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NEWS AND COMMENTARY

Evolution of species
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Explosive speciation in a cricket

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A recently published phylogeny of Hawaiian cricket species adds to the ongoing debate about the importance of sexual selection in speciation. The phylogeny implies that the genus has speciated faster than any other arthropod, and that it may have been changes in sexual behaviour that drove this rapid speciation.

The flora and fauna of Hawaii provide numerous examples of the radiation of single or few lineages into numerous endemic species (Simon, 1987). The best-known example are the *Drosophila* (Kaneshiro and Boake, 1987), but the flies are only one of several Hawaiian groups to have undergone dramatic radiations. Dan Otte (1989) originally discovered a radiation in the endemic cricket genus *Laupala*, and described many species from his surveys, largely based on calling song variation. Mendelson and Shaw (2005) have recently published a phylogeny of Hawaiian *Laupala* from which they derive the two eye-catching conclusions that these provide the fastest described speciation rate of any arthropod (and are exceeded only by cichlid fish), and that this rapid speciation has been driven primarily by changes in sexual behaviour.

The well-understood recent geological history of Hawaii allows an unusually clearcut calibration of the speciation rate. The oldest islands are around 5 million years old and the largest, main island is only around 0.5 million years old. Hence, multiple species endemic to the big island must be extremely recent. Mendelson and Shaw (2005) constructed a phylogeny of 25 species of *Laupala* using AFLP markers. These are anonymous but easily generated molecular markers that allow inference of phylogeny from band sharing. Their neighbour-joining tree was well resolved and, as well as allowing estimates of the age of clades, reveal the pattern of island hopping that these animals have undertaken (Figure 1). The tree shows that at least two lineages – they have sampled around two-thirds of the described species – have invaded the big island. Curiously, one has radiated into six species, whereas the other (*L. cerasina*) has not.

Calculations of speciation rate in *Laupala* imply that the radiation within the big island corresponds to a rate of over 4 species per million years; the number of species in any clade grows as an exponential function of time. Interestingly, as you broaden the calculation to include those from older islands, the rate declines to fewer than one species per million years. Mendelson and Shaw (2005) interpret this as meaning that older species are not sampled due to extinction, although an alternative might be that the younger islands encourage faster rates of speciation for some reason. For example, the youngest island is much bigger and perhaps ecologically more diverse than the others. A frustration in all comparative studies of speciation rates is the impossibility of distinguishing the interaction between speciation and extinction, which together determine the growth or decline of clades.

A rate of four species per million years is extremely high. Coyne and Orr (2004) published the most recent compilation of estimated speciation intervals and the equivalent value in their table is exceeded only by African lake cichlids, widely understood to be another classic example of 'explosive speciation' (curiously, horses have a negative speciation interval, which must be of some concern to horse conservationists).

Are crickets the Michael Schumachers of terrestrial speciation? Perhaps, but the fact that there are around 500 species of *Drosophila* endemic to Hawaii (with as many species endemic to the big island as were included in Mendelson and Shaw's complete phylogeny) suggests that flies would probably beat the crickets when analysed comparatively. However, chromosomal evidence shows that flies have also invaded the islands repeatedly, so it is not certain which of the Hawaiian radiations is the fastest.

Clearly, the process of founding new populations on habitat islands promotes speciation, sometimes extremely rapidly. What drives this? The second conclusion of Mendelson and Shaw (2005) is that variation in sexual behaviour has driven this rapid speciation.

The crickets are ecological generalists with no temporal separation of mating period. The calling songs of males attract receptive females, and Shaw and colleagues have previously shown that females have genetically determined preferences for the male song types found in their own species. Thus, song and preference divergence are thought likely to contribute to speciation within the crickets (Shaw and Parsons 2002). Again, there is a parallel with the African cichlids where body colour differs most between sister species and is a trait used in mate choice by females.

However, the direct evidence that sexual behaviour drives this speciation is less clear. It is difficult to study more than a few species pairs in any great detail and so the role of song in limiting gene flow between most species is not tested. Studies of other cricket species have shown that speciation can occur without changes in acoustic communication, especially in allopatry, and that some single species can be polymorphic in song patterns (eg Ritchie, 1996). The source of selection causing the divergence of sexual behaviour is also unclear, although Mendelson and Shaw seem to favour sexual selection or reinforcing selection. Such traits could also evolve by the optimisation of sexual communication or species recognition in different habitats, or simply genetic drift.

