Population Dynamic Principles [and Discussion]

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Population dynamic principles

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SUMMARY

Although the causes of population extinction, locally and globally, are many, varied and idiosyncratic when individual species are considered, there are nevertheless some basic general constraints and ground rules that make some species more extinction-prone than others. This paper reviews their implications for the ultimate and proximate causes of extinction. Phenomena reviewed include: a positive correlation between local abundance and size of geographic range, putting some populations in 'double jeopardy'; smaller average range sizes in the tropics; metapopulation dynamic processes that can spread risk, but only if the spatial correlation between fluctuations of conspecific populations is low; the influence of body size and trophic position; and phylogenetic constraints on range sizes and abundance.

1. INTRODUCTION

The death of an individual, a population, or an entire species can have many causes, even if one ultimately delivers the *coup de grâce*. Are there, however, general rules and constraints that may help us better understand rarity and extinction?

Simberloff (1986) and Caughley (1994) both provide succinct reviews of the literature on extinctions, and seek to draw some general conclusions. It is useful, for example, to draw a distinction between processes that make populations rare in the first place (what Simberloff calls the 'ultimate causes of extinction', and Caughley refers to as 'the declining population paradigm') and processes that may finally cause extinction, once populations are small (Simberloff's 'proximate causes', and Caughley's 'small population paradigm'). Proximate causes are why small populations still die out, even when protected. They are generally agreed to include demographic and environmental stochasticity, genetic deterioration, and social dysfunction, although the relative contributions of these four harbingers of doom are not well understood.

Ultimate causes of extinction – why species are, or become, rare in the first place – are a different matter. Throughout human history, formerly widespread and abundant species have been made rare and vulnerable to the proximate causes of extinction by hunting, habitat destruction, and pollution. Some species are naturally rare (many island endemics, for example), although they too may be made even rarer by man. It is currently unclear whether naturally rare and anthropogenically rare species differ in fundamental ways to the risks of extinction from proximate causes. I touch on this problem at the end of the paper.

It is not my intention to repeat existing reviews of the four proximate causes of extinction. Instead, I will review a number of less familiar, and sometimes contentious, issues that may contribute to both ulti-

mate and proximate causes. I am particularly concerned to see if there are general patterns and rules that may make particular taxa, in particular places, more or less prone to rarity and ultimately to extinction. I have not, generally, made a distinction between the local extinction of populations and the global extinction of species; 'there is no fundamental distinction to be made between the extinction of a local population and the extinction of a species other than . . . the species becomes extinct with the extinction of the last local population' (Andrewartha & Birch 1954, p. 665.)

2. POPULATION ABUNDANCE AND GEOGRAPHIC RANGE

(a) *Local abundance and size of range*

Rarity, which predisposes populations or entire species to extinction via proximate causes, is actually a rather complicated phenomenon; there are several ways of being rare (Rabinowitz 1986), involving both the size of a species' geographic range, and population abundance within that range. Interestingly, on average, population abundances and species' geographic ranges are not independent entities (Hanski 1982; Brown 1984; Lawton 1993). Within particular taxa and geographic regions, species with large ranges tend to have greater local abundances at sites where they occur than do geographically more restricted species. Examples include plants, birds mammals, fish and a variety of invertebrates from molluscs and mites to zooplankton and insects (Gaston & Lawton 1990). There is usually considerable unexplained variation in these plots, so that an individual species can be widespread but rare everywhere, or locally common but with a small total geographic range (Rabinowitz 1986). Nevertheless, the general pattern appears to be robust, despite problems with definitions of geo-

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graphic range (Gaston 1991), concerns about sampling artefacts, and occasional negative correlations (Gaston & Lawton 1990) that occur under somewhat unusual circumstances (see Lawton (1993) for a brief discussion of these problems).

Despite its theoretical and practical interest, the positive correlation between range and abundance is not well understood. Theoretically, there are a number of ways in which such a correlation might be generated (Lawton 1993; Hanski *et al.* 1994). The simplest, proposed by Brown (1984), is that species able to exploit a wide range of resources (species with 'broad niches') become both widespread and locally abundant. Several metapopulation dynamic models also predict positive correlations between geographic range measured as the number (or proportion) of patches occupied and population density within patches (Gyllenberg & Hanski 1992). Positive correlations in these models are a product of the 'rescue effect' (immigration reduces the risk of local extinction), mortality during migration, and difficulties in establishing new populations.

