Thus, selection on genital anatomy of both sexes may be similar to that producing sperm competition. Dewsbury[23] suggested a very similar scenario in regard to copulatory behavior, and it seems reasonable to regard the anatomy and behavior of copulation as a functional unit.

The vaginal code/tumblers hypothesis is easily converted to an intraspecific context, which may explain why attempts to identify the vaginal codes of vole species yielded identifiable but not exclusive copulatory modes[24–26]. Eberhard[2] observed that in insects, anatomical differences *per se* do not prevent nonconspecifics from copulating; this is also the case in mammals.

The concept of intraspecific selection on anatomical, physiological and neural/behavioral features presents at least as valid a context for hypotheses of genital evolution in mammals as the interspecific context. There may even be a continuum from wholly interspecific, exclusionary model to a completely intraspecific, internally selective one. This broad concept may offer a superior context for formulating and testing hypotheses, per species, than the current array allows.

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Range, Population Abundance and Conservation

John H. Lawton

Several patterns in the distribution and abundance of organisms have now been documented. They include broad (but not universal) positive correlations between range sizes and population abundances; a decline in the proportion of sites occupied and in average population densities from the centre to the edge of a species' range, with either unimodal or multimodal peaks of abundance and occupancy in the core of the range; and intriguing, but still poorly documented phylogenetic effects on both range size and abundance. All these patterns require further work to establish their generality, and all of them lack generally agreed explanations. They are important, however, not only theoretically but also practically, because of the constraints and opportunities they appear to provide for the management and conservation of species.

The abundance of species and the size of the area over which they are recorded (i.e. the size of their geographic range) are not indepen-

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dent[1,2]. Within particular taxa, species occurring over large geographic areas tend to have greater local abundances at sites where they occur than do geographically more restricted species. Examples include plants, birds (Fig. 1a), mammals, fish and a variety of invertebrates from molluscs and mites to zooplankton and insects[3–6]. Knowledge of the phenomenon has a long pedigree; in 1922 the botanist J.C. Willis noted that localized species were often rare within their limited geographic ranges[7].

There is usually considerable unexplained variation in these plots, so that an individual species can be widespread but rare everywhere, or locally common despite having only a small total geographic range[8]. Nevertheless, the average trends are important for conservation because they warn that geographically restricted taxa tend also to have small local populations, potentially making them doubly vulnerable.

Despite its theoretical and practical interest the pattern is not well understood. There are some *inverse* relationships (e.g. Fig. 1b), and a minority of studies report no correlation[3] (although given the nature of much of the data, this is no great surprise). There are also technical problems in defining exactly what is meant by size of geographic range. A thoughtful discussion on terminology is provided by Gaston[5]. I will use some of his ideas later. Concern has also been expressed that the correlation is a statistical artifact, because species with low average population densities are
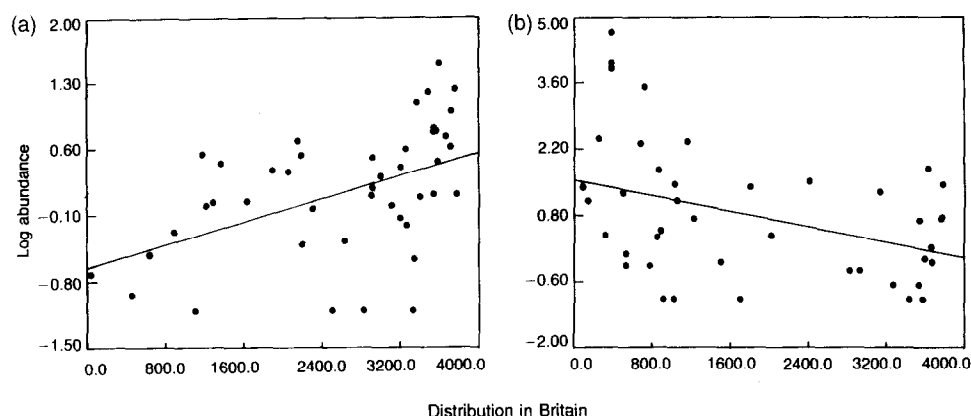
Fig. 1. (a) Example of a typical positive correlation between local abundance and size of geographic range for British breeding birds. Abundances are average number of singing territorial males in Eastern wood, a 16 ha oak wood in south east England, between 1949 and 1975 (excluding 1957). Distribution in Britain is the total number of 10 km squares with possible, probable or confirmed breeding in Britain and Ireland[47] ($r = 0.48$; $p < 0.001$). (b) A more unusual negative correlation between the number of breeding pairs of birds on Handa island, between 1976 and 1984, and geographic range in Britain measured as in (a) ($r = -0.41$; $p < 0.01$) (modified from Ref. 3).