There is perhaps a potential problem of defining species partly on song differences, then concluding that song divergence is driving speciation. The species need to be confirmed with independent genetic data such as the AFLP studies, but unfortunately their phylogeny only includes one population of most species, so it is not yet possible to ask whether the species definitions are supported by greater genetic distances between species than between populations within species. There is conflict in the resolution of species using different genetic markers (Shaw, 2002). AFLPs have been used to study multiple populations of *L. cerasina* and confirm this is a good species (Parsons and Shaw, 2001; Mendelson *et al*, 2004).

Laupala provide another example of extremely rapid radiation on Hawaii. There is great debate about the relative importance of adaptive radiation *versus* founder events in speciation, particularly here. Either of these processes could be expected to influence the potentially delicate coevolution of courtship traits and female preferences,
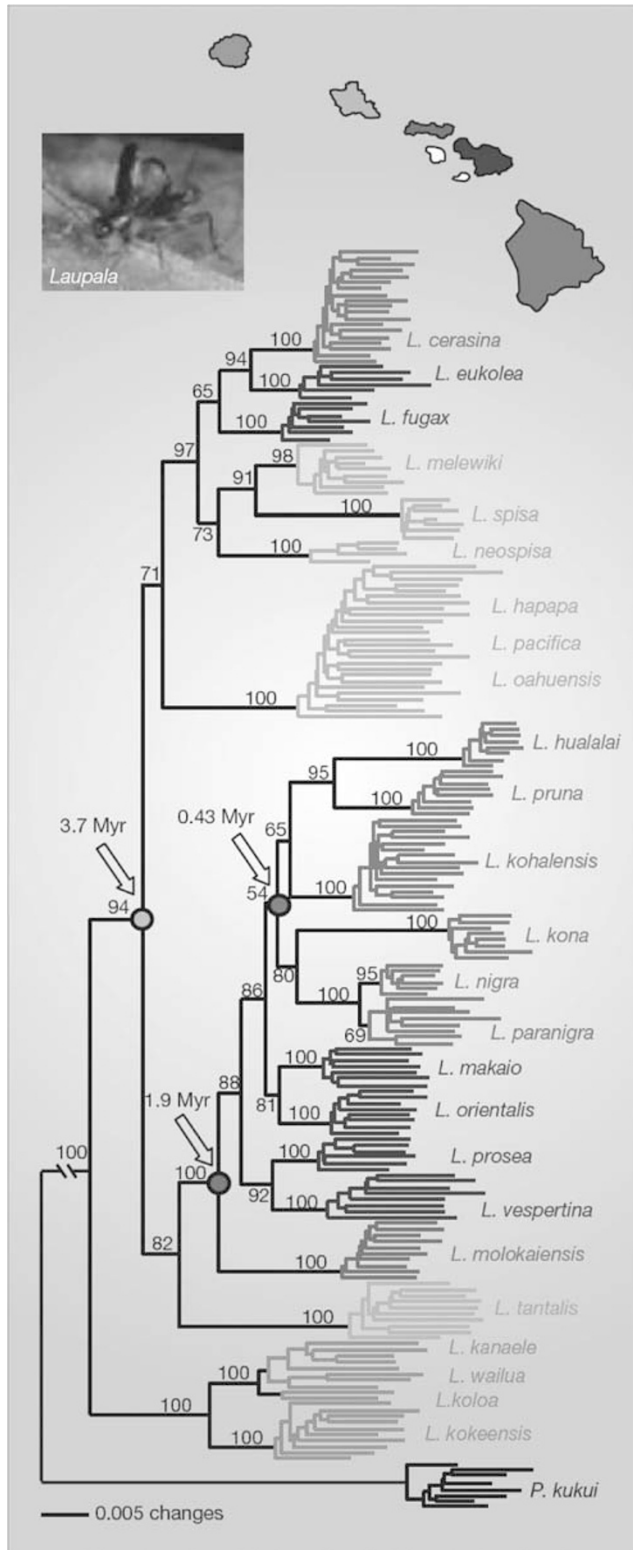
which can play a major role in limiting gene flow between developing species. *Laupala* could prove a more clearcut example of divergence in sexually selected traits primarily driving rapid speciation than the more famous Hawaiian flies (Panhuis *et al*, 2001), but more work is needed to confirm the causes of song and preference divergence, and their influence on gene flow.

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Figure 1 Phylogeny of 25 (of 38 described) *Laupala* species based on AFLP markers. Terminal taxa are individuals and branches are shaded to indicate the island of origin (shown in the top right of the picture). Arrows indicate the ages of three most recent common ancestors used to estimate rates of speciation (reproduced from Mendelson and Shaw, 2005).