

NEWS AND COMMENTARY

Evolutionary genetics

A ring of species

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A long-standing model illustrating how new species can arise through 'circular overlap', without interruption of gene flow through intervening populations, has now been confirmed among passerine birds (Irwin *et al.*, 2005). The new study of the Eurasian greenish warbler (*Phylloscopus trochiloides*) complex shows that reproductive isolation, the hallmark of biological species, can arise through 'isolation-by-distance' (Slatkin, 1993), such that large distances themselves restrict gene flow. The question of how species arise, the 'mystery of mysteries' as Darwin put it, has received much recent attention (Coyne and Orr, 2004). Birds have featured prominently as subjects in speciation research, in particular, illustrating the classic *allopatric model* of speciation through geographic separation. The recently deceased Ernst Mayr, one of the most outspoken proponents of the *allopatric* speciation model, was also the first to outline clearly a *nonallopatric* alternative, which he called 'speciation by circular overlap' (see Figure 1). This intuitively plausible idea actually goes back to the German biologists Bernhard Rensch and Geyr von Schweppenburg and was based on their observations of the Great Tit (*Parus major*) complex in Eurasia and the circumpolar Herring Gull (*Larus argentatus*) group, respectively. However, when these and other potential 'ring species' like the *Ensatina* salamanders of western North America were studied in detail (Wake, 1997; Kvist *et al.*, 2003; Liebers *et al.*, 2004), the *allopatric* divergence model seemed to explain the genetic data better than the ring species model did. In most cases, fragmentation of ranges, and thus divergence in geographic isolation, has happened at some point before the circular range around an uninhabitable barrier closed. This is not to say that isolation-by-distance was unimportant, but the crucial question remained whether it is sufficient to lead to reproductive isolation.

This question has now been answered positively by Irwin and colleagues' (2005) study of the greenish warbler complex, which provides the most convincing case to date in support of the ring species model. Greenish warblers

are small, drab-looking songbirds living in forested habitats across much of Eurasia and around the Himalayan mountain system. It had been known for some time that north of the Tibetan plateau, a huge treeless desert uninhabitable to a forest-dwelling warbler, there are two forms of greenish warbler that differ in plumage and song, but do not interbreed (*viridanus* in the west, *plumbeitarsus* in the east). These populations coexist as distinct biological species in the Siberian lowlands, but are connected through an until recently contiguous breeding range all around the Central Asian mountains. Using amplified fragment length polymorphism markers to survey a large number of anonymous nuclear gene loci, Irwin and co-workers show that there is a genetic continuum throughout this ring-shaped range, except in the zone of overlap in Siberia, where genetic divergence reaches its maximum. The physical distance around the ring is about 9000 km, orders of magnitude larger than the distance an average young greenish warbler will travel from its birth place to its later breeding territory. Genetic distance is strongly correlated with geographic distance

throughout the ring of intergrading populations, except in the zone of overlap, where this correlation breaks down abruptly.

Historically, this situation most likely arose when ancestors of today's greenish warblers from a refugium somewhere south of the Himalayas spread northwards on both sides of the mountain range. Separated by larger and larger intervening distances, the peripheral populations diverged as they were exposed to different selection pressures leading to differences in morphology, plumage and song. All conditions specified by the ring species model are met: a contiguous ring-shaped range with genetic continuity throughout, but a sharp genetic break where the ring has closed.

Two aspects are important in the warbler example that might distinguish it from other cases of potential ring species that have since been discredited. First, sexual selection is important in these songbirds, and it seems to be song characteristics that are most strongly selected by females when choosing a mate. This opens the door for a Fisherian run-away process in which different song parameters may be selected between geographically distant populations. True enough, song characteristics best distinguish the *sympatric* (overlapping) populations of *viridanus* and *plumbeitarsus* warblers in Siberia, although variation in song parameters, just like the genetic make-up of populations, was found to be continuous as one travels from the overlap zone

