

Nestedness and discontinuities in species-range-size distributions

Gaston's¹ discussion of the patterns and mechanisms shaping distribution curves of species-range-sizes leaves out two important issues related to scale and hierarchical structuring of biota. Several papers²⁻⁴ provide evidence that species distributions are nested, that is, overlapping in a particular manner in which species with broad ranges often contain much smaller ranges of other species. In nested systems, range-size distributions should be positively skewed because of the structural limitations on the number of large size-ranges.

'Nestedness' may give an even richer insight into ties among patterns of distribution, ecological determinants and speciation processes that were hinted at by Gaston¹. In particular, the niche breakage metaphor for species ranges would be easier to make if those ranges were seen as being influenced by ecological factors such as hierarchical habitat structure and community assembly, which involves a generalist-specialist gradient of habitat use. Habitat specialists have ecological ranges that are often nested within those of generalists⁵. It is possible that this community-level observation is but a hint of a more general mechanism responsible for patterns that span several spatial scales and that range size is correlated with ecological range of species. If this is the case, the wealth of ecological information could be used when interpreting biogeographical patterns, including prediction.

Another observation adds to this suggested link between the habitat level and geographical level pattern. Nested use of habitat necessarily implies discontinuities in ecological range distributions⁶. Such discontinuities were found in a variety of taxa, from marine foraminiferans to coral reef fishes and desert rodents. Notably, discontinuities in geographical ranges have also been found in North American birds of prey⁶ (data in Brown⁷). The discontinuities, while corroborating the hierarchical perspective, imply a potential change of focus away from the preoccupation with the log-normal statistics of distribution to other modes of description and analysis. For example, it may be useful to determine how nestedness and discontinuities correlate with habitat heterogeneity and fragmentation, both factors being fundamental to conservation, biodiversity maintenance and speciation dynamics.

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Reply from K.J. Gaston

Nestedness and discontinuities, as Kolasa observes, are two issues that I did not address explicitly in my review of species-range-size distributions¹. Neglect of at least some potentially significant issues was inevitable given constraints on available space. However, I would also suggest that, while these topics should not be forgotten, the importance of nestedness and discontinuities for an understanding of geographic range-size distributions remains, at present, arguable.

Plainly, the distributions of species in some assemblages are nested to a greater degree than one would expect by chance. Nonetheless, most published examples are at the scale of regional rather than entire geographic distributions (meso- as opposed to macro-scales); the ranges of the more widespread species in many analyses often extend well beyond the bounds of the study, embracing other sets of species that the study does not include (indeed it is plausible that the geographic ranges of widespread species perhaps embrace several otherwise largely exclusive nested sets of species). Patterson and Brown² observe that three conditions appear to be necessary for nested community structure: (1) a common biogeographic history, (2) generally similar contemporary environments, and (3) hierarchical sets of ecological relationships among the species. If we accept that this is so, then, on average, nestedness becomes increasingly less likely as the geographic extent and the taxonomic breadth of a study increase. In this sense, it seems unlikely that nestedness hints at a general mechanism for structuring range-size distributions, which spans multiple spatial scales and hence applies to frequency distributions of the entire geographic range-sizes of species as well as smaller areas.

In a similar vein, there appears to be little indisputable evidence for discontinuities in the frequency distributions of the overall geographic range-sizes of species. As illustrated by recent debate about the form of species-body-size distributions, detecting such discontinuities objectively may not be straightforward^{3,4}. In consequence, we cannot be certain that they do not exist in geographic range-size distributions, and the topic certainly deserves close attention. Frustratingly, the difficulties of determining genuine discontinuities are likely to be particularly acute when species numbers are comparatively small, and hence apply with perhaps greater force at the scales at which nestedness is typically studied.

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Ethology and sea turtle conservation

The call made by Curio¹ in a recent *TREE* Perspective for a more active role for ethologists in conservation is laudable. The examples given from avian conservation show how some projects have benefited recently from behavioural studies, increasing their overall success. In the case of sea turtles, conservationists have long known that the study of behaviour can help in the design and application of successful management strategies, as the following examples show.

One of the most extensively studied behaviours of sea turtles is the seaward orientation of hatchlings. Generally, the young emerge at night from their nest cavities on sandy tropical or subtropical beaches and scramble towards the ocean, despite not being able to see the ocean from turtle-eye level. More than two decades ago, careful examinations of their seafinding revealed that hatchlings are phototropotactic (for example, see Ref. 2). This was confirmed by reports of hatchlings becoming desiccated or being crushed to death by cars as they headed away from the ocean towards the artificial lights of nearby buildings or streets^{3,4}. One of the more creative solutions to the problem of 'misorientation' of sea turtle hatchlings due to artificial lights is the use of low-pressure sodium lamps for lighting at night. Behavioural studies of loggerhead sea turtle (*Caretta caretta*) hatchlings showed that they were repelled by the particular wavelengths emitted by such lights⁵.

