Species-range-size distributions: patterns, mechanisms and implications

Kevin J. Gaston

There are a number of curious lacunae and asymmetries in the study of population and community ecology. Until recently, there has been little interest in species-range-size distributions (i.e. the frequency distributions of the geographic range sizes of species), whereas enormous interest has been paid to the closely related species-abundance distributions. However, the growing need to understand species-range-size distributions, and the improved availability of appropriate data, have stimulated a number of recent studies. This work is supported by the growth in evidence that many features of the structure of local species assemblages can only be understood with reference to regional scale phenomena[1], and the emergence of macroecology as a field of study[2].

Species-range-size distributions have received remarkably little attention in contrast to species-abundance distributions. However, recognition of the importance of regional scale phenomena for local assemblage structure, and the emergence of 'macroecology', have begun to change this situation. A growing number of studies suggests that these distributions are, in general, approximately lognormal, although interpretation is complicated by a variety of factors. Assuming the distribution pattern to be real, it can be viewed in terms of evolutionary and ecological determinants of species occurrences, although their relative significance remains unclear. The form of the distribution has a variety of important consequences, particularly for inventories of faunas and floras and for conservation.

Kevin Gaston is at the Dept of Animal and Plant Sciences, University of Sheffield, Sheffield, UK S10 2TN.

The principal spatial pattern in range sizes is that associated with latitude, with the mean or median increasing from tropical to temperate regions for several groups[10-15]. There are, however, a growing number of exceptions[14-18]. Other spatial patterns of variation are associated with longitude[13,17] (e.g. average range sizes of North American mammals increase to the east[13]), and continent[9,11,17] (e.g. North American mammals have a smaller median range size than Australian mammals, which in turn have a smaller median range size than Palaearctic mammals[17]).

Between the upper and lower limits, and regardless of the magnitude of the mean, the sizes of the geographic ranges of species within a taxonomic assemblage are invariably distributed according to a 'hollow curve'[4,10,19] (i.e. strongly right-skewed) (Fig. 1). Typically, this distribution seems to be roughly lognormal[2,4,9,13] (Fig. 2). While this may serve as a first approximation, few species-range-size distributions have actually been tested for their fit to this model; claims of lognormality are often based on the tendency of a logarithmic transformation to generate a roughly symmetrical frequency distribution of range sizes. Where this fit has been examined explicitly, some significant departures have been documented. For example, for the New World avifauna, the frequency distribution of logarithmically transformed range sizes is significantly left-skewed[41].

Patterns in range-size distributions

The breadth of geographic range sizes exhibited by individual species is enormous. At one extreme lie those that are distributed virtually globally in the terrestrial or marine realms. For example, the barn owl (*Tyto alba*) is frequently regarded as the most widely distributed terrestrial bird, occurring on virtually all major land masses and many islands. At the other extreme lie those species with apparently only a very few or perhaps a single extant wild individual (e.g. Spix's macaw, *Cyanopsitta spixii*), and those confined to habitat patches of very limited spatial extent (e.g. some desert fish species). The limits to species-range-size distributions for taxonomic assemblages may thus embrace areas spanning many orders of magnitude.

The mean geographic range sizes of species can differ markedly between higher taxa. Various generalizations have been suggested, such as: (1) the range sizes of species in terrestrial taxa are, on average, narrower than those of marine taxa; (2) protists have larger geographic ranges than metazoa; and (3) plants and insects have narrower ranges than vertebrates[3-5]. Robust empirical analyses of higher taxonomic differences in range sizes are scarce because of the difficulties in obtaining comparable data for different groups. Those published largely concern vertebrates. From these it appears that in North America the average range sizes of species increase from fish to amphibians to mammals to birds[6-8], and in Australia from anuran amphibians to lizards to snakes[9]. Similar differences might be thought to exist between functional or trophic groups. However, the situation appears complex, with few generalizations as yet apparent, although among mammals, carnivores repeatedly tend to have larger mean geographic range sizes than do most herbivores[10,11].

Interpretation of range-size distributions

Comparison of the form of observed species-range-size distributions (both with each other and with statistical models) and their interpretation may be complicated by a number of factors. These complications have received surprisingly little attention, and deserve more study.

