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## Bimodal hybrid zones and the scale of a snail

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In their recent *TREE* perspective, Jiggins and Mallet discussed the intriguing distinction between unimodal hybrid zones (where the hybrid zone is made up largely of recombinant genotypes) and bimodal zones (where recombinants form the minority)<sup>1</sup>. They indicated that bimodality is associated with assortative mating, and that it might be the stage where parapatric speciation and reinforcement take place.

Two aspects of uni- or bimodality remain unexplored in their paper. The first of these is the fact that deciding whether a zone is uni- or bimodal depends on the sampling scale. A unimodal hybrid zone would be classified as bimodal if the sampling area was larger than the zone itself, which is a real possibility in organisms where limited capacities for dispersal produce extremely narrow hybrid zones. The second aspect, which might warrant more attention, is the fact that a single hybrid zone might be unimodal in some places and bimodal in other places, depending on the environmental circumstances.

Both these phenomena are present in the hybrid zone between the land snails *Albinaria hippolyti aphrodite* and *Albinaria hippolyti harmonia* in Crete. This zone runs for a distance of approximately 10 km along a cliff where rugged terrain changes into more gently undulating hills<sup>2</sup>. In places where the environmental transition is gradual, the hybrid zone is more than 300 m wide. Where the ecotone is more abrupt, the hybrid zone can be as narrow as a few metres. Using a standard sampling area of 10 × 10 metres (and based on morphological hybrid indices and allozymes<sup>3</sup>), we would have to classify the 300 m hybrid zone as unimodal and the narrow hybrid zone as bimodal. Choosing a larger sampling area would render both situations bimodal, whereas unimodality would appear at extremely small sampling areas.

The histogramical representation of any hybrid zone should not be used to infer speciation without reference to the ratio between the sampling area and the dispersal distance of the organism under study. As it happens, in *Albinaria*, dispersal is only of the order of one metre per year<sup>4</sup>, thus assortative mating and reinforcement are unlikely where the hybrid zone is wide because parental types are not within cruising range of one another, whereas they might be in the narrower sections of the zone.

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### References

- 1 Jiggins, C.D. and Mallet, J. (2000) Bimodal hybrid zones and speciation. *Trends Ecol. Evol.* 15, 250–255
- 2 Schilthuizen, M. and Gittenberger, E. (1994) Parallel evolution of an *sAat* 'hybrizyme' in

hybrid zones in *Albinaria hippolyti* (Boettger). *Heredity* 73, 244–248

- 3 Schilthuizen, M. and Lombaerts, M. (1995) Life on the edge: a hybrid zone in *Albinaria hippolyti* from Crete. *Biol. J. Linn. Soc.* 54, 111–138
- 4 Schilthuizen, M. and Lombaerts, M. (1994) Population structure and levels of gene flow in the Mediterranean land snail *Albinaria corrugata* (Pulmonata: Clausiliidae). *Evolution* 48, 577–586

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## Reply from C.D. Jiggins and J. Mallet

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Schilthuizen's comments<sup>1</sup> highlight two important aspects of bimodality in hybrid zones. First, perhaps we did not emphasize enough that, when identifying bimodality and measuring linkage disequilibria within a zone, it is critically important that samples represent locally panmictic populations<sup>2</sup>. It is a well known result of standard population genetics that mixing geographic samples with divergent gene frequencies will create artificial heterozygote deficits and linkage disequilibria; it is the local bimodality and concomitant deviations from Hardy–Weinberg or linkage equilibrium that are of special interest in the study of speciation. Of course, in practice, 'local populations' might be difficult to define. If present, bimodality should be evident at the smallest spatial scale at which it is feasible to sample, provided this is small relative to the dispersal distance of the organism concerned. We would probably consider the *Albinaria* zone to be unimodal throughout because 'unimodality would appear at extremely small sampling areas'.

Bimodality can also be difficult to detect because many loci might be undifferentiated. If there are few loci examined, each with small frequency differences between taxa, many heterozygotes and pairwise recombinant genotypes might be present locally, thus leading to unimodal distribution on a hybrid-index plot. Adding more loci, especially if more strongly differentiated, will give greater statistical power to detect bimodality. On a plot of hybrid index, the tg2 9ex,tnhus