

models propose that perpetual antagonistic coevolution between males and females drives divergence in postmating characters that eventually will confer reproductive isolation among allopatric populations. Besides representing a significant departure from conventional views over the catalysts of speciation, the general importance of sexual conflict to species diversification arises from the proposed ubiquity of antagonistic coevolution between the sexes. A new study by Arnqvist *et al.* tests these contentions by assessing whether rates of speciation in insects covary with the intensity of postmating sexual conflict.

Arnqvist *et al.* use a series of phylogenetic contrasts to compare extant species richness in pairs of related insect clades that differ in the opportunity for postmating sexual conflict. These comparisons are made between polyandrous and monandrous insect groups. Under polyandry, there should be ample opportunity for postmating sexual conflict, and therefore also for antagonistic coevolution between the sexes, because the ejaculates of several males compete over fertilization within the female. Even if male

traits convey costs to females, they will be favored if they enhance his reproductive success. In contrast, the opportunity for postmating sexual conflict will be absent or minimal in monandrous species. They find that species diversity, as predicted, is significantly higher in insects groups in which females mate with many males compared with groups where females mate only once. Because the two clades in a given contrast share a common ancestor, this difference in species richness reflects a higher rate of speciation in the polyandrous clade relative to the monandrous clade. By examining the potential confounding effects of differences in the trophic ecology, range of geographic distribution and latitude between poly- and monandrous clades, they show that this conclusion is not only robust to but was actually strengthened when such effects were controlled for. Their study doesn't examine whether differences in the 'opportunity' for sexual conflict between polyandrous and monandrous insects actually correspond to differing amounts of postmating reproductive divergence. However, to the extent that this

association holds, their results do suggest that increased rates of speciation are an evolutionary corollary of divergence in postmating characters.

Further study is needed to decipher what processes actually drive the rapid divergence of postmating characters. Nevertheless, whether this divergence can be ascribed to the opportunity for postmating sexual conflict, or some other postmating sexual selection, the effect on rates of speciation is indeed intriguing. Arnqvist *et al.*'s study suggests that by studying the evolutionary dynamics of these postmating characters we can gain insight into the processes generating patterns of diversity.

L. Lacey Knowles

University of Arizona, USA
(knowles@u.arizona.edu)

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Finding Mr Right: good genes and multiple mating by females

Understanding why males and females multiply mate is at the heart of behavioural ecology. Generally, theory suggests that while a male's reproductive success is limited by the number of mates he has, a female's success is limited by the number of viable eggs she produces. Since sperm is relatively cheap and plentiful, a female should be able to maximize her reproductive success by mating with only a single male. However, females of most animal species mate with more than one male (sometimes referred to as polyandry). This apparent contradiction with the theory has motivated extensive research over the past decade. A large number of empirical studies, particularly in insects, have now shown that males provide material resources to their mates. These resources can include such things as nutrients that the female consumes, care for her offspring, or protection from predators, and are referred to as direct benefits. Females that mate with multiple males can therefore acquire more resources and increase their reproductive success. Direct benefits provide a satisfying resolution to the apparent paradox of polyandry. However, in some mating systems, males provide only sperm (genes) and no direct benefits, yet females still multiply mate. In these systems, females might benefit indirectly by obtaining good genes or genes that better complement their own. When it is difficult to assess male quality prior to copulation, these females may mate with multiple males and rely on post-copulatory cues, such as sperm competitiveness, to select the ideal father. A recent study on guppies provides some much needed empirical evidence showing that females do in fact mate with multiple males in search of good genes.

Jon Evans and Anne Magurran¹ examine the predator avoidance abilities of juvenile guppies that were produced by females that had either mated with four different males or a single male four times. They show that multiply mated females produce offspring that have better developed schooling and predator escape behaviours. Because male guppies provide no direct benefits, they attribute these results to good genes. Evans and Magurran¹ also show that multiply mated females produce larger broods with a shorter gestation time. However, this latter result might also be explained by potential sperm limitation in the females mated to only a single male. Nevertheless, this study provides compelling evidence that females mate with multiple males in search of good genes.

Although the importance of polyandry and postcopulatory paternity biasing or 'cryptic female choice' is becoming clear, little is still known about the proximate mechanisms involved. For example, females might play a passive role, only facilitating sperm competition, or they might play an active role by removing undesired sperm. The fact that females may be in search of not only good genes, but genes that better complement their own, might help to explain apparent disparities in mate choice, and warrants consideration in mate choice studies. Evidently, promiscuity is not only rewarding for males, but also females.

Bryan D. Neff

Cornell University, Ithaca, NY, USA
(bdn5@cornell.edu)

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How does recombination affect phylogeny estimation?