A broadly positive correlation between size of range and population abundance carries two important messages when assessing extinction risks. First, all else being equal, species that are most at risk from proximate causes are those with small geographic ranges, because they will, on average, also be locally rare, even in areas where they occur. Nature has double jeopardy built into her game plan.

Second, this double jeopardy may be particularly serious when populations and ranges are artificially reduced and threatened by ultimate causes of extinction. Reductions in range, via habitat destruction or extirpation by hunting, ought eventually to result in a reduction in population density in surviving populations, even when protected. Reversing these arguments, overall reductions in population density (e.g. by pollution, hunting or, for migrants, problems on the wintering grounds) should result in correlated reductions in range size, in the absence of any habitat destruction. These empirical predictions are confirmed by metapopulation dynamic models (see, for example, Lande 1991; Gyllenberg & Hanski 1992; Lawton *et al.* 1994) but they are not easily derived from Brown's explanation for the positive correlation between range and abundance, and I know of no unequivocal experimental tests. I find it remarkable that such an important problem has not attracted more experimental and practical attention.

(b) *Tropical versus temperate ranges and abundances*

A second empirical pattern that may influence extinction risk is an apparent decline in the average sizes of species' ranges within comparable taxa, as one moves from higher to lower latitudes (Rapoport 1982). Stevens (1989) documents declines in range size towards the tropics for groups as diverse as trees, molluscs, fish, amphibians and reptiles, and mammals (although not all recent analyses confirm the pattern:

see, for example, Ricklefs & Latham (1992); see Lawton *et al.* (1994) for a brief review).

A decline in average range sizes from the poles to the tropics need not, of course, mean that average local population abundances of comparable taxa are also lower in the tropics; too many other key variables change along this same gradient. It is therefore intriguing that latitude alone explains 46.7% of variation in population densities in a major compendium of data assembled by Currie & Fritz (1993). Average population densities increase linearly from the equator towards the poles in invertebrates, ectothermic vertebrates, mammals and birds. At any one latitude, densities range over four or more orders of magnitude within these groups, but the overall trend is clear and consistent with a decline in range sizes towards the tropics.

Taken at face value, both trends must make tropical taxa more prone to extinction from human activities, particularly habitat destruction, compared with equivalent temperate taxa. Starkly, clearing $1000\ km^2$ of tropical forest will, on average, pose a much greater threat of extinction to inhabitants living at low average densities, in small ranges, than clearing an equivalent area of temperate forest; of the 1029 species of birds in the world listed in Rands (1991) as threatened with global extinction, 442 live in tropical forests, more than twice as many as in the next most important habitat, wetlands (although many other factors also contribute to this depressing statistic).

3. VARIATIONS IN ABUNDANCE WITHIN GEOGRAPHIC RANGES

(a) *Textures of abundance*

One reason why the correlation between size of geographic range and local abundance is fuzzy is that species are not evenly distributed throughout their range (Brown 1984; Wiens 1989). Very crudely, densities are often envisaged as being greatest near the centre of a range, and least near the boundaries (see, for example, Hengeveld & Haeck 1982). In practice, textures of distribution and abundance are often more complex than a gradual decline from the centre to the edge of the range, with multi-modal patterns of abundance being common and perhaps even the norm (Taylor & Taylor 1979; Brown 1984; Root 1988; Wiens 1989).

Because average abundances vary across species' ranges, it follows that one or more of the key demographic rates (birth, death, immigration and emigration) also change across the range, in response to changes in environment and resources (Richards 1961; Huffaker & Messanger 1964). Some recently documented examples are provided by Randall (1982), Rogers & Randolph (1986) and Caughley *et al.* (1988). At some point close to the range boundary, rates of population increase from low densities (r) must on average be zero. Beyond the point where $r = 0$, 'sink populations' (Pulliam 1988) with negative average r may be sustained by immigration from

'source populations', in which overall population performance (but not necessarily density) is higher.

(b) Implications for extinction

One interesting consequence of variations in population processes across a species' range is that attempts to restore populations by reintroductions into historical, but currently unoccupied, parts of a range are less likely to fail (the reintroduced population is less likely to become extinct) in the core of the former distribution than on its periphery or beyond it. Consistent with this prediction, 76% of 133 documented translocations (reintroductions) of birds and mammals into former core areas succeeded, compared with 48% of 54 translocations to the periphery or beyond (Griffith *et al.* 1989).

