Bimodal hybrid zones and the scale of a snail

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)[1]. 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[2]. 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 3 10 metres (and based on morphological hybrid indices and allozymes[3]), 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 histographical 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[4], 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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Reply from C.D. Jiggins and J. Mallet

Schilthuizen's comments[1] 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[2]. 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 two peaks might slowly pull apart as more loci are added. Part of the problem is the loss of resolution involved in representing a multidimensional (multilocus) property – bimodality – on a two-dimensional hybrid-index plot. Likelihood analysis of multilocus genotypes[3] is a more appropriate statistical method and should detect bimodality with greater sensitivity; hybrid-index plots[2] are merely a useful means of data display.

Second, there is often considerable variation between populations within a single zone. Given the ubiquity of ecological differentiation across hybrid zones, it is not surprising that environmental variation, such as that described by Schilthuizen, should affect the genetic structure of hybrid zone populations. In the case of *Albinaria*, it appears that the width of the hybrid zone is primarily affected, thus leading to difficulty in choosing a suitable sampling scale. However, the degree of bimodality can also vary. As with sympatric sibling species[4], the local strength of disruptive natural selection might vary in space and time. Alternatively, habitat and population structure, leading to differences in dispersal pattern, can have similar effects: in *Bombina* hybrid zones, most populations are unimodal but some are nearly bimodal where the habitat is more patchy[2]. Although in individual cases it is often difficult to determine whether divergence between hybridizing taxa occurred *in situ* or in allopatry, such variation in bimodality is exactly the pattern expected if hybrid zone populations represent transitional stages in a process of gradual parapatric speciation.

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Spite in social insects

In a past *TREE* News & Comment, Gadagkar[1] asked the question 'can animals be spiteful?'; that is, do they ever harm another without a gain in personal reproduction. The cited examples[1], the killing of chicks in gulls and egg cannibalism in sticklebacks, were later shown to be better interpreted as plain selfishness[2]. This led Keller *et al.*[2] to conclude that 'spiteful animals are still to be discovered'. Here, we draw attention to recent work on conflict in insect societies, which reveals several clear examples of spiteful actions.

The first class of examples are behaviours that Wilson[3] termed spiteful. He proposed that harmful behaviour could, in the absence of personal benefits, be favoured through benefits to a third party (Fig. 1). Consider sex-ratio biasing in ants[4], where workers kill their brothers to increase the production of more valuable sister queens (fratricide; Fig. 1). Fratricide, although detrimental to the male recipients, is not carried out to benefit the personal reproduction of the worker because
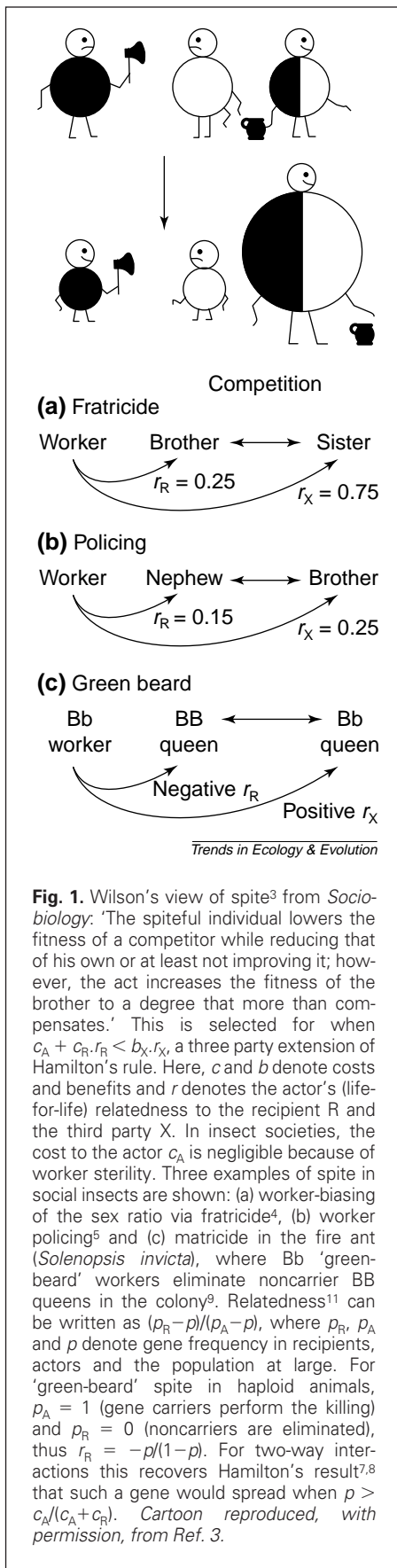
Fig. 1. Wilson's view of spite[3] from *Socio-biology*: 'The spiteful individual lowers the fitness of a competitor while reducing that of his own or at least not improving it; how-ever, the act increases the fitness of the brother to a degree that more than com-pensates.' This is selected for when $c_A + c_R.r_R < b_X.r_X$, a three party extension of Hamilton's rule. Here, c and b denote costs and benefits and r denotes the actor's (life-for-life) relatedness to the recipient R and the third party X. In insect societies, the cost to the actor c_A is negligible because of worker sterility. Three examples of spite in social insects are shown: (a) worker-biasing of the sex ratio via fratricide[4], (b) worker policing[5] and (c) matricide in the fire ant (*Solenopsis invicta*), where Bb 'green-beard' workers eliminate noncarrier BB queens in the colony[9]. Relatedness[11] can be written as $(p_R - p)/(p_A - p)$, where p_R, p_A and p denote gene frequency in recipients, actors and the population at large. For 'green-beard' spite in haploid animals, $p_A = 1$ (gene carriers perform the killing) and $p_R = 0$ (noncarriers are eliminated), thus $r_R = -p/(1-p)$. For two-way inter-actions this recovers Hamilton's result[7,8] that such a gene would spread when $p > c_A/(c_A + c_R)$. *Cartoon reproduced, with permission, from Ref. 3.*

