

How fast do crossbills speciate? On assortative mating and vocalizations

The question of whether sympatric speciation (i.e. reproductive isolation of populations with overlapping distributions) is a source of biodiversity has always been controversial. So far, mounting evidence from only a few species, for example African lacustrine cichlids, African widowbirds and phytophagous insects, supports the notion that it occurs in nature. In the latter two, host shifts can lead to genetic isolation of the population that has shifted.

A potential new example comes from Eurasian and North American crossbills. The North American red crossbill (*Loxia*

curvirostra) can be divided into sibling species that differ in vocalizations, with positive assortative mating between males and females of the same vocal type. Moreover, crossbills with the same vocalizations share allozyme patterns, whereas other vocal types differ in allozyme patterns and bill morphology. Worldwide, some host race formation and subsequent speciation has obviously occurred allopatrically (i.e. when geographically isolated) in island populations such as those of Hispanolia (*L. megaplaga*), Scotland (*L. scotica*) and perhaps Corsica (*L. curvirostra corsicana*). However, in North

America, red crossbills are continental sibling species that occur sympatrically over large areas and disperse over long distances, making a sympatric origin of these sibling species probable. For sympatric speciation and subsequent species coexistence to occur, two conditions must be met: genetic isolation and ecological diversification of the incipient species. The coevolution of American crossbills and conifer species has already been demonstrated, and provides evidence for ecological diversification. The numerous conifer species in North America provide a huge variety of different cone structures, which must have been a necessary condition for host–race formation. The incipient species can coexist because specialization reduces competition. But, how do incipient species come about? Crossbills are highly social; if songs are learned (as with other finches) cultural evolution is likely to occur within cohesive groups. The preference for mates of the same vocal type (i.e. positive assortative mating) can then ultimately lead to genetic isolation.

Magnus Robb¹ now publishes extensive evidence that European crossbills also fall into discrete vocalization patterns. Of the six types he observed in The Netherlands alone, four were still present at the start of the breeding season, and the males and females in all the observed pairs belonged to the same vocal type. Two vocal types were found breeding sympatrically in the area. Importantly, unlike North America, there is little evidence that European crossbill populations can be divided into groups that differ in bill morphology. In addition, specialist species feeding on pine (*L. scotica* and *L. pytyopsittacus*) often occur sympatrically with *L. recurvirostra* in Europe, excluding the possibility of specialization on pine for the latter. Therefore, in Europe, low conifer diversity and interspecific competition might have prevented the formation of host races and morphological differentiation.

In both America and Europe dialect formation has evolved in association with assortative mating. In America there is differentiation both of the feeding niche and of morphology and sibling species can be recognized. In Europe there is no such differentiation both of the feeding niches, no apparent differentiation of the morphology and no evidence of sympatric speciation. The evidence presently available suggests, thus, that cultural evolution of vocalizations and assortative mating among birds of the same vocal type facilitate the generation of new species, provided that sufficient opportunity for ecological differentiation is present.

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Plant defense: signals in insect eggs

Like many adaptations, plant defenses operate with a high level of economy. Given the variable nature of herbivory, and the potential ecological and energetic costs of defense, many plants employ defenses that are induced following initial attack. In addition, some defenses are more effective when inducible. Three recent papers^{1–3} describe an extreme level of precision in a plant's response to the least damaging (yet with the most potential to damage) stage of an herbivore: its eggs. A useful distinction in the type of plant defense, be it induced or constitutively expressed, is that some act directly on herbivores and others act indirectly by involving a third party – usually predators or parasitoids. Although both can be effective, direct defenses are not generally lethal and indirect defenses might act late or reduce plant damage only minimally. These observations have led to the questions: (1) how strong a selective impact do herbivores really have on plants?; and (2) has coevolution resulted in moderately strong defenses and counterdefenses, with nowhere left to go? These articles describe wonderful and detailed natural history that challenges these questions, by describing systems in which plants actively respond to oviposition by an herbivore by killing the eggs directly or by attracting natural enemies that eat them before they hatch. In both of these cases, a constitutive strategy would probably not be an effective defense.

Doss *et al.*¹ show, using field trials, that it is probable that a single gene in peas is responsible for the growth of undifferentiated cells (neoplasm) upon oviposition by the pea weevil. The small, tumor-like growth impedes the entrance of neonate larvae (direct defense). The authors characterize a new class of compounds from weevils (called Bruchins) that elicit the neoplasm formation on the pods, but not on stems or leaves of peas and several other legumes. Meiners *et al.*³ show that female elm leaf beetles cause

elms to emit volatiles upon oviposition. These induced volatiles attract parasitoids of the beetle eggs in the laboratory (indirect defense). Amazingly, the volatiles are mediated by the highly conserved jasmonic acid pathway, they are systemically released by the plant, and they are specific to the species of elm and ovipositing beetle. These studies are reminiscent of previous reports of plant hypersensitivity in response to herbivore oviposition that resulted in egg desiccation or drop from the plant. However, the mechanistic detail in both studies reduces the possibility that the induction was a result of bacterial contamination.

Induced defense against the eggs of herbivores provides a novel level of complexity in plant–herbivore interactions, hinting towards how strong herbivore impacts can be, and opens the door for ongoing coevolution. There must be strong selection for herbivores to avoid producing signals in eggs that the plants perceive – the authors suggest that perhaps these signals are intimately involved in primary insect functions. Such interactions between not-so-passive plants and the apparently passive stages of herbivores are probably common in nature, but herbivore eggs are small and thus often out of sight.

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