It also follows that wholesale persecution or habitat destruction may leave isolated populations of high conservation importance in marginal habitats. Relict populations of bontebok (*Damaliscus dorcas dorcas*), an antelope, in the fynbos of Cape Province, South Africe (van Wilgen *et al.* 1992) and of red kites (*Milvus milvus*), a raptor, in south–central Wales on the very edge of its European range (Cramp & Simmons 1980) are good examples. Such populations may have very low rates of increase (well below that which the species can achieve in better habitat), making their survival even more precarious. *In extremis* some populations may persist only because of immigration from the core; destruction of the source guarantees the ultimate extinction of the sink population, making its conservation impossible (Harrison *et al.* 1988; Harrison 1991).

Finally, as noted in §2, if overall population numbers decline because of falling birth rates or rising death rates, we expect ranges to contract anyway, even in the absence of habitat destruction. If the original range had a single, well-defined centre, ranges should collapse towards that core; if there were originally multiple modes, contraction and fragmentation into former 'hot spots' seems more likely.

For reasons that are not entirely clear, there have been rather few attempts to document and link patterns of population decline with changes in species' distributions (Hengeveld 1989). A drastic decline during the 20th Century by British populations of a skipper butterfly, *Hesperia comma*, left a scattered and highly fragmented population in 46 or fewer refugia by the mid-1950s (Thomas & Jones 1993). However, as Wilcove & Terborgh (1984) show for some North American birds, range fragmentation does not always accompany decline. The highly endangered Kirtland's warbler (*Dendroica kirtlandii*) withdrew to the historical centre of its range, leaving peripheral areas virtually empty, as populations collapsed by 60% between 1961 and 1971.

Which type of range decline poses the greater threat of ultimate extinction? Fragmentation and isolation may exacerbate population declines in remaining areas via metapopulation processes; contraction towards a single core area may avoid these problems but puts all the conservation eggs into one geographical basket. A growing body of data and theory addresses the problems of extinction risk in a few large (in the limit, one) and many small, fragmented populations, and it is to these questions that we now turn.

(c) Extinction risks in one to few large against many small populations

Imagine two species with identical total numbers of individuals. One (call it A) occurs as a single, large, panmictic population, the other (B) as a series of separate, fragmented populations. Which is most vulnerable to the proximate causes of extinction (Pimm 1993)? There is no simple answer, and indeed only vaguely useful contingent answers. It depends, amongst other things, on the extent to which populations of B are isolated from one another, and the degree to which chance events strike populations of B independently or in synchrony (their spatial correlation).

If B's fragmented populations are totally isolated, then each is, on average, more vulnerable than the large population of A to the four causes of proximate extinction (Soulé 1987; Bengtsson 1993); however, it is unclear without knowing a great deal more about the system whether all the populations of B will die out before A. A counter-argument, for example, is that a major catastrophe, such as disease or fire, may sweep through the range of A and wipe it out, whereas isolated populations of B may escape and survive for a time. More generally, catastrophies reduce the numerical advantages A has over populations of B (Mangel & Tier 1993). So there is no simple answer.

Total isolation is, however, extreme. Usually, metapopulations enjoy some exchange of individuals, allowing small populations of B to be 'rescued', and those that go extinct to re-establish via immigration. Is it now better to be A than B? Fragmentation into metapopulations increased extinction probabilities for laboratory stocks of *Drosophila pseudobscura* and *D. hydei* (Forney & Gilpin 1989), and model populations reveal broadly similar results when extinctions are primarily due to demographic stochasticity (Burkey 1989). However, if environmental stochasticity is large and spatially uncorrelated, it may favour B, rather than A (Burkey 1993), because fragmentation spreads risk (den Boer 1981). (Note that no models currently incorporate the effects of fragmentation with all four causes of proximate extinction; if they did, genetic effects and social dysfunction could override the benefits of spreading of risk in metapopulations.)

A major problem in this debate is lack of knowledge about synchrony of fluctuations, driven by environmental stochasticity, in spatially separated conspecific populations. Increasing spatial synchrony decreases the expected lifetime of metapopulations (by reducing risk spreading and thus making the separate populations of B behave, in aggregate, more like A) (see, for example, Harrison & Quinn 1989). This problem has recently been reviewed and addressed by Hanski & Woiwod (1993), who show that, for British moths and aphids, spatial synchrony between conspecific populations declines, as expected, with increasing distance between them, but synchrony remains positive at all

distances up to 800 km. Spatial synchrony is itself positively correlated with temporal variability in local populations (except in geometrid moths); that is, the more similar fluctuations of conspecific populations are in space, the larger they are in time.