workers are effectively sterile. Instead, the gain to the actor comes indirectly via benefits to sister queens. Worker sex-allocation biasing conforms to Wilson's[3] concept of spite: a harmful interaction that is offset by an indirect benefit to related individuals. Wilson's definition separates two distinct processes. Sex-ratio biasing could also occur through preferential feeding of sister larvae[4] – nepotistic altruism, whereas it actually involves harm to males[4] – spite. Worker policing in honey bees[5], where workers invest time in the destruction of worker-laid male eggs, thus facilitating their replacement with more valuable queen-laid male eggs[5,6], is similarly spiteful (Fig. 1).

But, does Hamilton's more stringent view of spite ever occur[7,8]? He argued that spite could evolve with only two parties, but required highly specific conditions[7,8]. Amazingly, the recently discovered 'green-beard' matricide in the fire ant (*Solenopsis invicta*)[9,10] has all the conditions Hamilton predicted (Fig. 1): (1) kin discrimination – a 'green beard' gene that enables workers to identify nongene carrier queens; (2) a low cost to the actor – in fact, no cost because fire ant workers are sterile; and (3) negative relatedness, from the perspective of the green beard locus, because the killed queens are less likely than random to possess the green beard gene[10]. As the antithesis of altruistic behaviour, the harm to non-kin is sufficient to cause the spread of spite, without requiring any indirect benefits[7,8] (Fig. 1). However, there might also be indirect benefits to 'green-beard' carrier queens, meaning spite is also favoured by Wilson's condition[3].

In the fire ant, spite has evolved as Hamilton predicted[7,8], but is it widespread in the animal kingdom? It will be interesting to look for but, as Hamilton himself pointed out, spite is likely to be rare due to the stringent conditions for its evolution[7,8]. It is no coincidence that the famously altruistic insect societies provide the most compelling examples of spite. In the course of social evolution, insect workers have become actually or effectively sterile, thus overcoming the major obstacle in the evolution of spite – cost to personal reproduction[7,8].

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Mitochondrial recombination or coevolution of sites?

A recent *TREE* News & Comment by Hey[1], discussing the possibility of recombination in human mtDNA, examined, in particular, the recent findings of Awadalla *et al.*[2] Awadalla *et al.* inferred recombination from negative correlations between linkage disequilibrium and distance between polymorphisms. Hey provides two other explanations for such a pattern: (1) nearby mutations could have a tendency to arise in concert; and (2) data-recording errors might be more likely to occur in independent sequences – those collected in different runs that tend to be farther apart.

As an extension to (1), it is also possible that combinations of variants are maintained in concert by selection. Perhaps the best example of this feature is the compensatory changes that we see in rRNA and tRNA genes to maintain the secondary structure of stems[3–7]. These types of secondary structures are also found in control regions[7,8] and some polypeptide-coding regions[9].

In general terms, variants within a gene or region are more likely to be subject to some sort of contextual dependence leading to cohesive coevolution of nearby sites, which could contribute towards the effect documented by Awadalla *et al.*[2] Differences among regions in rates of synonymous substitution or codon usage[10] could, in theory, also be factors. More direct observation, or more unequivocal evidence (such as interspecific hybrid genomes[11]), is required as proof of recombination in mtDNA.

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