less likely to be encountered in broad geographic surveys[9], generating a spurious positive correlation between local abundance and the number of sites where the species has been recorded[1,3]. However, for many well studied taxa such as birds, where both ranges and abundances are very accurately recorded, it seems extremely unlikely that the relationship is entirely spurious.

Explanations for range:abundance correlations

Brown's hypothesis

Theoretically, there is a number of ways in which a positive correlation between size of geographic range and local abundance might be generated. The simplest, proposed by J.H. Brown[1], is that species able to exploit a wide range of resources (species with 'broad niches') become both widespread and locally abundant. Empirical tests are equivocal. For example, birds breeding on several types of Finnish mires (habitat generalists) have larger geographic ranges than habitat specialists, although they are not more abundant locally[6]; North American mammals with large ranges also occur in more habitats than species with small ranges[10]; and the most abundant desert lizards on three continents[11] have moderate niche breadths, whilst rare species include the entire spectrum from extreme specialists to broad generalists. Some of these data support, but others are hard to reconcile with Brown's hypothesis.

Data of a very different kind on the fate of species' introductions are also pertinent. Herbivorous insects released as biological control agents against alien weeds in a new country, and birds released on Hawaiian islands, are more likely to establish the more widespread and abundant the species are in their native environments[12-14]. If characteristics that favour invasion ability include ecological flexibility (broad niches), Brown's hypothesis receives some support, but more critical tests are desirable.

When local abundances are measured in unusual habitats (i.e. the 'reference habitat' differs markedly from the spectrum of habitats in the geographic region of interest) Brown's hypothesis predicts a negative relationship between range, and local abundance in the unusual reference habitat[3]. Consistent with this argument, there are negative relationships between local abundances of birds on Handa island (an oceanic island on the extreme north-western fringe of Europe) and the extent of species' geographic ranges, both in Britain (Fig. 1b) and in Europe as a whole (where the majority of habitats differ markedly from those on Handa)[3]. Similar results were obtained by Ford[15] for abundances of birds in woodland study plots on the eastern edge of Australia, and their continent-wide geographic distributions. The dominant habitats in Australia are deserts, not woodland.

To summarize, whilst Brown's hypothesis makes good intuitive sense, and has some data that are consistent with it, other data do not support it. Niche breadths are, in any case, notoriously difficult to measure and to interpret in an objective way[16]; critical, direct tests of Brown's hypothesis are therefore likely to remain elusive for some time.

Models

Several metapopulation dynamic models predict positive correlations between geographic range measured as the number (or proportion) of patches occupied (*area of occupancy* in Gaston's[5] terminology) and population density within patches[17-20]. Positive correlations are a product of the 'rescue effect' (immigration reduces the risk of extinction), mortality during migration, and difficulties in establishing new populations[18,20]; for certain parameter values, one of these models[18] also generates negative correlations. A rather different, statistical model based on the consequences of patch selection by individual organisms also yields positive (but not negative) range:abundance plots[21]. All these models seem most appropriate as descriptions of population dynamics and distributions at local and intermediate scales (see Ref. 17 for further discussions); they are less satisfactory as explanations for processes operating on continental scales. They also suffer from the potentially serious problem that on current evidence[22] many, perhaps most species, do not conform to the classical assumptions of metapopulation dynamic theory (in which extinctions and balancing recolonizations take place on similar time-scales across discrete habitat patches), despite the model's intuitive appeal.