Range-size measures

No standard methodology exists for measuring the sizes of species' geographic ranges[4]. Rather, a host of techniques have been applied (Box 1) on data of differing resolution (Box 2), capturing different, and sometimes fundamentally distinct, features of a species' spatial distribution. In particular, a division can be made between measures of extent of occurrence and area of occupancy – the former being the distance or area between the outermost limits to a species' occurrence, and the latter being the (smaller) area over which the species is actually found[4]. In addition, some methods serve differentially to weight areas in which species occur at many sites or at high densities[20]. Even when expressed in similar units, there can be substantial differences
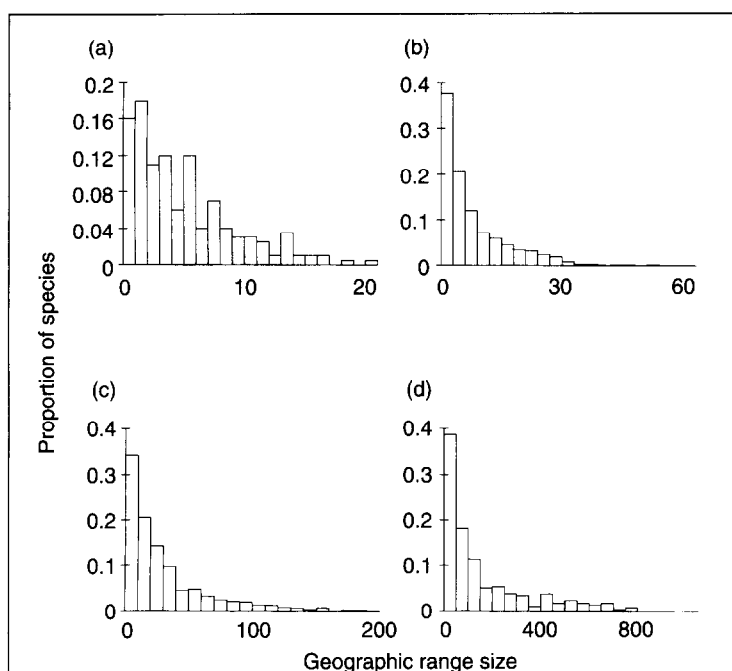
© 1996, Elsevier Science Ltd

Fig. 1. Some examples of species-range-size distributions. (a) Proportion of species of land birds with extents of occurrence of different sizes (10^6 km^2) in North America. *Redrawn from Ref. 2.* (b) Proportion of species of birds occupying different numbers of 611 000 km^2 grid squares in the New World. *Redrawn from Ref. 41.* (c) Proportion of species of passerine birds occupying different numbers of 2° × 2° grid squares in Africa south of 20°N. *Redrawn from Ref. 35.* (d) Proportion of species of passerine birds occupying different numbers of 100 × 100 km grid squares in Australia. *Redrawn from Ref. 19.* The differences in the measures of range size used and the way in which distributions are summarized exemplify the difficulties of making comparisons between studies.

in range sizes measured using different methods. For example, Hollander *et al.*[21] calculate the range of a teiid lizard in California, the orange-throated whiptail (*Cnemidophorus hyperythrus*), to be: 11 300 km^2, based on the area delineated by the entire range boundary; 6900 km^2 based on suitable habitat types within this boundary; and 2200 km^2 based on frequently used spectral classes (from satellite imagery). Although there may be significant positive interspecific relationships between range sizes quantified using different measures[9,20], substantial variance may occur.
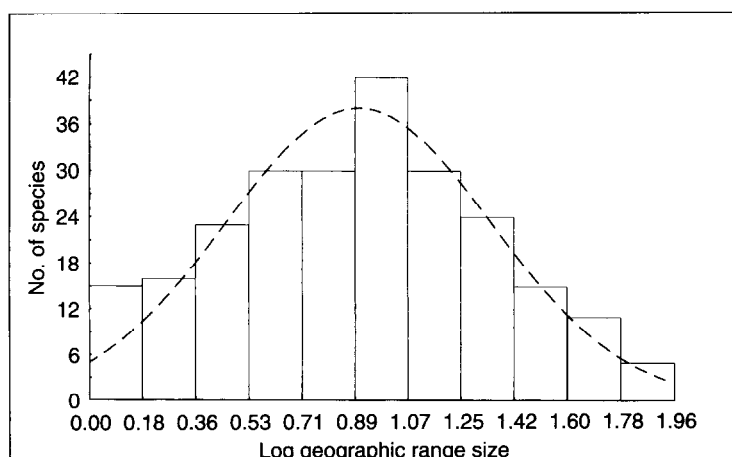

Fig. 2. Species-range-size distribution for $\log_{10}$-transformed global geographic range sizes of bumblebee species. Range sizes measured as the number of 611 000 km^2 grid squares occupied, with approximately 10% of recorded occurrences interpolated (P.H. Williams, unpublished).

