

NEWS AND VIEWS

PERSPECTIVE

Incipient ring speciation revealed by a migratory divide

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Ever since Ernst Mayr (1942) called ring species the ‘perfect demonstration of speciation’, they have attracted much interest from researchers examining how two species evolve from one. In a ring species, two sympatric and reproductively isolated forms are connected by a long chain of intermediate populations that encircle a geographic barrier. Ring species have the potential to demonstrate that speciation can occur without complete geographic isolation, in contrast to the classic model of allopatric speciation. They also allow researchers to examine the causes of reproductive isolation in the contact zone and to use spatial variation to infer the steps by which speciation occurs. According to the classical definition, a ring species must have (i) gradual variation through a chain of populations connecting two divergent and sympatric forms, and (ii) complete or nearly complete reproductive isolation between the terminal forms. But evolutionary biologists now recognize that the process of speciation might often occur with some periods of geographic contact and hybridization between diverging forms; during these phases, even partial reproductive isolation can limit gene flow and permit further divergence to occur. In this issue Bensch *et al.* (2009) make an exciting and important contribution by extending the ring species concept to a case in which the divergence is much younger and not yet advanced to full reproductive isolation. Their study of geographic variation in willow warblers (*Phylloscopus trochilus*; Fig. 1) provides a beautiful example of gradual variation through a ring of populations connecting two forms that are partially reproductively isolated where they meet, possibly due to divergent migratory behaviours of the terminal forms.

Keywords: hybridization, *Phylloscopus trochilus*, ring species, seasonal migration, speciation, willow warbler

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Bensch *et al.* present an unusually comprehensive and thorough study of within-species geographic variation. Using data from more than 1700 birds from 77 sampling sites, a truly remarkable



Fig. 1 A male willow warbler resembling the southeastern-migrating form (*Phylloscopus trochilus acredula*), on its breeding territory in central Sweden. (Photo: Anders Hedenström).

sampling effort especially for a study of birds, Bensch *et al.* measured variation in molecular markers, morphometrics (i.e. body shape and size), plumage colour, and feather isotopes (which provide an indication of wintering location). They use these data to reconstruct the likely biogeographic history for willow warblers surrounding the Baltic Sea. Previous work (see references in Bensch *et al.* 2009) had suggested that there is a narrow contact zone between a southern form (*P. t. trochilus*) and a northern form (*P. t. acredula*) in central Sweden. There are two main possibilities for how this situation arose. First, the two forms might have undergone divergence in geographically separated refugia during the last period of Pleistocene glaciation. Second, the two forms might have arisen from a single population that expanded around the Baltic Sea and invaded Sweden along two pathways, one from the north and one from the south. In this second scenario, the divergence between the terminal forms occurred without any period of complete geographic isolation. Rather, divergence built up according to a pattern of ‘isolation by distance’ within a continuously distributed species.

The data strongly support the single-refugium hypothesis. Mitochondrial and microsatellite markers show little geographic variation, consistent with a single ancestral population. The pattern of trait variation around the eastern and southern sides of the Baltic Sea is gradual and discordant between traits, indicating no particular area of transition between distinct forms. In contrast, within Sweden each of the studied traits changes dramatically in the same region, between 62° and 63° north latitude, suggesting a secondary contact zone. The overall pattern is one of a ring of forms in which there is only a single area

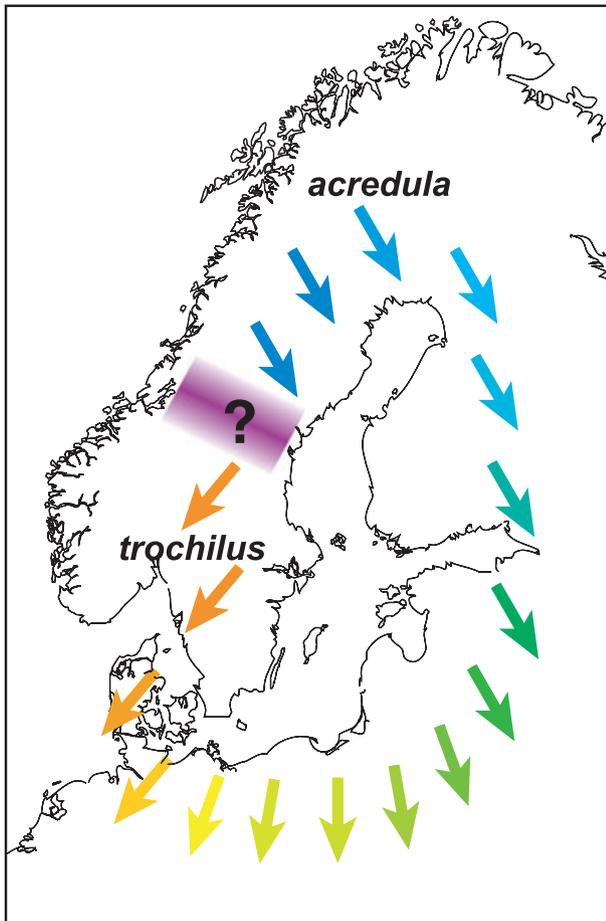


Fig. 2 Map showing gradual variation in apparent average fall migratory orientation (arrows) and genetic characteristics (colour) in a ring of willow warbler breeding populations surrounding the Baltic Sea. The purple line represents the narrow hybrid zone between divergent migratory forms (*Phylloscopus trochilus acredula* in northern Sweden, and *P. t. trochilus* in southern Sweden), with the question mark suggesting that hybrids may experience low fitness because of inferior migratory behaviour.

of sharp and concordant change in traits. This is the pattern expected in a ring species; the only difficulty with applying the classical ring species concept to the willow warblers is that there is substantial hybridization, and presumably gene flow, in the contact zone between the two Swedish forms.