Given the growing implicit or explicit reliance on metapopulation dynamic theory in designing conservation strategies, it would be both wise and valuable to have independent field tests of this family of models, although the work involved will be considerable. For those species that do persist as classical metapopulations, the implications for conservation are profound, and depressing. Very generally, if local abundance and proportion of sites occupied are positively correlated for metapopulation dynamic reasons, then reducing the number of sites at which a species is found (for example by habitat destruction) will reduce population densities at remaining, undisturbed, sites; and reducing population densities within sites (by hunting or habitat degradation) may lead inevitably to a reduction in the number of sites occupied, even if those sites are

protected. Other models and some empirical data yield broadly similar messages (e.g. Ref. 23).

Textures of abundance within geographic ranges

One obvious reason why the correlation between size of geographic range and local abundance must inevitably be weak is that species are not evenly distributed throughout their range[1,4]. All bird watchers know that maps in field-guides merely define each species' *extent of occurrence*[5], and that species differ markedly in abundance within, and may be entirely absent from, large areas delimited by field-guide range maps, either because suitable habitats are lacking, or because not all suitable habitats are currently occupied. For instance water voles (*Arvicola terrestris*), small aquatic mammals that form colonies close to water, were absent from 45% of sites surveyed on river banks throughout their extent of occurance in the North York Moors National Park in England because the habitat was unsuitable; and of the sites that were suitable, about 30% nevertheless lacked voles because they were too isolated, and/or because of predation by mink (*Mustela vison*)[24].

Very crudely, densities tend to be greatest near the centre of the range, and decline towards the boundaries[1,4,25]. Brown[1] argues that two phenomena are involved. First, species tend to inhabit a progressively smaller proportion of local patches towards the edge of their range (area of occupancy[5] declines); and, consistent both with metapopulation models and Brown's own hypothesis (see previous section), average population densities within occupied patches also decline. It would be valuable to have more documentation of these patterns from a variety of taxa (see Refs 25–27 for some pioneering examples). 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[1,4,28,29].

Because average abundances vary across species' ranges, it follows that one or more of the key demographic rates (birth, death, immi-

gration and emigration) also change across the range, in response to changes in environment and resources; that is, a species' population dynamics must be very different near the centre compared with the edge of its range[30,31] (Fig. 2a). Important, recently documented examples of markedly different population dynamics across species ranges are provided by both insects[32,33] and mammals[34]. 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 = zero, 'sink populations'[35] with negative average r may be sustained by immigration from 'source populations' deeper within the geographic range, where overall population performance (but not necessarily density) is higher. These insights carry several important messages for conservation.

First, attempts to restore populations by reintroductions into historical, but currently unoccupied parts of species' ranges are more likely to succeed into the core of the former range than on the periphery or beyond it; 76% of 133 translocations (reintroductions) of birds and mammals into former core areas succeeded, compared with 48% of 54 translocations to the periphery or beyond[36].

Second, wholesale persecution or habitat destruction may leave isolated populations of high conservation importance in marginal habitats (the 'where we find them now is not where they want to be' phenomenon) (Fig. 2b). Relict populations of takahe (*Porphyrio mantelli*), a flightless rail, in the Murcheson Mountains of New Zealand and of red kites (*Milvus milvus*), a raptor, in south-central Wales on the very edge of its European range, 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 conservation even more difficult. *In extremis* some populations may persist only because of immigration from the core; destruction of the source would make the long-term conservation of such sink populations virtually impossible[22,37].