Where range sizes have been expressed in terms of the numbers of sites occupied by species (more typical when considering patterns in regional occurrences than in entire geographic range sizes), range-size distributions have been found to be well described by a log-series model (e.g. Refs 22,23). Given that only a small proportion of possible sites is sampled to determine species occurrences, differences in the most appropriate models may reflect the level of sampling.

Measurement errors

Assuming constant sampling effort, species that have lower local densities will, on average, tend to be recorded from a smaller proportion of the sites at which they actually occur than species that have higher densities. Accepting that the local density of a species is genuinely positively correlated with the number of sites at which it occurs[24,25], this will mean that the occurrence of narrowly distributed species is disproportionately underestimated when compared with that of widely distributed species.

The above effect may, of course, be confounded by unequal sampling effort, or reporting, among taxa and across space. The spatial occurrences of many rare species may, in fact, be disproportionately well mapped, simply because they are rare or of particular conservation interest. Likewise, the effects of sampling effort on measures of the extents of species' occurrences may be reduced if, as is very often the case, there is a disproportionate likelihood that occurrences that extend the known extreme limits of species' geographic ranges are reported.

Temporal considerations

The spatial patterns of occurrence of few, if any, species are constant in ecological time. Rather, populations are established, undergo growth, decline and extinction. For practical reasons, it is virtually impossible to determine the spatial occurrence of a species at any given moment (except over small areas for relatively long-lived and immobile organisms, such as trees and corals) – distributional information tends, therefore, to be integrated over time. This may inflate measured range sizes, particularly for species that exhibit short generation times, high mobility or metapopulation dynamics. Such effects may differentially affect species that have a larger area of occupancy to extent of occurrence ratio; species that, at the spatial resolution of interest, are found throughout their extent of occurrence will suffer minimal inflation.

The chosen time period may also affect the observed distribution; for example, the pattern of occurrence of perhaps most organisms differs before and after major human influences.

Missing species

Species-range-size distributions may be biased because species are missing from them. This may be because data are not available about their spatial occurrences, because they remain undiscovered, or because they have recently become extinct. These effects are most likely to influence the left-hand part of the distribution. Data are least likely to be available for narrowly distributed species, and these species tend to be described later and to have greater likelihoods of extinction[26-28].

Assemblage of interest

All studies of range-size distributions to date have concerned groups of taxonomically closely related species; broader community-based analyses have not been

performed. Moreover, most studies have concerned assemblages associated with particular continents or biogeographic regions. In these cases, species with geographic ranges that extend beyond the bounds of these areas, or that have a given proportion of the areas of their ranges beyond these bounds, are often excluded. One effect of this constraint will be to limit artificially the upper boundary of the species-range-size distribution. Careful distinction needs to be made between (1) the overall species-range-size distribution of a taxonomic assemblage, (2) the distribution for those species endemic to a defined area, and (3) the distribution based on the patterns of occurrences of all the species in the assemblage but only in the defined area.

Mechanisms structuring range-size distributions

If we accept that species-range-size distributions are genuinely approximately lognormal, then what generates this pattern? From a statistical viewpoint, it simply may be regarded as an outcome of the central limit theorem and the interplay of many independent factors (see Ref. 29). However, there are other ways of viewing the issue. These have seldom explicitly been explored (but see Ref. 8), and the links between evolutionary and ecological paradigms are ill-developed.

Temporal trajectories

In the context of evolutionary time, species-range-size distributions can be seen as summarizing a slice across the temporal trajectories of the sizes of the geographic ranges of the species in an assemblage. The ranges of different species may be in phases of expansion, decline or stasis. As yet, there is no generally accepted model for the long-term (speciation to extinction) temporal dynamics of species'

geographic range sizes. While some analyses suggest that periods of increase and decrease are relatively brief, and that most time is passed close to the maximum range size achieved, others suggest that most time is spent in range-size increase, or that range sizes undergo marked oscillations through time and exhibit no repeated patterns[4,30]. The determination of any broad generalizations, should they exist, may provide an historical basis for understanding species-range-size distributions. This would necessitate, in particular, an understanding of any interactions between the form of dynamics and the mean or maximum range size that species attain over their lifespans, any long-term patterns in the interspecific mean and variance of range sizes, and temporal variation in the rates of speciation and extinction.

