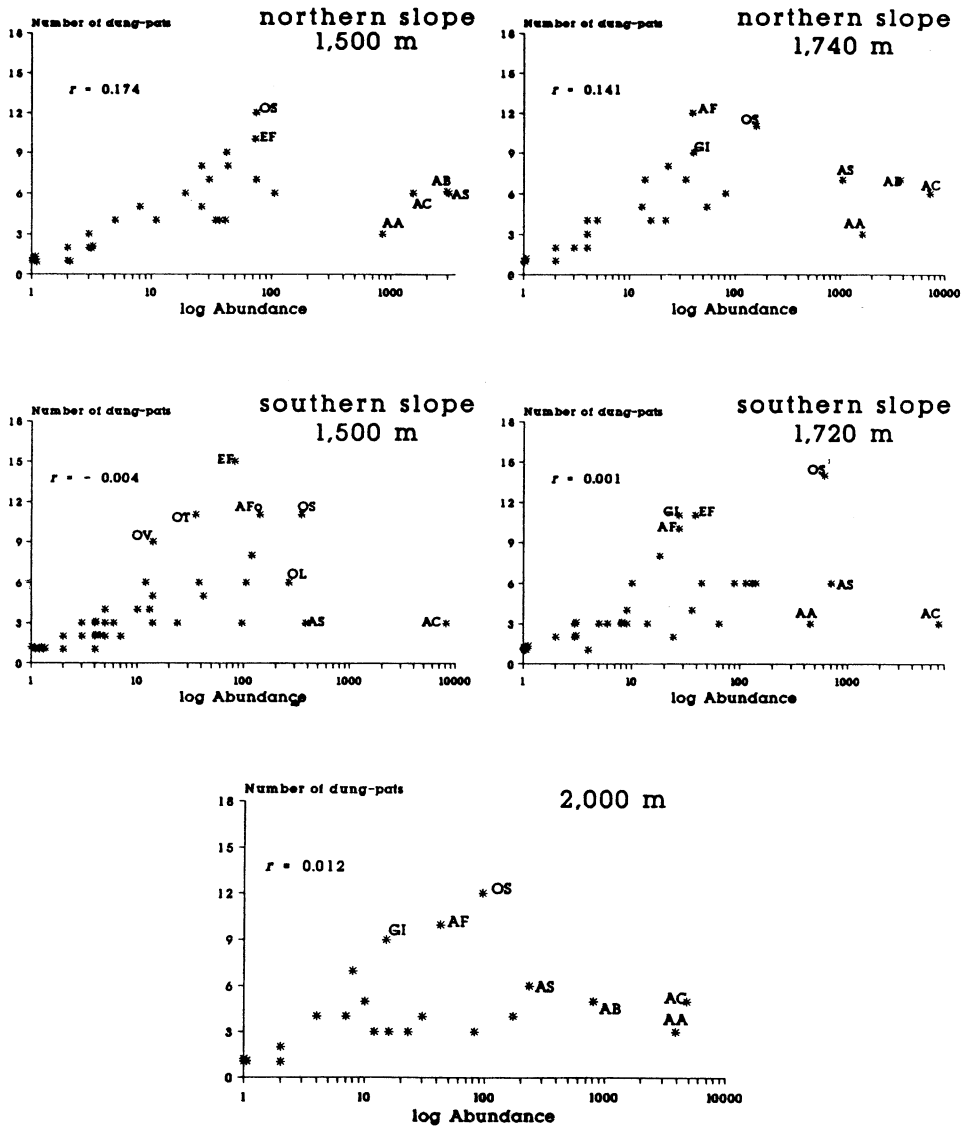


FIG. 3. — Relation between the logarithm of abundance of each species and the number of dung pats in which they were found for any one of five sampling stations. Abbreviations as in figure 1.

It is difficult to determine the size of the area of distribution for a species from this group of organisms. As a first approximation, each of the species has been included in three chorologic categories, as proposed by LA GRECA (1964):