We may tentatively draw three conclusions. First, fragmented populations will have to be separated by many hundreds of kilometres before they can be guaranteed to fluctuate independently in response to environmental stochasticity. Second, those populations most at risk from environmental stochasticity (i.e. those that fluctuate most) are apparently also at greatest risk of regional extinction because they show the greatest spatial synchrony; here is another double jeopardy. Third, because spatial synchrony decreases the expected lifetime of metapopulations, risks of extinction are probably lower in a few large populations than in many small ones. Risks of inbreeding and social dysfunction are also lower in larger populations. Given a choice, current evidence therefore suggests that it is better to have all our population eggs in one or a few large geographical baskets (A) than many smaller ones (B).

(d) Biology interacts with populations to change spatial patterns

It is unlikely that patterns of population decline and fragmentation are independent of the details of species' life histories and breeding systems. Is there any evidence, for instance, that some species have attributes that favour the persistence of very isolated populations, reducing the likelihood of extinction? Quinn *et al.* (1994) analysed the U.K. distributions of 139 species of scarce native British plants, mapped on a scale of 10 km × 10 km. The species examined occurred in 16–100 of these '10 km squares'. Quinn *et al.* refer to occupied 10 km squares as 'loci', because they are not strictly populations. Nevertheless, in the absence of any better information, the distributions of loci are instructive.

The loci of all 139 species are more aggregated than expected by chance, but some are more aggregated than others. Not surprisingly, habitat plays a significant role in determining patterns of aggregation at this scale, but so do two attributes of the plants themselves.

Species with seeds adapted for long-distance dispersal have less strongly aggregated loci than species with more feeble dispersal abilities, consistent with metapopulation dynamic theory. In other words, fragmentation and isolation of populations poses a greater threat of extinction for species with poor dispersal abilities than for good dispersers, and it is the most isolated populations that go first.

More unexpectedly, obligate cross-pollinated plants have very few weakly aggregated species; they mainly have strongly aggregated loci. In contrast, species that can self-pollinate frequently have loci that are weakly aggregated. It is surprising that this result shows up at such a coarse scale, but it is consistent with the hypothesis that isolation of obligate outcrossers reduces their chance of reproductive success (Kunin

1992). Self-compatible plants may establish, and persist in, very isolated localities.

A recent survey of the literature by Kunin & Gaston (1993) suggests that locally rare and geographically restricted species in many other taxa, from mosses and vascular plants to protozoa, insects and mammals, may have characteristics that differ from commoner relatives, including lower levels of self-incompatibility, and poorer dispersal abilities. As in Quinn *et al.*'s study, some of these characteristics may contribute to, and exacerbate, one or more aspects of rarity, whereas others promote the persistence of rare populations. Whether any can be viewed as evolved adaptations to rarity (Kunin & Gaston 1993), and whether there are any differences between the characteristics of naturally rare against anthropogenically rare species, is a much more difficult question. I return to the problem briefly in the final section.

Summarizing, extant patterns of species' distributions – where populations persist after human impacts – are not immutable echoes of former ranges. Nor do all species react in the same way to similar abuses. Current ranges reflect biology and history, with some taxa apparently more prone to local, regional and ultimately global extinction than others.

4. BODY SIZE AND TROPHIC POSITION

In a search for useful indicators of vulnerability to extinction, adult body size and trophic position might appear to offer some predictive power, at least for animals. Body size and trophic position are clearly correlated, but not perfectly, and common sense suggests that the ultimate causes of extinction driven by human activities differentially threaten larger herbivores and predators.

Unexpectedly, for birds at least, body size (from 10 g to 10 000 g) has no power to predict rates of population increase or decline in a global sample of threatened species from 12 families occupying various trophic levels (Green & Hirons 1991). I find these results surprising, and counter-intuitive; it would be interesting to repeat the analyses controlling for generation time and taxonomy.

(a) Body size as a predictor of proximate causes of extinction

Can we do better with the proximate causes of extinction? For example, if populations of two species differing in body mass by an order of magnitude both contain equal numbers of a few individuals, or if the two species are confined to a fixed area at natural densities, which population is most likely to persist, the larger- or the smaller-bodied one?