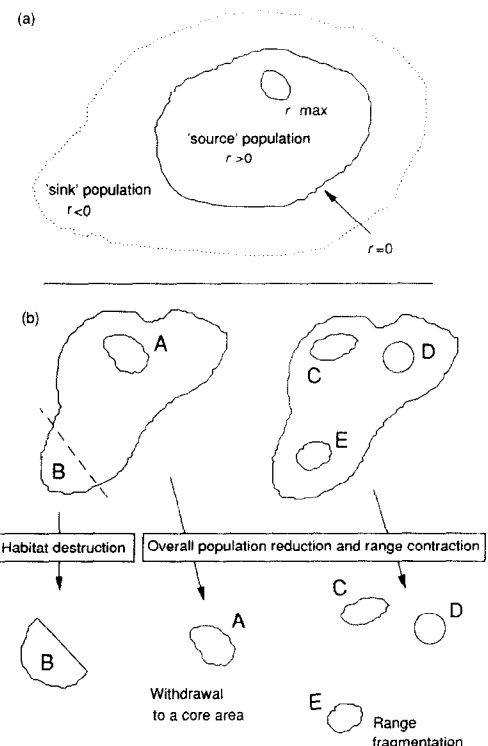Third, widespread changes in the environment (e.g. pollution, hunting, or for migrants, problems on

Fig. 2. Hypothetical species ranges. (a) Species are assumed to have maximum intrinsic rates of increase, r, towards the centre of their range (N.B. it does not follow that this is also the region with maximum abundances). Values decline away from this central region, to a point where average rates of increase are zero[18]; populations and individuals may occur beyond this region, but only as 'sinks' from 'source' populations[35] deeper within the range. (b) Population abundances vary across species ranges, tending to be higher towards the (shaded) centre of the range; peak abundances may be reached in just one area (A) or several different parts of the range (C–E). Habitat destruction may leave a species surviving only in very marginal habitats (B). Overall reductions in population abundances may cause contraction of species ranges to a single region (A), or to range fragmentation (C–E).

the wintering grounds) that lead to a general decline in population abundance via an increasing death rate or falling birth rate, should result in overall range contraction in the absence of habitat destruction. If the original range had a single, well defined centre, we expect range contraction towards that core; if there were originally multiple modes, we expect range contraction *and* fragmentation into former hot spots (Fig. 2b).

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[38] shows that declines in European populations of fir trees (*Abies* spp.) were accompanied by range fragmentation. But as Wilcove and Terborgh[39] show for population declines of some North American birds, this is by no means always the case. The highly endangered Kirtland's warbler (*Dendroica*

kirtlandii) for example, withdrew to the historical centre of its range, leaving peripheral areas virtually empty, as populations collapsed by 60% between 1961 and 1971.

As already pointed out, fragmentation or contraction to a single core area presumably depends at least in part upon textures of population abundance within the original range (uni- versus multi-modal) (Fig. 2b). Patterns of decline must also be influenced by the pace and extent of habitat destruction in a species' former range. It is difficult to know which type of range decline poses the greater threat for conservation efforts. 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.

Ranges and abundances in evolutionary time

Population density and size of geographic range are usually thought of as labile species' attributes determined by processes operating in ecological time; that is we expect abundances particularly, and ranges occasionally to be dynamic and variable over time periods of, say $10-10^3$ years. But 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, which links local abundance and size of range to a complex, elusive, albeit obviously evolved characteristic of species, namely fundamental niche breadth.

One group of studies centres on the 'taxon cycle' for birds on West Indian islands[7,40]. Among passerines, putatively older taxa occur on fewer islands, have more restricted habitat distributions and tend to have reduced population densities. It would be intriguing to revisit these analyses using independently derived, molecular criteria for species' ages.

A second group of studies also involves birds, and finds quite unexpected phylogenetic effects on patterns in species' abundances which, if real, imply constraints on

the size of bird populations that extend back over millions of years. Briefly summarizing a complex literature, we expect a rough, inverse correlation between body size and population density in animals (mice are commoner than elephants). But if we examine body-size:abundance plots for species within individual tribes of birds, there are significantly more *positive* relationships than expected (large-bodied species are commoner than small-bodied species) in taxonomically more ancient tribes (measured in various ways, but based on molecular phylogenies)[41-43].

