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The tails of two geckos tell the story of dispersal in a fragmented landscape

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Abstract

The fragmentation of habitat is a major cause of biodiversity loss. However, while numerous studies have suggested that reducing the size of populations and isolating them on fragments leads ultimately to the extinction of a species (small isolated populations are extinction prone), the evidence has been rather conjectural. This is because dispersal is so difficult to measure and isolation difficult to confirm. In past studies, evidence that populations become small and isolated on fragments, leading to declines, has relied on spatial patterns of distribution and abundance. Thus, a species not trapped in the matrix in which fragments are embedded might be assumed isolated on fragments, and if low in abundance on fragments compared to continuous habitat is assumed to have declined on fragments due to this isolation. However, without accurately measuring the degree of isolation, it is difficult to distinguish the role of isolation from other important causes of population decline that are correlated with fragment and population size, such as habitat degradation. Developments in molecular techniques and statistical methods now make it possible to measure isolation. Refreshingly, in this issue Hoehn *et al.* analyse microsatellite DNA with a suite of statistical methods to show convincingly that a declining species of gecko suffers from greater isolation on habitat fragments than a contrasting gecko that is able to disperse between fragments and hence persist in the severely fragmented wheatbelt of Western Australia.

The Western Australian wheatbelt is a region outstanding both for its endemic biodiversity, and for its degree of habitat fragmentation (7% of the original habitat remains) and history of extinctions (the region has already lost five other gecko species). It is the perfect setting to illustrate the power of modern genetic techniques in getting to the bottom of why one species is at risk of extinction in a fragmented landscape while another persists. Using DNA samples taken from the tails of two gecko species (Fig. 1), the study compares the reticulated velvet gecko (*Oedura reticulata*) whose populations are declining in the fragmented wheatbelt, to a more widespread gecko (*Gehra variegata*) that maintains persistent populations in the fragmented landscape. While the declining species is endemic to the southwest corner of Australia and is a habitat specialist, preferring the arboreal haven of smooth-barked *Eucalyptus* woodland, the persistent species is widespread in southern

Australia, and is a habitat generalist, although neither species can live in the hostile wheat fields that comprise the matrix in which habitat fragments are embedded (Fig. 2).

An elegant feature of the study by Hoehn *et al.* (2007) is the crossed comparison of unfragmented to fragmented habitat and declining to persistent species. They show that the genetic structure and diversity of both species have been affected by habitat fragmentation by comparing the fragmented populations with populations in the continuous habitat of nature reserves. In the fragmented landscape, genetic diversity is lower and the genetic structure of both geckos reflects the subdivision of the population into habitat fragments, whereas individuals in continuous woodland appear to belong to one well-mixed population. While indices of genetic structure are almost the same for both species in the continuous habitat, the declining species is more strongly structured among fragments than the persistent species, consistent with the hypothesis that the declining species is suffering from greater isolation on fragments.

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Fig. 1 The reticulated velvet gecko, *Oedura reticulata*, is gradually disappearing from the landscape because it is isolated on habitat fragments (top), while the better disperser, the tree dtella, *Gehyra variegata*, persists (bottom). (Photos M. Hoehn)

While the genetic structure measured by general indices such as F_{ST} and G_{ST} is consistent with some degree of isolation for both species, such structure can also arise demographically or be driven by underlying environmental variation. Therefore, a vital task was to discover whether

the greater genetic structure in the declining species is because its dispersal is more limited than the persistent species. Curiously, in previous work, the persistent species had emerged as the species with smaller populations, suggesting it should be the more vulnerable of the two species (Sarre *et al.* 1996; Wiegand *et al.* 2001). Clearly something was protecting the gecko with smaller populations from extinction and an early hypothesis was formed that its higher dispersal ability is behind its greater persistence (Sarre *et al.* 1996; Wiegand *et al.* 2001). But the hypothesis had to wait for the better molecular techniques and statistical methods used here to be tested.

Hoehn *et al.* use three lines of evidence to show that the dispersal rates of the two geckos determine their persistence. First they show that genetic differentiation in fragment populations and the geographical distance between them are correlated in the persistent species but not in the declining species. Considering this evidence alone, there are two possible explanations for the lack of correlation in the declining species: (i) either dispersal is so limited that fragment populations are completely isolated from one another, or (ii) dispersal is so great that the network of fragments comprises a single, well-mixed population. In contrast, the persistent species falls between these two extremes, the positive correlation demonstrating that its dispersal is limited by the distance between fragments. The second and third lines of evidence differentiate between the two possibilities for the declining species, suggesting that almost complete isolation on habitat fragments is the most likely explanation.

In the second line of evidence, the study used spatial autocorrelation analysis, a distance-based analysis with finer resolution than the initial isolation-by-distance test. This analysis revealed genetic structure in the declining gecko at a scale of 100 m, but that genetic structure disappears entirely at about 500 m. In other words, dispersal between fragments occurs in the declining species after all, but only if habitat fragments are very close together. In



Fig. 2 Native woodland fragment surrounded by a hostile sea of wheat in the Western Australian wheatbelt. (Photo: M. Hoehn)

comparison, populations of the persistent species were spatially autocorrelated at larger scales and suggested dispersal of up to about 1 km between fragments, twice as far as the declining species.

In the third and clinching line of evidence, the study used assignment tests, which attempt to determine which population an individual is from. This suggested that only half as many individuals of the declining species had dispersed between fragments compared to the persistent species. The assignment tests confirmed that the declining species is unable to disperse between fragments separated by more than 500 m, whereas the persistent species can disperse between fragments separated by as much as 1 km. The agreement between all three lines of evidence makes a convincing case.

To summarize, the study was able to pin down how far the geckos move, how many individuals had moved between fragments, and ultimately how their populations are structured in the fragmented landscape and continuous woodland (are there many small populations or one large population?). Data on infrequent dispersal events are the holy grail of research on habitat fragmentation because they are needed to know how populations are structured at the between-fragment scale and hence to draw inference about the likelihood of persistence. Until the techniques illustrated in this study, such data were almost impossible to obtain. It is exciting to see these methods applied and how powerful the level of inference

can be when all the information is combined. As molecular technology and associated statistical methods continue to improve, we can expect ever finer resolution of dispersal, which will revolutionize the study of habitat fragmentation and indeed the wider field of spatial ecology.

References

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Dr Kendi Davies studies the spatial dynamics of communities and populations in fragmented and invaded ecosystems. Dr Brett Melbourne is a theoretical ecologist and studies the spatio-temporal dynamics of persistence, coexistence and invasion. Their research has led to a greater understanding of why some species persist in fragmented landscapes while other species do not.
