FORUM FORUM FORUM

FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

How large is a species' geographic range?

Kevin J. Gaston, Biodiversity Division, Dept of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Many patterns of community structure will not be understood without reference to processes operating at regional and geographical scales (Cornell 1985a, b, Ricklefs 1987, Brown and Maurer 1989, Lawton 1990). This realisation doubtless has been a prime motivation behind many recent studies of patterns in the sizes of species geographic ranges, and how these interact with such characteristics as local abundances, body sizes and trophic habits (Brown 1984, Brown and Maurer 1987, 1989, Bowers 1988, Gaston 1990, Gaston and Lawton 1990a, b, Pagel et al. 1991). It is thus somewhat curious to find that few of these studies explicitly state what they believe the size of a species geographic range, measured by whatever method, actually represents. This situation is made the more troublesome because different studies seem to be measuring different things. Thus, whilst Reaka (1980) quantifies species geographic ranges in terms of the numbers of degrees of latitude and longitude over which they have been recorded, and regards the numbers of $5° \times 5°$ quadrats in which they were recorded as a measure of another aspect of their distribution, Schoener (1987) and Ford (1990) use numbers of occupied quadrats as a measure of geographic range size.

This paper examines some of the ways in which the size of species geographic ranges could be measured, what these measures mean, and how they relate to one another.

What is a geographic range?

No species occurs everywhere, yet every extant species occurs somewhere. At its crudest a species geographic range is little more than a description of the regions in which its individuals have been recorded. Thus, for example, Corbet and Hill (1990) list the geographic range of the wolf *Canis lupus* as 'Palaearctic (except N. Africa), India, Alaska, Canada, Mexico, U.S.A.', that of the water chevrotain *Hyemoschus aquaticus* as 'Sierra Leone – W. Uganda', and that of the blackbuck *Antilope cervicapra* as 'India'. Such descriptions tend to emphasise the location of the limits to a species occurrence, and may be more detailed, or even more sweeping, depending upon the information available and the objectives in providing it.

Perhaps the simplest way of trying to quantify a species geographic range is to sum the areas of the regions in its description. Thus, for example, Spitzer and Lěps (1989) assign species of European noctuid moths to one of six geographic range categories, from largest to smallest, cosmopolitan, palaearctic + paleotropical, holarctic, palaearctic, eurosiberian, and european (Lěps and Spitzer 1990 perform a similar analysis). This is a measure, albeit a crude one, of a species' *extent of occurrence.* It can be refined using more comprehensive information on the localities at which species have been recorded. Thus, extent of occurrence is often quantified in terms of the latitudinal or longitudinal extent of these localities (Reaka 1980, Stevens 1989, Dennis and Shreeve 1991), or of the size of the smallest area contained within an imaginary boundary line which encloses all of them (Anderson 1977, 1984a, b, 1985, Glazier 1980). The majority of field guides and many taxonomic works depict species distributions as a solid block of occupancy, and commonly provide the basis for the latter calculations. A variety of criteria are available by which the position of the boundary line can be determined, though it is usually fitted by eye.

The extent of a species occurrence is one of two markedly different ways of essentially defining what a species geographic range is. The alternative is to regard it as the *area of occupancy* of a species. Measures of species extent of occurrence include regions which, whilst falling within the limits of its occurrence, are not actually occupied by it. This may be because these areas are entirely unsuitable, or simply uncolonised at the present. When a species' geographic range is viewed as an area of occupancy, such regions are not included.

In principle this distinction between species geographic ranges as extents of occurrence and as areas of occupancy is a straightforward one. Unfortunately, it is complicated by two things. First, the extent of occurrence of a species is difficult to interpret when its individuals are distributed amongst two or more geographically isolated groups, and certainly means something somewhat different from that of a species which is more uniformly distributed between its limits. Methods have been developed to identify such isolates, with bounds often being drawn about the limits of occurrence of each separately, and the species extent of occurrence being regarded as the sum of the measures of each of these (Rapoport 1982). However, what is regarded as an isolate is a matter of scale, the finer the scale the more isolates (Erickson 1945), and it is plain that once one starts to identify isolates one rapidly starts to measure a species area of occupancy and not its extent of occurrence.