Speciation patterns

In a related vein, species-range-size distributions might also be regarded in terms of patterns of range division that result in speciation, with ranges of different sizes having different likelihoods of giving rise to new species. This parallels various niche-breakage models (in which resources are subdivided among species in given ways) for species-abundance distributions[31]. Evidence for which range sizes are more likely to speciate is, however, remarkably divergent. Some studies suggest that larger ranges are more likely to give rise to new species, other studies suggest that small ranges are more likely to do so[32]. Whether this reflects different aspects of a more general pattern or a taxon and/or region dependency is unclear. Nor is it obvious the extent to which an understanding of range-size distributions founded on speciation patterns would have to incorporate information on the temporal dynamics of range sizes post-speciation – curiously, temporal dynamics have not been a major concern in studies of niche-breakage models for species-abundance distributions.

Ecological determinants

At any one time, the range sizes attained by species can potentially be limited by a number of factors. These include habitat availability, dispersal and establishment abilities, competitors, predators and parasites, climatic and/or environmental tolerances and various (often very important) historical considerations. Given this variety, there is no reason for there being any significant interspecific correlation between range size and any one of these factors, thus

their use is potentially severely limited in predicting the form of species-range-size distributions. Nonetheless, positive relationships have been reported between habitat availability, habitat generalism, breadth of environmental tolerance, and dispersal ability of the species in a taxonomic assemblage and the present sizes of their geographic ranges (for reviews, see Refs 4,33,34). In many cases, the effects are weak. However, no attempt has been made to determine the proportion of variation in the range sizes of species in an assemblage that can be 'explained' by a number of different variables, although this may well be substantial; habitat abundance and/or the breadth of habitat usage alone often appear to be of major importance in determining between-species differences in range size.

The general, positive, interspecific relationship between local abundance and range size has been explained in terms of the similarity of the ecological characteristics (especially breadth of resource usage) that permit species to become locally more abundant and geographically more widespread (for discussion, see Refs 2,4,30). This suggests that similarities in species-abundance distributions and species-range-size distributions could have some common mechanistic basis, and that in some sense species-range-size distributions are simply species-abundance distributions writ large. Moreover, it emphasizes that important insights are likely to be gained by applying a population dynamic approach to modelling species-range-size distributions.

Some implications of range-size distributions

Whatever the causes, the strong right skew to species-range-size distributions has some important consequences. First, it results in a dramatic increase in the effort required to inventory regional and global faunas and floras; most species do not occur in most regions (and, at least at large spatial scales, ranges are not simply geographically nested). Equally, however, the continuum of range sizes in a taxon argues for the importance of large-scale taxonomic revisions and faunal overviews. Second, it means that the documentation of patterns of spatial turnover in species identities is crucial to an understanding of regional assemblage structure, although many basic facets of such turnover remain poorly explored. Third, it means that the composition of the assemblage with which widespread and often well-studied species interact (directly or indirectly) changes markedly across their geographic ranges. This may alter interpretation of patterns of adaptation and occurrence. Fourth, given that most species have small geographic range sizes, and that geographic range size and risk of extinction tend to be negatively correlated[4], it means that a disproportionate number of species need to be screened if those with a high likelihood of loss are to be identified.

References

1 Ricklefs, R.E. and Schluter, D., eds (1993) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, University of Chicago Press
2 Brown, J.H. (1995) *Macroecology*, University of Chicago Press
3 Fenchel, T. (1993) **There are more small than large species?** *Oikos* 68, 375–378
4 Gaston, K.J. (1994) *Rarity*, Chapman & Hall