Plants also provide evidence for phylogenetic effects on both distribution and abundance. In nine regions of North America, rare plants (loosely defined as extent of occurrence, area of occupancy or local abundance, or by combinations of these attributes) are significantly over represented in certain families (Scrophulariaceae, Lamiaceae) and under represented in others (Rosaceae)[44]. 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[45]. These results imply stasis in genus-level attributes determining distributions that have been stable for at least 10 million years. Woody taxa, in contrast, do not show the pattern.

Phylogenetic constraints on range sizes have also been reported for animals. The Gulf and Atlantic Coastal Plain of North America contains one of the most diverse and best preserved molluscan faunas of the late Cretaceous. Individual species of bivalves and gastropods from these fossil assemblages achieved characteristic range-sizes relatively early in their history; once evolved, species' range sizes changed relatively little[46]. Moreover, pairs of closely related species have statistically similar range sizes, which Jablonski[46] describes as 'in effect heritable at the species level'. One could argue with this precise form of words; the pattern remains.

Taken together, these studies imply that both range sizes and local abundances are somehow constrained and determined by phylogeny, at least in some taxa; in other words evolutionary history

leaves a signal on distribution and abundance detectable through the noise of contemporary ecological events. Quite what this might mean for conservation is unclear, but we may draw two tentative conclusions, prefaced by the remark that humankind is currently changing the distributions and abundances of many (possibly most) organisms on earth at a pace that has no antecedents in evolutionary time.

General effects of phylogeny on size of range and abundance are by no means proven. But if they turn out to be at least reasonably common (and there is not much time to find out!), they imply that species phylogenetically predisposed to low population densities and small geographic ranges will be unusually vulnerable to exploitation and habitat destruction. Paradoxically, however, they may also be pre-adapted to, and easier to maintain as, small populations in isolated reserves than formerly abundant and widespread species. Second, current assaults on the distributions and abundances of organisms mean that human forces acting in ecological time will increasingly dominate large-scale ecology. Stripped of technical jargon this means that the earth's surviving biota will persist in what is little more than a large botanical garden-come-zoological park.

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Toward a Cognitive Ecology

Leslie A. Real

The emergence of cognitive psychology as the dominant approach to understanding human behaviors and actions acknowledges the importance of internal mental operations in generating specific behavioral responses to sets of external stimuli. Traditional behaviorist interpretations that rely primarily on external inputs as the precursors of action have been largely replaced by cognitive approaches. The main intent of this article is to outline the major areas that require exploration if we wish to apply fully the principles and insight of cognitive science to behavioral ecology.

The recognition that humans, in large measure, construct representations of the environment through subjective mental operations (i.e. we are responsible for "generating our own output") constitutes a genuine intellectual revolution comparable to the behaviorist revolution of the 1920s and 1930s that it seeks to replace[1]. The application of cognitive techniques and approaches to issues in animal behavior, however, is in its infancy. Nonetheless, there have been some substantial

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attempts to recast animal behavior within a cognitive framework[2] and to apply cognitive principles while interpreting the evolution and ecology of the behavior of organisms in their natural environments[3–11]. Cognitive analyses in behavioral ecology have been, however, rather haphazard and have not been incorporated into the broad spectrum of the cognitive sciences.

Cognitive analyses are predicated on three underlying processes. First, information from the environment filtered through the organism's senses is translated and encoded into some form that can be stored and manipulated by brain functions. Secondly, stored information is manipulated through computational operations executed in the nervous system. And lastly, the equilibrium configuration of the manipulated sensory data generates particular 'representations' of the environment in which action must take place. The belief that these three processes underlie all organismal actions is what constitutes the 'computational–

representational' approach to animal behavior[2].

From an evolutionary perspective, different 'representations' of information from the environment can lead to different fitness consequences. Some computational algorithms or schemes used to process information may lead to representations of the environment that increase reproduction and survival relative to other potential schemes for processing and representing this same set of information[4,5]. Computational algorithms can differ in their efficiencies, accuracy, and in their ultimate representational state. For example, the central tendency of a distribution can be represented by the arithmetic, geometric or harmonic mean. The three computational schemes generate different numerical characterization of central tendency given the same data, and under some circumstances one of the three potential characterizations may prove most appropriate for a given environment or task. How organisms