Again, there is no universally agreed answer, although the theoretical framework is reasonably well understood. Other things being equal, population persistence is more likely when average population size is large rather than small; when fluctuations in numbers are small, not large; and when recovery from low numbers is fast rather than slow. All these characteristics can be correlated with body size, but

not necessarily in ways that act consistently to either promote or reduce the risk of extinction, and not apparently in ways that are consistent across all taxa and body sizes. Space precludes a thorough summary of a complex literature, but some of the more pertinent points are as follows.

Although on a scale from invertebrates to whales, small-bodied species occur at higher average population densities than large-bodied species, densities vary by several orders of magnitude in organisms of one body size, and, within local assemblages and communities, body size usually explains none, or virtually none, of the observed variation in average population numbers (Blackburn *et al.* 1993; Blackburn & Lawton 1994). A knowledge of body size alone does not, therefore, allow us to predict which species will be vulnerable to extinction because they occur at low densities. We need to know numbers.

Second, although population variability seems a relatively easy concept, measuring it correctly is not simple (McArdle *et al.* 1990); links between observed variation in numbers and risk of population extinction are far from straightforward (McArdle & Gaston 1993); and population variability itself is correlated with body size in complex ways, both theoretically and empirically (Gaston & Lawton 1988; Pimm 1991; Sutherland & Baillie 1993). The best we can say is that, on present evidence, and with some exceptions, populations of large-bodied species fluctuate less on an annual basis than smaller-bodied taxa (see Pimm (1991) for a review), making large-bodied species less likely to fluctuate unexpectedly to extinction in the short term.

One consequence of this broad generalization is that small, isolated populations of insects, endangered butterflies, for example, are much more likely to fluctuate to extinction than equally isolated populations of birds of similar average population size, even when afforded maximum protection. Within more closely related taxa, populations of large-bodied species also appear less extinction-prone than related, small-bodied species, including *Daphnia* (Bengtsson 1993), shrews in the genus *Sorex* (Peltonen & Hanski 1991), and possibly some birds (Gotelli & Graves 1990).

However, more complex patterns have been claimed for local extinctions of birds on U.K. islands (Pimm *et al.* 1988). This latter analysis suggests that, below a population size of about seven breeding pairs, the probability of extinction is smaller for large-bodied species than small-bodied species, with the risks reversing in larger populations. A reanalysis does not confirm this result (Tracy & George 1992); I have sympathy and disagreements with both sides of this debate, and believe that the matter is still unresolved.

(b) *Trophic position*

Vulnerability to local extinction is unlikely to be independent of where species fit into food chains. For example, simple models predict that populations at the top of long food chains are more likely to become extinct than those at lower levels in the noisy, real

world (Pimm & Lawton 1977); and that intermediate species that suffer both predation and competition from higher-level 'omnivorous' predators are vulnerable to extinction (Pimm & Lawton 1978; Polis *et al.* 1989). Both predictions have some support (see, for example, Spiller & Schoener 1990; Jenkins *et al.* 1992). Pimm (1991) reviews the whole problem of how trophic position may influence population dynamics and persistence.

The problem is to distinguish trophic position per se from other confounding variables, not least body size (which tends to be bigger at higher trophic levels in predator food chains), and other natural history details (some of which will also be correlated with body size). The prediction that higher trophic levels are more vulnerable to environmental stochasticity, for example (see previous paragraph), appears inconsistent with the claim for greater population persistence in larger-bodied species (made in § 4a), unless other things are factored out. Data and experiments that address these problems are very few.

One pioneer experiment bears examination. In small aquatic microcosms with protozoan predators and bacterial prey, involving various combinations of species in food webs of different complexity, prey became extinct more often than predator populations, and extinctions were associated with increasing species richness (Lawler 1993). However, these results were sensitive to exactly which species were in the microcosms; as Lawlor notes, the characteristics of individual species matter as much as the abstract trophic web in which they sit.

Perhaps for these reasons, and contrary to expectations, it has proved extremely difficult to detect a consistent tendency for differential extinction of species at higher trophic levels, either in the fossil record (Jablonski 1986) or as a consequence of habitat fragmentation in extant communities (Mikkelson 1993, and references therein). Mikkelson's analyses suggest that all trophic levels lose species *pro rata*, so that proportions of species in different trophic categories remain constant as diversity falls.