5 Rapoport, E.H. (1994) **Remarks on marine and continental biogeography: an areographical viewpoint**, *Philos. Trans. R. Soc. London Ser. B* 343, 71–78
6 Anderson, S. (1984) **Geographic ranges of North American birds**, *Am. Mus. Novit.* 2785, 1–17
7 Anderson, S. (1984) **Areography of North American fishes, amphibians and reptiles**, *Am. Mus. Novit.* 2802, 1–16
8 Anderson, S. (1985) **The theory of range-size (RS) distributions**, *Am. Mus. Novit.* 2833, 1–20
9 Anderson, S. and Marcus, L.F. (1992) **Areography of Australian tetrapods**, *Aust. J. Zool.* 40, 627–651
10 Rapoport, E.H. (1982) *Areography: Geographical Strategies of Species*, Pergamon
11 Letcher, A.J. and Harvey, P.H. (1994) **Variation in geographical range size among mammals of the Palearctic**, *Am. Nat.* 144, 30–42
12 Stevens, G.C. (1989) **The latitudinal gradient in geographical range: how so many species coexist in the tropics**, *Am. Nat.* 133, 240–256
13 Pagel, M.D., May, R.M. and Collie, A.R. (1991) **Ecological aspects of the geographical distribution and diversity of mammalian species**, *Am. Nat.* 137, 791–815
14 Macpherson, E. and Duarte, C.M. (1994) **Patterns in species richness, size, and latitudinal range of East Atlantic fishes**, *Ecography* 17, 242–248
15 Ruggiero, A. (1994) **Latitudinal correlates of the sizes of mammalian geographical ranges in South America**, *J. Biogeog.* 21, 545–559
16 Rohde, K., Heap, M. and Heap, D. (1993) **Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness**, *Am. Nat.* 142, 1–16
17 Smith, F.D.M., May, R.M. and Harvey, P.H. (1994) **Geographical ranges of Australian mammals**, *J. Anim. Ecol.* 63, 441–450
18 Roy, K., Jablonski, D. and Valentine, J.W. (1994) **Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for Rapoport's rule**, *Proc. Natl Acad. Sci. USA* 91, 8871–8874
19 Schoener, T.W. (1987) **The geographical distribution of rarity**, *Oecologia* 74, 161–173
20 Maurer, B.A. (1994) *Geographical Population Analysis: Tools for the Analysis of Biodiversity*, Blackwell
21 Hollander, A.D., Davis, F.W. and Stoms, D.M. (1994) **Hierarchical representations of species distributions using maps, images and sighting data**, in *Mapping the Diversity of Nature* (Miller, R.I., ed.), pp. 71–88, Chapman & Hall
22 Buzas, M.A. *et al.* (1982) **On the distribution of species occurrence**, *Paleobiology* 8, 143–150
23 Buzas, M.A. and Culver, S.J. (1991) **Species diversity and dispersal of benthic Foraminifera**, *BioScience* 41, 483–489
24 Brown, J.H. (1984) **On the relationship between abundance and distribution of species**, *Am. Nat.* 124, 255–279
25 Gaston, K.J. and Lawton, J.H. (1990) **Effects of scale and habitat on the relationship between regional distribution and local abundance**, *Oikos* 58, 329–335
26 Mace, G.M. (1994) **An investigation into methods for categorizing the conservation status of species**, in *Large-scale Ecology and Conservation Biology* (Edwards, P.J., May, R.M. and Webb, N.R., eds), pp. 293–312, Blackwell
27 Gaston, K.J., Blackburn, T.M. and Loder, N. (1995) **Which species are described first?: the case of North American butterflies**, *Biodiv. Conserv.* 4, 119–127
28 Patterson, B.D. (1994) **Accumulating knowledge on the dimensions of biodiversity: systematic perspectives on Neotropical mammals**, *Biodiv. Lett.* 2, 79–86
29 May, R.M. (1975) **Patterns of species abundance and diversity**, in *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 81–120, Harvard University Press
30 Lawton, J.H. (1993) **Range, population abundance and conservation**, *Trends Ecol. Evol.* 8, 409–413
31 Tokeshi, M. (1993) **Species abundance patterns and community structure**, *Adv. Ecol. Res.* 24, 111–186
32 Chown, S.L. **Speciation and rarity: separating cause from consequence**, in *The Biology of Rarity* (Kunin, W.E. and Gaston, K.J., eds), Chapman & Hall (in press)

33 Kunin, W.E. and Gaston, K.J. (1993) **The biology of rarity: patterns, causes and consequences,** *Trends Ecol. Evol.* 8, 298–301

34 Gaston, K.J. and Kunin, W.E. **Rare–common differences: an over-view,** in *The Biology of Rarity* (Kunin, W.E. and Gaston, K.J., eds), Chapman & Hall (in press)

35 Pomeroy, D. and Ssekabiira, D. (1990) **An analysis of the distributions of terrestrial birds in Africa,** *Afr. J. Ecol.* 28, 1–13

36 Gaston, K.J. **What is rarity?** in *The Biology of Rarity* (Kunin, W.E. and Gaston, K.J., eds), Chapman & Hall (in press)

37 Williamson, M.H. and Lawton, J.H. (1991) **Fractal geometry of ecological habitats,** in *Habitat Structure: the Physical Arrangements of Objects in Space* (Bell, S.S., McCoy, E.D. and Mushinsky, H.R., eds), pp. 69–86, Chapman & Hall