Behavioural studies of adults may also be useful in conservation programmes. In the case of loggerhead turtles in Florida, it was discovered that nesting females are attracted to the silhouettes of tall condominium buildings on an urban beach: their nests tend to be clustered in front of them on the beach⁶. It has been found that shade from these same buildings can lower the sand temperature at turtle nest depth⁷. As the direction of sexual differentiation in sea turtle hatchlings is determined by incubation temperatures⁸, it is likely that such behaviour can alter the sex ratio of the hatchlings. Thus, behavioural information is important for developing management plans.

One of the most promising areas of overlap between conservation and ethology is in the assessment of conservation strategies themselves. For instance, a recent study has shown that when confronted by dense low-lying vegetation on the beach, sea turtle hatchlings cannot successfully find the ocean⁹. This has implications for choosing proper sites in the relocation of nests, which is a common technique used by many conservation programmes. Also, several studies have focused on the potentially negative impacts of tourists on the behaviour of nesting adults^{10,11}. As ecotourism has been described as 'an economic incentive to conserve sea turtles' by the IUCN - The World Conservation Union¹², it is encouraging to see that sea turtle conservationists are evaluating ecotourism in

terms of its behavioural effects as well as its financial benefits. It is hoped that other conservation areas will follow this example.

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Behavioural deception

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Theoretical models predict that deception should occur even in stable signalling systems. Assessment of the prevalence of deception and its importance has, however, been hampered by the lack of a rigorous definition of what constitutes deception and by the anecdotal nature of much of the literature. For an interaction to qualify as deception, the receiver of the 'deceptive' signal must incur a cost. While this cost is often clear in interspecific interactions, it is more difficult to evaluate in interactions between members of the same species. A systematic approach to the study of deception, including the use of experimental techniques to elicit deceptive behaviour, is now required. Such an approach may enable us to address a crucial question in social evolution – whether animals are capable of manipulating the minds of others, or merely their behaviour.

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Although behavioural deception is expected to be a natural consequence of selfish behaviour¹, certain signals are truthful. Honest signalling is favoured where there is no conflict of interest between the sender and receiver of the signal, for example when species identity is being signalled². Honest signalling also occurs where the high costs of being deceived have selected for discriminating receivers who respond only to intrinsically unfalsifiable signals^{3–5}. Zahavi^{6,7} proposed that, in situations where individuals can profit from deception, honest signals must be more expensive to make than is necessary to convey the relevant information – they are a 'handicap' – and consequently, in order for a system of biological signalling to be stable, signals must be costly and honest. The stability of such a system results from its resistance to cheats; as the ability to signal is directly related to fitness, deceptive signalling is not possible. However, further analysis of models of Zahavi's handicap principle has shown that deception can occur in a stable signalling system, provided that it does so at sufficiently low levels^{8,9}. Deception can also exist at intermediate levels where the

costs to receivers of being deceived are low compared to the cost of probing, for example in status signalling in birds¹⁰.

Many examples of manipulative behaviour by animals are claimed to be indicative of deception, but the lack of a generally accepted definition has led to confusion about what exactly constitutes deception. We advocate a functional definition:

An interaction qualifies as behavioural deception when, as the result of the behaviour of the signaller, the receiver registers a certain situation that is not in reality occurring. As a result of the interaction, the signaller benefits, while the receiver pays a cost.

This definition makes no assumptions about the underlying mechanisms by which deception is controlled. It also highlights the importance of considering the cost paid by the receiver when deciding whether a particular interaction constitutes deception. According to our definition, if the receiver pays no cost, or indeed derives benefit from the interaction, the application of the label 'deception' is inappropriate. The assessment of this cost is often straightforward in inter-

specific interactions but is more difficult in intraspecific interactions.

Interspecific deception

The costs of interspecific deception are particularly obvious in the context of predator–prey interactions, where much exploitative signalling occurs. For example, adults and large juveniles of the salticid spider, *Portia fimbriata*, deceive females of another salticid species, genus *Euryattus*, by mimicking the tactile signals that their males give during courtship¹¹. The nest of female *Euryattus* sp. consists of a rolled up leaf that is suspended by silk threads. When *Euryattus* males are courting, they attract females by rocking this nest, manipulating the threads with leg movements. The predatory *P. fimbriata* mimic these leg movements and consume the females that approach them. A similar deceit, which involves mimicry of chemical signals, is used by bolas spiders¹², such as *Mastophora cornigera*¹³. While hunting, this spider secretes a blend of chemicals that resembles the pheromone mixture secreted by females of the species' moth prey¹³. Individual spiders appear to produce different blends of such chemical signals, suggesting that they exploit different prey species¹³. Visual attractants can also be exploited in predator–prey interactions. Lloyd's well-known work¹⁴ documents how the firefly *Photuris versicolor* attracts and then preys upon the males of another firefly species, *Photinus macdermotti*, by imitating the flashing pattern of *P. macdermotti* females.

In these examples of predators deceiving prey, the deception is stable because the frequency of dishonest signals is low. Most signals are 'honest' – they are given by a conspecific – and failure to respond to them, in terms of lost reproductive opportunities, is costly. Thus, only a change in the signal of the deceived species will reduce the efficacy of the deception.

Prey species also employ behavioural deception to exploit their predators. Distraction displays, which serve to lure predators away from vulnerable offspring, have evolved in a number of bird species. Often, such displays consist of