The second complication to the distinction between species geographic ranges as extents of occurrence and as areas of occupancy is almost the inverse of the previous one. That is, that the area within the bounds of a species occurrence tends to be used in some circumstances as a reasonably refined measure of its extent of occurrence and in others as a very crude measure of its area of occupancy. More refined measures of areas of occupancy include the total number of localities at which species have been found (McAllister et al. 1986, Gaston and Lawton 1988), and the number of squares of a grid, placed over a map of the region of interest, in which they have been recorded (Lawton and Schroeder 1977, Schoener 1987, Ford 1990). The relationship between the crude and more refined measures is akin to that between 'crude' and 'ecological' population densities. 'Crude' densities are measured over some arbitrarily chosen area, whilst 'ecological' densities are measured over the area of habitat actually used by the organisms concerned (Robinson and Redford 1986). Clearly, areal measures based on the number of squares of a grid in which a species has been recorded will move from being crude to being refined measures as the mapping scale becomes finer. They will also tend at the same time to become increasingly different from measures of areal extent of occurrence.

The most refined measure of a species area of occupancy is probably the sum of the areas of the home ranges (or equivalent) of all individuals, reduced to account for zones where these overlap one another (though this may be almost impossible to measure in most cases). At this point the area of occupancy of a species is close to becoming a measure of its abundance. Hengeveld (1990 and references therein) has repeatedly argued that species geographic ranges should not be viewed independently of their abundances, and the above method is an extreme form of his position. In this context, it might also be noted that Root (1988) and Lack (1986) integrate crude measures of abundance into atlas maps of species extents of occurrence and areas of occupancy, respectively.

Combined, the complications associated with differentiating between extents of occurrence and areas of occupancy might explain why many authors fail to make it explicit what aspect of a species distribution they are referring to when producing measures of its geographic range. Thus, for example, despite discussing the area of species geographic ranges at some length, neither Udvardy (1969) nor Rapoport (1982) clearly distinguishes between the two definitions.

It is perhaps worth observing that there are yet other closely related measures of the geographic distribution of individuals. Thus, for example, one might determine the *proportion* of the area within the range boundaries that is occupied by a species (the 'distribution' of Dennis and Shreeve 1991, and distinct from measures of the proportion of a defined set of sites occupied by each species in a given assemblage, as used in studies of regional distributions, eg. Hanski 1982) This would be a relative measure of area not an absolute one. To my knowledge, such measures have not, to date, been interpreted as species geographic ranges.

Extent of occurrence or area of occupancy?

Ignoring for a moment some of the practical problems in differentiating between species extents of occurrence and areas of occupancy, for what kinds of ecological problems are the two interpretations of a species geographic range size most appropriate?

Species extents of occurrence have repeatedly been used in addressing questions of dispersal, invasion, and the dynamics of geographical range size (Elton 1958, Reaka 1980, Williamson and Brown 1986, Hengeveld 1989). Here, the emphasis has very much been upon the factors determining the limits to species ranges, and how these limits change in time and space. Measures of extent of occurrence clearly contribute much in this context to understanding why particular species occur where they do. However, as pointed out elsewhere (Gaston 1990), although they have rarely been used in this field, species areas of occupancy might provide yet further insights. Thus, if we are to develop a comprehensive understanding of patterns of distribution we should, for example, be interested not simply in how species extents of occurrence decline through time as their geographic ranges contract, but also in how the area of occupancy within those limits changes.