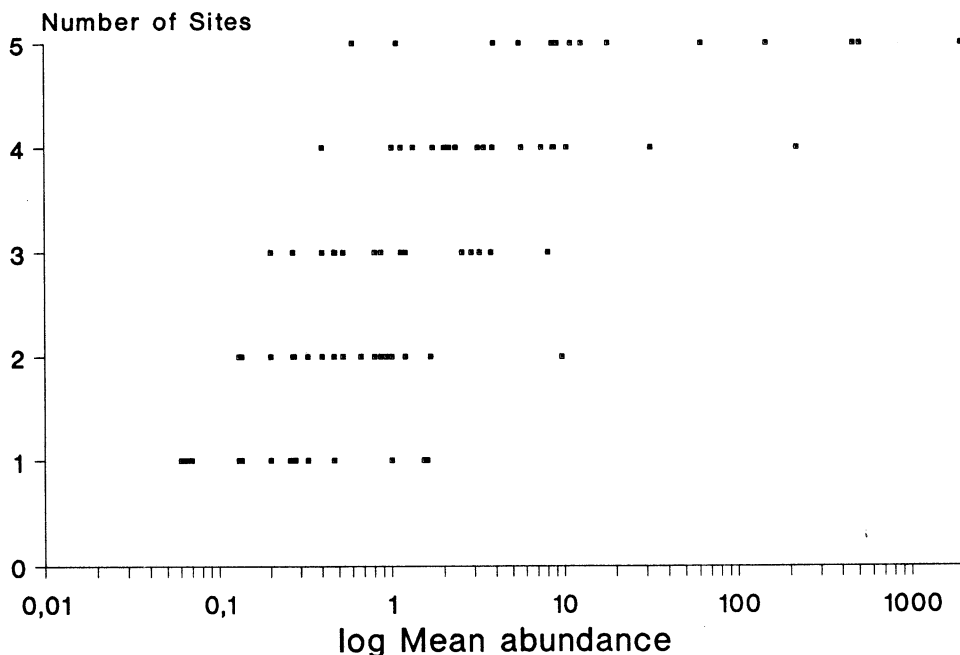


FIG. 4. – Relation between average abundance per dung pat and the number of sampling sites in which each species occurred in each of the six sample periods.

i) Widely-distributed species, those with a Cosmopolitan, Euosiberian, Euro-central-asiatic, Euro-asiatic, Palearctic or Holartic distribution.

ii) Less-widely-distributed species, such as Mediterranean or Euroturanic ones.

iii) Restrictedly-distributed species, endemic to the Iberian peninsula.

The distribution according to different abundance class (fig. 5) of the number of species classified as to these three categories shows that species with lesser population density are not usually geographically widely distributed and that species with large local populations are, above all else, widely distributed. The frequencies of the less-widely-distributed species and the widely-distributed ones are significantly different ($\chi^2=10.74$, $df=4$, $P < 0.05$). Nevertheless, distribution area varies among species in practically all the abundance classes.

DISCUSSION

In each one of the sampling periods, the larger the population of a species, the more frequently they occur in the dung pats and in the samples, which is what one would expect. This relation lacks biological implication if "distribution" is defined as the frequency with which a species occurs in a group of samples (WRIGHT, 1991). So for data derived from a sample population captured over a small region one can expect the above-mentioned relation to hold, since the larger the average abundance of a species, the greater the probability that they occur in a larger

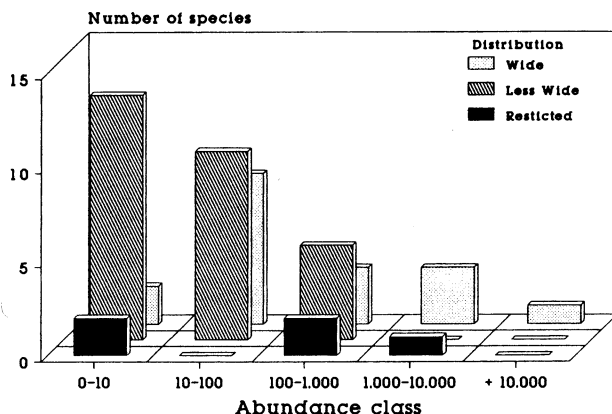


FIG. 5. – Number of species with different distribution area size according to their regional abundance in the sampling area.

number of samples. Even so, examination of the relation between the abundance and distribution of species found in sample units or samples (local scale) leads to some interesting considerations.

Statistically significant positive correlations are seen to occur only in data from individual months. However, if species distribution data comes from dung pats belonging to samples taken in several months, positive correlations between abundance and distribution do not occur (fig. 3). This is due to the appearance of species characterized by explosive population growth rates and brief seasonal occurrence, which only occur in the dung pats during their brief phenological periods. Actually, only broad phenology species are present in samples from more than 50% of total dung pats.

In some monthly samples there are species that are well distributed among the dung pats of the examined area (some 20 km²); but these species may, or may not, be characterized by large abundances. Those species that appeared in a large number of dung pats, and with large populations, all belong to the genus *Aphodius*, dominant in northern Europe (HANSKI, 1986). Their specimens are of a small size (between 5 mm and 9 mm in length), which enables them to maintain large populations within the dung pat microhabitats. In general, these species seem to be spatially or seasonally limited. *A. bonvouloiri*, *A. affinis*, *A. contaminatus* and *A. sphacelatus* are all species that only inhabit the upper half of Iberian peninsula mountains. *A. bonvouloiri* is an endemism restricted to the central mountains of the Iberian peninsula, while the other three species can be said to have a European or Euro-central-Asiatic type of distribution (DELLACASA, 1983). Seasonally, two are strictly autumnal (*A. affinis* and *A. contaminatus*), one strictly occurs in the spring (*A. bonvouloiri*), while only *A. sphacelatus* is autumnal-spring (LOBO, 1992).