5. PHYLOGENETIC CONSTRAINTS

Two of the most important variables that determine risks of extinction, namely population density and size of geographic range, are usually thought of as labile attributes of species set by processes operating in ecological time; however, there are also poorly understood, intriguing hints of effects operating in evolutionary time. Obviously, individuals, not species, are the units of selection; nevertheless, data now exist suggesting that both range and abundance are persistent, species' characteristics. The idea is implicit in Brown's hypothesis (1984), which links local abundance and size of range to a complex, elusive, albeit obviously evolved characteristic of species, namely fundamental niche breadth. One implication of these studies is that some taxa are more extinction-prone than others.

The data are summarized by Lawton (1993). One group of studies centres on the 'taxon cycle' for birds

on West Indian islands (Ricklefs & Cox 1978; Ricklefs 1989). Among passerines, putatively older taxa occur on fewer islands, have more restricted habitat distributions, and tend to have reduced population densities. They would appear to be particularly sensitive to human impacts.

A second group of studies also involves birds, and finds quite unexpected phylogenetic effects on patterns in species' abundances as a function of body size. Briefly summarizing a complex literature, body size: abundance plots for species within individual tribes of birds show significantly more positive relations than expected (large-bodied species are commoner than small-bodied species) in taxonomically more ancient tribes (Cotgreave & Harvey 1991; Nee *et al.* 1991; Blackburn *et al.* 1994). This pattern is not well understood, but at least in part it could be the product of differential extinctions of large-bodied, rare species over long periods of time (although this suggestion sits uncomfortably with some of the data and theory discussed in § 4).

Plants also provide evidence for phylogenetic effects on distribution and abundance. Rare North American plants (loosely defined by range, local abundance, or both) are significantly over-represented in certain families (Scrophulariaceae, Lamiaceae) and under-represented in others (Rosaceae) (Schwartz 1993). More unexpectedly, disjunct taxa within extant genera of herbaceous perennial plants, relict in temperate eastern Asia and eastern North America, have significantly correlated range sizes, implying stasis in genus-level attributes determining distributions that have been stable for at least 10 Ma (Ricklefs & Latham 1992). Unfortunately, we have no idea what characteristics of these taxa promote commonness or rarity.

Phylogenetic constraints on range sizes have also been reported for animals. Individual species of bivalves and gastropods from late Cretaceous fossil assemblages in North America achieved characteristic range sizes relatively early in their history; once evolved, species' range sizes changed relatively little. Moreover, pairs of closely related species have statistically similar range sizes (Jablonski 1987). Again, why this should be is unclear, but the fossil record also shows that locally endemic species with small geographic ranges have a much higher chance of extinction than more cosmopolitan genera (Raup & Jablonski 1993).

If we accept that these patterns are real (which is not certain), they mean two things. First, some taxa (genera, tribes, families) are more extinction-prone than others, but we have no idea why. Second, species phylogenetically predisposed to low population densities and small geographic ranges will be unusually vulnerable to the ultimate causes of extinction, in the form of exploitation and habitat destruction. Paradoxically, however, they may also be less prone to the proximate causes of extinction because they are pre-adapted to life as small populations on isolated reserves, compared with formerly more abundant and widespread species (see also Kunin & Gaston (1993), and § 3*d* above). The problem deserves more urgent attention.

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Discussion

G. DAILY (*University of California, Berkeley, U.S.A.*). As Professor Lawton indicates, the influence of body size on a species' vulnerability to extinction is complex and poorly understood. One potentially important factor is interspecific social status, often well correlated with body size. It appears that in some groups of organisms where interference competition for common resources operates, high social status confers an advantage in persisting in human-controlled habitat. This observation has been made in a few, but none the less interesting and important, communities, e.g. some ants, birds, and geckos. To the extent that social status is correlated with body size, this observation suggests a conter-intuitive policy implication. In groups where interference is important, large tracts of habitat may be required to support the smaller-bodied species.

I. NEWTON (*Institute of Terrestrial Ecology, Monks Wood, Cambridgeshire, U.K.*). Professor Lawton referred to the 'double jeopardy' of low numbers and restricted range. But many animals, notably birds and fish, often have two ranges in different parts of the world, using one for breeding and the other for 'wintering'. In some respects, such species may face twice the extinction risks of year-round residents, because they are vulnerable to adverse events on both breeding and wintering areas (and in some species also on migration routes). For example, recent declines in some European birds have been linked to detrimental changes in their African wintering areas. In what ways does Professor Lawton think that we could take migration considerations into account in assessing the extinction risks for such mobile animals?

J. H. LAWTON. I believe that migratory species will be doubly vulnerable to habitat losses and population declines on their breeding grounds and on their wintering grounds. They may also be vulnerable to these pressures whilst on migration.