It is actually difficult to see many ecological problems where *only* measures of species extents of occurrence could profitably be used (though they probably yield the most useful information for more strictly biogeographical problems of species origins and distribution). The converse is less true. A whole group of problems can be identified for which use of extent of occurrence measures is distinctly hazardous. Because many environmental parameters show 'reddened spectra' (Williamson 1987 and references therein), their heterogeneity increasing with area, species extents of occurrence will inevitably tend to be correlated with the heterogeneity in these parameters. Thus, for example, the numbers of habitats, the range of temperatures and the range of levels of precipitation recorded within the extent of occurrence will all tend to be positively correlated with the magnitude of this extent. However, this says very little about the biologies of the species concerned, they may all occur within just one habitat type at a narrow range of temperatures and levels of precipitation. It is only through measuring species geographic ranges in terms of areas of occupancy that artefactual correlations with environmental factors will be avoided.

Measures of area of occupancy seem to be most appropriate for a wide variety of other problems. Examples of two particularly important ones will suffice. First, a large proportion of recent papers utilising measures of range size have been concerned with the interaction between species geographic distributions and local population abundances (Schoener 1987, Brown and Maurer 1989, Arita et al. 1990, Ford 1990, Gaston and Lawton 1990a). The principle hypothesis under test has been Brown's (1984) proposal that species able to exploit a wide range of resources are able to occupy a larger number of sites and become locally abundant, and therefore that species distributions and local abundances will tend to be positively related. It is plain that the most appropriate measure of range size here is one of area of occupancy. Nonetheless, many (but not all) studies have used either the area within the limits to species occurrences (Brown and Maurer 1987), or numbers of squares occupied of exceedingly coarse grid maps (Bock and Ricklefs 1983, Bock 1984). As stated earlier, these methods are the least able to resolve between extents of occurrence and areas of occupancy, and it would be interesting to see what effect using range measures of different quality has upon the interaction observed between distribution and abundance for a particular species assemblage.

A second example where area of occupancy measures are particularly relevant is in the study of the relationship between the number of insect species associated with a particular species of plant, and the geographic range of the plant. Again, this is an interaction with a large literature (Strong et al. 1984, Jones and Lawton 1991, and references in both). A number of methods have been employed to quantify species distributions, from Stevens' (1986) crude calculation of the magnitude of plant geographic ranges as 'the area of a rectangle defined by the two major perpendicular axes of the plant's distribution', through Fowler and Lawton's (1982) and Kennedy and Southwood's (1984) estimates of the numbers of tetrads (2 km × 2 km) in which a plant had been recorded, to Claridge and Evans (1990) use of quite accurate censuses of the actual areas species occupied. Despite this diversity of approaches, several studies make it plain that the desired quantity is a species area of occupancy (Kennedy and Southwood 1984, Claridge and Evans 1990). Claridge and Evans (1990) demonstrate that the crudity with which this is measured can have important effects upon the relationship that is observed between numbers of associated insect species and plant distribution, perhaps helping to explain why the observed correlation coefficients tend to vary so much (Strong et al. 1984). No systematic study has been undertaken, however, to explore this issue. Moreover, it seems likely that the numbers of species of insect associated with a plant might be affected not only by its area of occupancy, but also by its extent of occurrence, suggesting that an attempt to dissect the two effects might prove profitable.

In conclusion

The term 'geographic range' is part of the everyday vocabulary of ecologists. Growing interest in the role of large scale processes in determining the structure of local communities has necessitated quantifying this aspect of species distributions, and in so doing highlighted the lack of conformity as to precisely what it is. Although two distinctly different ways of measuring species geographical distributions can be recognised, their extent of occurrence and their area of occupancy, the relative crudity of distributional information make their separation more difficult in practice. To what extent they are truly independent is as yet hard to assess. Species with wide extents of occurrence are likely to have large areas of occupancy, whilst species with narrow extents of occurrence are likely to have small areas of occupancy. Of more interest is the magnitude of the correlation between the two measures. This is likely to depend a great deal on the particular species assemblage being studied, the precise way in which the measures are made, and such things as the relative frequencies of habitat generalism and specialism amongst its species. Much may be learned if studies involving measures of species range size seek to quantify them in several ways (McAllister et al. 1986), and report their interactions.