38 Maurer, B.A. and Heywood, S.G. (1993) **Geographic range fragmentation and abundance in Neotropical migratory birds,** *Conserv. Biol.* 7, 501–509

39 Virkkala, R. (1993) **Ranges of northern forest passerines: a fractal analysis,** *Oikos* 67, 218–226

40 Gautestad, A.O. and Mysterud, I. (1994) **Fractal analysis of population ranges: methodological problems and challenges,** *Oikos* 69, 154–157

Reference added in proof

41 Blackburn, T.M. and Gaston, K.J. (1996) **Spatial patterns in the geographic ranges of bird species in the New World,** *Philos. Trans. R. Soc. London* (in press)

Inbreeding avoidance in animals

Anne Pusey and Marisa Wolf

Inbreeding depression has been extensively documented in captive animals, and progress has been made in understanding its causes (Box 1). However, data on inbreeding depression under natural conditions have been very slow to accumulate. Inbreeding between closely related animals is difficult to detect in the field because it is rare in many species and also because the frequent occurrence of mating with multiple partners means that genetic techniques are often necessary to detect truly inbred offspring. Although there seems little reason not to extrapolate from data on captive animals, given the mechanisms involved in inbreeding depression, this paucity of field data has led some to question the strength of inbreeding depression as a selective force for the evolution of inbreeding avoidance mechanisms[12,13]. Table 1 gives several examples of the costs of inbreeding in natural populations. While differing in rigor of measurement, some of these examples indicate strong inbreeding depression, and three recent examples suggest that inbreeding depression may be underestimated in captivity. Inbred and outbred land snails (*Arianta arbustorum*)[22] and white-footed mice (*Peromyscus leucopus noveboracensis*)[23] were released into the field and their survival compared. Inbred individuals showed markedly lower survival, and the magnitude of the difference in survival between inbred and outbred individuals was much larger in the field than under laboratory conditions. In another study of an island population of song sparrows in which inbreeding coefficients were known from pedigrees, inbred individuals showed much lower survival than outbred individuals during a population crash caused by severe winter weather[21]. These studies illustrate both inbreeding depression and the influence of ecological factors on its severity (see also Refs 5,7).

Inbreeding depression will also be underestimated unless the lifetime performance of progeny is measured.

The phenomenon of inbreeding depression is well documented and behavioral adaptations for inbreeding avoidance have been described. However, there is debate over whether inbreeding depression is always an important selective force on behavior. Here, we summarize recent evidence for inbreeding depression under natural conditions, review inbreeding avoidance mechanisms, and discuss how these are influenced by social structure. We also examine the idea that animals have evolved mechanisms to avoid outbreeding.

Anne Pusey and Marisa Wolf are at the Dept of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St Paul, MN 55108, USA.

Some have suggested that inbred offspring that survive increased juvenile mortality may be fitter than outbred offspring[3,12], but although inbreeding depression may be expressed most strongly in early life stages, inbreeding also produces such deleterious consequences for adults as sperm deformities[18], sterility[5] and decreased courtship frequency[4], and inbreeding depression usually increases as more lifestages are included.

Table 1 indicates considerable variation in the severity of inbreeding depression, between species and between populations, and this is also found in captive studies. Ralls and Ballou[2] examined the effect of inbreeding on juvenile mortality in 40 populations of captive mammals and found an average inbreeding cost for first degree relatives ($r = 0.5$) of 0.33, but a range of -0.1–1.0 with no peak around the mean. Variation between taxa may be influenced by the particulars of their genetics. For example, inbreeding has a dramatic effect in some Hymenoptera because of their particular mechanism of sex determination[24]. Another source of variation in the severity of inbreeding depression between and within species is the inbreeding history of the population. When inbreeding is persistent, there is some evidence that inbreeding depression becomes less severe. This is attributed to the unmasking and purging of severely deleterious recessive alleles[5,6]. However, it is unlikely that purging can be so complete that inbreeding depression is only a temporary phenomenon. Purging of slightly deleterious mutations under moderate selection through inbreeding is less effective and fixation of such alleles is likely to occur through Müller's ratchet[1,5,6]. Inbreeding depression is still found in habitually selfing plants[1,5]. Among animals, habitually inbreeding social spiders have much smaller egg masses and lower juvenile survival than their outbred congeners, and this has been ascribed to inbreeding depression[25]. So the extent to which inbreeding reduces