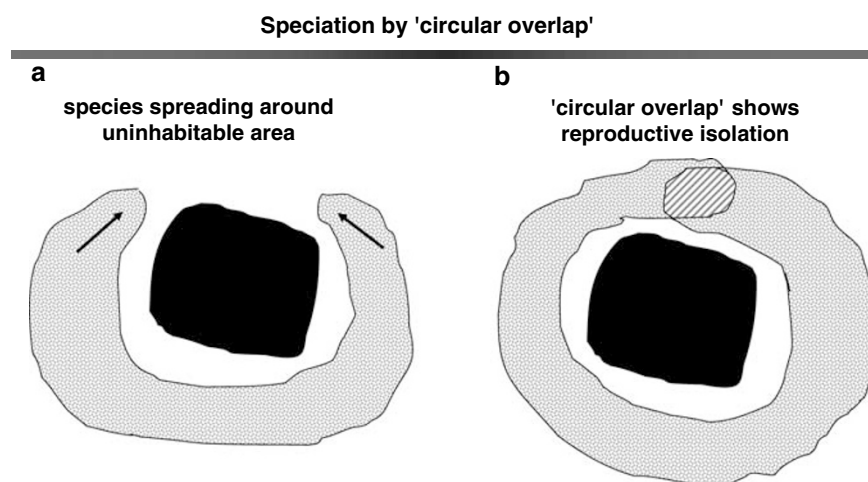


Figure 1 (a) Assume a species expands its breeding range (green), over many generations, around a large, uninhabitable area (black). The peripheral populations will differentiate genetically because gene flow between them would be effectively restricted as the distance between them becomes much larger than the average dispersal distance of the individuals. (b) When the peripheral populations come into contact on the other side of the uninhabitable area, thereby closing the ring, they might turn out to be reproductively isolated.

southward around the ring and back north on the other side (Irwin *et al.*, 2001). Second, there is a geographic bottleneck to gene flow in the southern section of the ring where it runs east-to-west along the steep, southern slope of the Himalayas (in Nepal and Kashmir). Here greenish warblers are restricted to a narrow altitudinal belt of tree-line habitat over quite some distance, which means that there must be relatively few individuals through which genes might pass from one side of the Himalayas to the other.

The question whether an interruption of gene flow by extrinsic factors is necessary to allow two populations to diverge to the extent of reproductively incompatible has been controversial for over a century. On the 'allopatric side' of the debate, proponents argue that even where speciation occurs in a relatively restricted geographic setting, say within a large lake, range fragmentation, that is, 'microallopatry', will occur through variations in lake level or discontinuous habitat distribution. Thus, it is very hard to empirically demonstrate the occurrence of sympatric speciation (within the same area) in the strict sense. Whether extrinsic interruption of gene flow is really required to set the scene for reproductive incompatibility to evolve can more easily be studied in the spatial than in the temporal dimension. The example of greenish warblers shows that two taxa are reproductively isolated at one point (or zone) in space, yet are connected through a belt of populations among which there is unimpeded gene flow. If reproductive isolation can be maintained in such a situation, there is no reason to assume that allopatric frag-

mentation was necessary to let this situation arise in the first place.

Coming back to the concept of sympatric speciation, one can conclude, by analogy, that it must be possible for reproductive isolation to arise without prior interruption of gene flow through extrinsic factors. However, the warbler example also points to the restrictive conditions that seem to be required for this to happen: divergent sexual selection on traits related to mating (eg song in warblers) between populations, and some sort of gene flow bottleneck such as an ecotone or habitat barrier not easily crossed by dispersing individuals.

Once divergence has reached a stage where at least some hybrid fitness disadvantage occurs, the reproductive barrier may be strengthened through reinforcement. In an elegant theoretical model, Servedio and Saetre (2003) proposed that divergent selection on mating-related traits and genes affecting reproductive compatibility may act like a positive feedback loop, which will reinforce both pre- and postzygotic barriers. This should be so because genes related to mate selection and those involved in reproductive functions often become closely linked on the sex chromosomes, thus reducing recombination between them. Whether reinforcement has been important in creating reproductive isolation between the forms of greenish warbler remains to be studied, but results in other songbirds (*Ficedula* flycatchers) are highly supportive (Saetre *et al.*, 2003).

The greenish warbler case shows that not only the well-known model organisms such as *Drosophila* or the mouse can provide important new insights into

speciation mechanisms, but that research on natural populations is indispensable. The warblers offer rare opportunities for future research on the behavior and effects of speciation-related genes in natural populations. Along with current advances in our understanding of the genetic basis of bird song, it may soon be possible to reveal more direct links at the molecular level between mate selection and reproductive (in)compatibility.

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