This paper has glossed over many of the complexities to the structure of species geographic ranges. These include the fact that they do not have true edges (MacArthur 1972), that the inclusion or exclusion of vagrant individuals may markedly alter perceived range extent, and that the distribution of individuals changes continually in space and in time. Only through continued attempts to improve the quality and quantity of distributional data will it be possible to explore their implications.

Acknowledgements – My thanks go to the referees of past papers who have shown a disturbing lack of agreement as to what a species geographic range is, and in so doing encouraged me to try and address the topic. S. Gaston, J. Lawton, P. Warren and M. Williamson kindly commented on the manuscript.

References

Anderson, S. 1977. Geographic ranges of North American terrestrial mammals. – Am. Mus. Nov. 2629.
– 1984a. Geographic ranges of North American birds. – Am. Mus. Nov. 2785.
– 1984b. Areography of North American fishes, amphibians and reptiles. – Am. Mus. Nov. 2802.
– 1985. The theory of range-size (RS) distributions. – Am. Mus. Nov. 2833.
Arita, H. T., Robinson, J. G. and Redford, K. H. 1990. Rarity in Neotropical forest mammals and its ecological correlates. – Conserv. Biol. 4: 181–192.
Bock, C. E. 1984. Geographical correlates of abundance vs. rarity in some North American winter landbirds. – Auk 101: 266–273.
– and Ricklefs, R. E. 1983. Range size and local abundance of some North American songbirds: a positive correlation. – Am. Nat. 122: 295–299.
Bowers, M. A. 1988. Relationships between local distribution and geographic range of desert heteromyid rodents. – Oikos 53: 303–308.
Brown, J. H. 1984. On the relationship between abundance and distribution of species. – Am. Nat. 124: 255–279.
– and Maurer, B. A. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. – Am. Nat. 130: 1–17.
– and Maurer, B. A. 1989. Macroecology: the division of food and space among species on continents. – Science 243: 1145–1150.
Claridge, M. F. and Evans, H. F. 1990. Species-area relationships: relevance to pest problems of British trees? – In: Watt, A. D., Leather, S. R., Hunter, M. D. and Kidd, N. A. C. (eds), Population dynamics of forest insects. Intercept, Andover, pp. 59–69.
Corbet, G. B. and Hill, J. E. 1980. A world list of mammalian species. – British Museum (Natural History) and Cornell Univ. Press, London.
Cornell, H. V. 1985a. Species assemblages of cynipid gall wasps are not saturated. – Am. Nat. 126: 565–569.
– 1985b. Local and regional richness of cynipine gall wasps on California oaks. – Ecology 66: 1247–1260.
Dennis, R. L. H. and Shreeve, T. G. 1991. Climatic change and the British butterfly fauna: opportunities and constraints. – Biol. Conserv. 55: 1–16.
Elton, C. S. 1958. The ecology of invasions by animals and plants. – Methuen, London.
Erickson, R. O. 1945. The *Clematis fremontii* var. *riehlii* population in the Ozarks. – Ann. Missouri Bot. Gard. 32: 413–460.
Ford, H. A. 1990. Relationships between distribution, abundance and foraging niche breadth in Australian land birds. – Ornis Scand. 21: 133–138.
Fowler, S. V. and Lawton, J. H. 1982. The effects of host-plant distribution and local abundance on the species richness of agromyzid flies attacking British Umbellifers. – Ecol. Ent. 7: 257–265.
Gaston, K. J. 1990. Patterns in the geographical ranges of species. – Biol. Rev. 65: 105–129.
– and Lawton, J. H. 1988. Patterns in body size, population dynamics and regional distribution of bracken herbivores. – Am. Nat. 132: 662–680.