Another group of species was found in the majority of dung pats of some samplings, but without large captured abundances. For instance, during June an average population of 4 specimens per dung pat of *Aphodius fimetarius* was found. The captured abundance of *A. bonvouloiri* were 128 times greater, but both species

appeared in more than 90% of dung pats. In October the abundance of *Geotrupes ibericus* was almost 350 times smaller (at 5.5 specimens per dung pat) than that of *A. contaminatus*; nevertheless, both species were found in all dung pats examined. *Onthophagus similis* and *Euoniticellus fulvus* also seem to be species which are well represented in dung pats, although their average captured abundances are small.

A. fimetarius and *O. similis* are probably the two western european species with greatest ecological capacity in their respective families (Aphodiidae and Scarabaeidae). *A. fimetarius* is considered to be bivoltine and euryoic (PAULIAN & BARAUD, 1982), highly resistant to temperature extremes and dryness (LANDIN, 1961). Its area of distribution takes in all of the Palearctic region, having been accidentally introduced in Australia and North America (DELLACASA, 1983), where it can be found in large populations (from 200 to 500 specimens per dung pat; MERRITT & ANDERSON, 1977). *Onthophagus similis* is a species of small size (6 mm, approximately) within its family; it is polymorphic (PALESTRINI, 1981) and widely distributed throughout the western Palearctic (PAULIAN & BARAUD, 1982). It is doubtlessly the most frequently occurring and abundant species of the Scarabaeidae in the Iberian peninsula. It colonizes all elevations, is of a broad phenology and varied trophic range (MARTIN-PIERA, 1984).

The majority of the species of the genus to which *Euoniticellus fulvus* belongs inhabit the Afrotropical region (CAMBEFORT, 1991). The behaviour of the Eurosiberian-Mediterranean species *E. fulvus* is extremely flexible; its feeding behaviour varies according to latitude (ROUGON & ROUGON, 1982). *E. fulvus* is the only European species of Scarabaeidae to have the entire egg, larval, and pupal development in dung pats, like *Aphodius* (dwellers). This uniqueness, coupled with its rapid development, is a major factor in the achieving of high population growth rates (HALFFTER & EDMONDS, 1982). It is one of the most abundant and frequently occurring Scarabaeoidea species in the Iberian peninsula. Lastly, the most frequently occurring coprophage species of the Geotrupidae family in the Iberian peninsula is surely *Geotrupes ibericus*; it is also the one with the broadest phenology. Its body size is considerable (between 20 mm and 25 mm in length); it was the only large-size species captured in the sample area in numbers in excess of one specimen per dung pat (LOBO, 1992). In this case one is dealing with a species endemic to the Iberian peninsula, as revealed by a study of its genital anatomy. It is externally very similar to its sister species *G. spiniger*, which is distributed throughout all of Europe and Asia Minor (BOGGETTI & ZUNINO, 1977).

It would seem that a species which forms large populations would also surely be locally well-distributed. Nevertheless, there are locally well-distributed species (ones which are found in more dung pats or more samples) which have not been caught in abundance. These species have usually a great ecological capacity (broader niche). In the case of this study's samples, having large abundance is not necessarily a characteristic of broad-niche species.

Highly ecological capacity possibly favours the spreading of spatial distribution on a local or regional scale. The relation between ecological capacity (broad niche) and population density does not have to be the norm, since a species may be adapted to very particular space-time ecological conditions and be locally abundant. Species may be represented in small local populations, but be well-distributed on a local scale, perhaps because their environmental tolerance allows them to colonize all the dung pats in a particular area despite environmental differences. An instance of this

is the case of *Geotrupes ibericus*, the only species of large body size found to be well-distributed throughout all the dung pats, and also relatively abundant. Body size might be a major factor which enhances a species environmental independence and heightens its competitive abilities (BARTHOLOMEW & HEINRICH, 1978; SCHOENER, 1983; BROWN & MAURER, 1987; HANSKI & CAMBEFORT, 1991).