Phylogenetic methodology is being increasingly used in diverse areas of biological sciences. Although there are many examples of the utility of a phylogenetic approach, all these studies rely on accurate estimates of phylogenetic relationships. Traditional methods of phylogeny estimation, such as maximum parsimony, minimum evolution or maximum likelihood, assume that a single evolutionary history underlies the sequences in question. However, the development of automatic PCR-based sequencing has led to the accumulation of a considerable amount of

population sequence data in which the presence of recombination – that allows for different parts of the sequences to have different phylogenetic histories – violates this fundamental assumption. Despite this fact, recombination has been traditionally ignored and its possible consequences neglected.

Schierup and Hein^{1,2} are the first to characterize thoroughly the effect of ignoring recombination in phylogenetic analysis. They use the coalescent with recombination to simulate recombining sequences, from which phylogenetic trees are inferred under the

assumption of no recombination – the way researchers typically analyse their nuclear or retroviral sequences. Schierup and Hein reveal that the consequences of ignoring recombination are many and relevant. Long terminal branches appear in a more star-shaped phylogeny, thus suggesting apparent exponential growth when the population size is actually constant. Parallel mutations are postulated to fit the data to a single tree, and rate heterogeneity among-sites is wrongly inferred. In addition, the molecular clock is lost, when in fact all lineages are evolving at the same rate. However, not all the effects of recombination are the same with different phylogenetic methods. While distance methods underestimate the time to the most common ancestor, maximum likelihood leads to an overestimate of the total number of mutations.

Values of the recombination parameter >8 in their simulations (i.e. .28 recombination events in the history of 20 sequences with 1000 bp) were found to have a large effect. How common is this amount of recombination in real data sets? The authors crunch some numbers and suggest that we would find these levels of recombination with just 100 bp in *Drosophila*, or 2000 bp in humans, although obviously the recombination rate varies extensively over the genome. They also analyse several empirical data sets, including viruses, a nuclear gene, and two mitochondrial data sets, and infer extensive recombination in all of them.

It is clear that recombination presents some important challenges to phylogenetic estimation. It would be nice to recognize when recombination might be a problem, but we are still in the dark regarding the performance of

recombination detection. In the future, researchers might aim to develop phylogenetic methods robust to recombination and also to characterize further the diversity of problems that recombination poses for sequence analysis.

David Posada

Brigham Young University, UT, USA
(david.posada@byu.edu)

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Evidence that specialists are special

Habitat fragmentation is recognized as a major threat to biological diversity. One of the most simple, but ingenious, ways of applying ecological theory to conservation problems linked to fragmentation is the use of species-area curves. The classic species-area relation is $S = cA^z$, where S is the number of species in a spatial area A , and c and z are constants. The constant z indicates how sensitive species richness is to marginal changes in habitat area, and is useful for scale-independent comparisons of species-area curves. Alternatively, one may be interested in assessing conservation status by how population densities change with habitat area, so-called 'individual-area' relationships. The idea here is that populations of only a small number of target species are quantified, enabling species-specific conservation measures. Steffan-Dewenter and Tscharrntke¹ have now added a new dimension to this problem, showing that life-history traits may be important mediators in developing conservation priorities based on species- and individual-area relationships.

The authors studied 61 butterfly species on 33 calcareous grasslands ranging from 300 to 76 000 m². They recorded numerous habitat, population and species variables, which permitted them to see how butterfly feeding niches were associated with individual-area and species-area curves. Each butterfly species was categorized into one of four feeding niches: polyphagous, oligophagous, strongly oligophagous, and monophagous. Steffan-Dewenter and Tscharrntke found that although total butterfly density decreases with habitat area, the density of a group of four monophagous species significantly increases. This would appear to be the first study to show that opposing responses of density to habitat area may be linked to resource specialization.

Steffan-Dewenter and Tscharrntke additionally discovered that when z -values were calculated for each level of food plant specialization, there was an increasing relationship between the rank level of specialization and z -values. What this means is that monophagous species richness is likely

to be more sensitive to habitat fragmentation than are more generalist species in this community. Moreover, in accord with theory, these authors show that specialists on higher trophic levels (i.e. monophagous and strongly oligophagous butterflies) are more sensitive to fragmentation than are species at lower trophic levels (the plant community).

This study should inspire both community ecologist and conservation biologist alike. Both the species number and population density approaches indicate that resource specialists in this butterfly community are more sensitive to decreases in habitat area than are generalists. Because specialists and not simply 'total diversity' can often be the target of conservation, the study by Steffan-Dewenter and Tscharrntke is unique in showing how species biology can be used to narrow-down conservation options.

Michael E. Hochberg

University of Montpellier II, France
(hochberg@evol.univ-montp2.fr)

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