– and Lawton, J. H. 1990a. Effects of scale and habitat on the relationship between regional distribution and local abundance. – Oikos 58: 329–335.
– and Lawton, J. H. 1990b. The population ecology of rare species. – J. Fish. Biol. 37 (Suppl. A): 97–104.
Glazier, D. S. 1980. Ecological shifts and the evolution of geographically restricted species of North American *Peromyscus* (mice). – J. Biogeog. 7: 63–83.
Hanski, I. 1982. Dynamics of regional distribution: the core-satellite species hypothesis. – Ann. Zool. Fennici 19: 65–73.
Hengeveld, R. 1989. Dynamics of biological invasions. – Chapman and Hall, London.
– 1990. Dynamic biogeography. – Cambridge Univ. Press, Cambridge.
Jones, C. G. and Lawton, J. H. 1991. Plant chemistry and insect species richness of British umbellifers. – J. Anim. Ecol. in press.
Kennedy, C. E. J. and Southwood, T. R. E. 1984. The number of species of insects associated with British trees: a re-analysis. – J. Anim. Ecol. 53: 455–478.
Lack, P. 1986. The atlas of wintering birds in Britain and Ireland. – Poyser, Calton.
Lawton, J. H. 1990. Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space. – Phil. Trans. R. Soc. Lond. B 330: 283–291.
– and Schroder, D. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. – Nature, Lond. 265: 137–140.
Lěps, J. and Spitzer, K. 1990. Ecological determinants of butterfly communities (Lepidoptera, Papilionoidea) in the Tam Dao mountains, Vietnam. – Acta Entomol. Bohemoslov. 87: 182–194.
MacArthur, R. H. 1972. Geographical ecology: patterns in the distributions of species. – Harper and Row, New York.
McAllister, D. E., Platania, S. P., Schueler, F. W., Baldwin, M. E. and Lee, D. S. 1986. Ichthyofaunal patterns on a geographic grid. – In: Hocutt, C. H. and Wiley, E. D. (eds), Zoogeography of freshwater fishes of North America. Wiley, New York, pp. 17–51.
Pagel, M. D., May, R. M. and Collie, A. 1991. Ecological aspects of the geographic distribution and diversity of mammal species. – Am. Nat. in press.
Rapoport, E. H. 1982. Areography: geographical strategies of species. – Pergamon, Oxford.
Reaka, M. L. 1980. Geographical range, life-history patterns, and body size in a guild of coral-dwelling mantis shrimps. – Evolution 34: 1019–1030.
Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. – Science 235: 167–171.
Robinson, J. G. and Redford, K. H. 1986. Body size, diet, and population density of neotropical forest mammals. – Am. Nat. 128: 665–680.
Root, T. 1988. Atlas of wintering North American birds. – Univ. of Chicago Press, Chicago.
Schoener, T. W. 1987. The geographical distribution of rarity. – Oecologia (Berl.) 74: 161–173.
Spitzer, K. and Lěps, J. 1988. Determinants of temporal variation in moth abundance. – Oikos 53: 31–36.
Stevens, G. C. 1986. Dissection of the species-area relationship among wood-boring insects and their host plants. – Am. Nat. 128: 35–46.
– 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. – Am. Nat. 133: 240–256.
Strong, D. R., Lawton, J. H. and Southwood, T. R. E. 1984.

Insects on plants: community patterns and mechanisms. – Blackwell, Oxford.

Udvardy, M. D. F. 1969. Dynamic zoogeography: with special reference to land animals. – Van Nostrand Reinhold, New York.

Williamson, M. 1987. Are communities ever stable? – In: Gray, A. J., Crawley, M. J. and Edwards, P. J. (eds), Colonization, succession and stability. Blackwell, Oxford, pp. 353–371.

Williamson, M. H. and Brown, K. C. 1986. The analysis and modelling of British invasions. – Phil. Trans. R. Soc. Lond. B. 314: 505–522.