In temperate regions, seasonal changes may comprise the main niche dimension for dung beetles (HANSKI & KOSKELA, 1977 and 1979; HANSKI 1980a; HOLTER, 1982; YASUDA, 1984), so it is difficult for a niche in such regions to be seasonally broad, and simultaneously narrow in other dimensions. This is the explanation for the observation that species found with greatest frequency in dung pats are those with a greater ecological capacity, not those with the largest abundances, when data from annual sampling of all the sites are considered. The hypothesis of BROWN (1984) would be correct in this case, since broader-niche species would be locally better distributed; the same hypothesis would fail in its supposition that broad-niche species form large populations. On the contrary, in the case of this study it seems that large-population species compensate for their lack of ecological capacity by massive reproduction in a very short seasonal period.

It is important to keep in mind that the seasonal occurrence and spatial gradients in the environment of a given region can be determining factors in the observed regional distributions of species. For this reason, to avoid anomalous results due to seasonal heterogeneity, data meant to be used to establish the relation between local abundance and distribution should be collected on a yearly basis; in the same manner, so as to avoid sampling problems due to spatial heterogeneity, data should be collected over the entire species range (BROWN & MAURER, 1987; GASTON & LAWTON, 1990).

When one examines the relation between abundance and regional distribution, one observes: i) Although wide regional distribution species are usually abundant locally, their average abundance may vary considerably. There were some species captured in the five sample sites in widely varying number (for example: *Aphodius scrofa* (Fabricius, 1787), $n=24$ and *A. affinis*, $n=6.862$). ii) The average abundance of species with a restricted regional distribution is never high; such species always occur with fewer than 10 individuals per dung pat.

In this case the relation between abundance and distribution is in complete agreement with that predicted by BROWN & MAURER (1987), for whom there were no species with restricted distribution and scarce local abundance, as they would be threatened with extinction. But it is also true that these species could be scarce due to their being located on the periphery of their area of distribution (RICKLEFS, 1972; BROWN, 1984), or to their being less detectable (BOCK, 1987). Furthermore, this case is also influenced by the fact that there is a lesser probability that species with smaller populations occur in all sites (WRIGHT, 1991). Neither do species exist which are of great abundance but of a restricted regional distribution (BROWN & MAURER, 1987). This pattern holds generally, although there are exceptions (BROWN, 1984; GASTON & LAWTON, 1990) that appear when the territory considered comprises peculiar habitats or includes species adapted to limited but productive resources.

It is difficult to analyse the relation between local abundance and geographic distribution in this faunistic group. Some patterns in agreement with previous results can be observed. Among species with high local abundance, the most frequent are those with wide-spread geographic distributions. Non-abundant species are not

usually geographically wide-spread, although the geographic distribution of species with a similar local abundance may vary considerably.

The "rescue effect hypothesis" as an explanation of the correlation between abundance and distribution is less valid on a geographic scale, as is the case with metapopulation dynamics. According to the "niche model", the wide geographic range of a species should, in many instances, be the result of climatic tolerance. It is to be expected that the more generalist a species is in one or more dimensions of its niche, the more abundant it will be locally, and the more widely distributed it will be on a local, regional and geographical scale. In the end, widening of the geographical range of a species may be the result of repeated enlargement of its range on an ecological scale (HANSKI, 1980b). However, historic factors would have exerted great pressure in this case. High tolerance of environmental conditions may allow a species to inhabit an enlarged area of distribution, to be more highly competitive and generate large local populations; but not all widely-distributed species necessarily share all these characteristics. There are many published cases of widely-distributed species which do not have large local populations (see, for example, RABINOWITZ, 1981 or BROWN & MAURER, 1987). The causal relationship between abundance and distribution can vary from species to species.

The "niche model" (BROWN, 1984) is ecologically reasonable, but perhaps too simple. Over a geographic scale historic factors could distort the abundance-distribution relationship. On a local and regional scale, high population densities are not necessarily linked with a broader niche. A species characterized by large populations might appear, found to be spatially or seasonally limited. Another possible exception might occur as follows: it is supposed that increased body size makes insect species more competitive (SCHOENER, 1983) and more independent of environmental conditions (BARTHOLOMEW & HEINRICH, 1978); perhaps that is why large-body-size species are generally widely distributed, but with small local populations (BROWN & MAURER, 1987); in this case, greater ecological capacity (broader niches) would mean smaller local populations.

As HANSKI (1991a) has pointed out, the "niche model" and the "rescue effect hypothesis" are not mutually exclusive explanations of the abundance-distribution relationship, but rather, complementary ones. Either can help to explain such a relationship although perhaps the correlation between abundance and distribution might be nothing more than a demonstration that, often times, the adaptive success of a species (measured by the average abundance of some populations, but the biomass would be a more correct measure) is associated with an expansion of these populations (measured by the size of the area they occupy).

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