However, in some hybrid zones, there can be substantial reduction in gene flow between forms, especially if there is strong selection against hybrids. Using estimates of dispersal and time since contact, Bensch *et al.* show that the cline is narrower than would be expected if there were no selection maintaining the cline. Moreover, they provide a highly plausible argument for the source of the selection: seasonal migratory behaviour.

Many young songbirds migrate between their breeding and wintering areas alone, at night, without any assistance from their parents. Thus, logic dictates, and experiments and observations have shown, that migratory behaviour often has a strong

genetic component (reviewed by Pulido 2007). In the case of the willow warbler, ringing recoveries and feather isotope analyses indicate that the two Swedish forms have distinct migratory routes, with *trochilus* migrating southwest via Spain to western Africa and *acredula* migrating southeast via the eastern Mediterranean and east Africa to southern Africa (Hedenström & Pettersson 1987; Bensch *et al.* 2006). It is thought that these two routes are favourable because they both avoid a difficult crossing of the Alps, the central Mediterranean, and the central Sahara. Thus, the hybrid zone in central Sweden provides an example of a migratory divide, a place where forms with divergent migratory routes come into contact. If hybrids have a mixture of alleles for the two migratory behaviours, it is likely that they will have inferior migratory behaviour, and hence, lower yearly survival. This could provide a powerful form of selection on hybrids, stabilizing the hybrid zone and resulting in limited gene flow across the zone (Irwin & Irwin 2005).

The possibility that hybrids in central Sweden suffer from inferior migratory behaviour raises a conundrum. The apparently gradual variation in feather isotopes and other traits around the southern and eastern side of the Baltic suggest there is gradual variation in migratory behaviour around that side of the ring. Why is it that there is no other narrow migratory divide? Bensch *et al.* suggest an interesting possibility, that willow warblers on the southeast side of the ring in fact take an intermediate migratory route (Fig. 2), flying across the central Mediterranean, and that this behaviour is not of particularly low fitness for those birds (this is consistent with the common observation of migrants over Italy). The difference is that these birds have been selected to optimize that route for many generations, whereas first-generation hybrids in central Sweden have a mixture of genes optimal for the highly divergent western and eastern migratory routes. While this possibility needs further testing, it illustrates an important principle of speciation theory: two populations can evolve in different directions along high-fitness 'ridges' in an adaptive landscape, but the resulting forms can be on opposite sides of an adaptive valley, resulting in selection against hybrids (Gavrilets 1997). Altogether, the Bensch *et al.* study provides some of the strongest evidence yet for the role of gradual divergence in migratory behaviour in promoting speciation (Irwin & Irwin 2005; Fig. 2).

The willow warbler study is also remarkable in its use of molecular evidence. Initial surveys using mitochondrial and microsatellite DNA revealed little evidence of any molecular differentiation between *trochilus* and *acredula*. But by surveying variation in more than 1000 nuclear markers (using AFLP) in a sample of birds from far northern and far southern Sweden, Bensch *et al.* identified two markers that differed strongly in frequency between the two forms. Bensch *et al.* were then able to design an efficient means of genotyping additional individuals at these markers, revealing a pattern of sharp and coincident change in central Sweden but more gradual variation around the eastern and southern side of the Baltic. This study illustrates that standard analyses of mitochondrial and microsatellite DNA may be quite limited in their power to reveal important patterns of intraspecific gene flow. It also focuses our attention on those small parts of the genome that are closely associated

with phenotypic patterns and, may be under selection, and raises the exciting possibility that these parts of the genome are also involved in reproductive isolation. According to some recent models of speciation (e.g. Wu 2001), divergence begins at a small part of the genome that is involved in generating reproductive isolation between incipient forms. Over time, the divergent fraction of the genome increases and the two forms become increasingly reproductively isolated. Thus, the approach used by Bensch *et al.* may be increasingly used to study the genetic basis for the early stages of speciation.

Despite their potential value, known ring species are rare (Irwin *et al.* 2001). Many proposed cases have been cast into doubt by further research, for example the herring gull (e.g. Liebers *et al.* 2004), the great tit (e.g. Päckert *et al.* 2005), and the crimson rosella (e.g. Ribot *et al.* 2009) species complexes. Generally, these cases have been rejected because of a lack of gradual and intermediate variation through the ring. Most researchers agree that there are only two known well-studied cases that closely approach the classic ring species model: the *Ensatina eschscholtzii* salamanders in California (e.g. Wake 2006) and the greenish warblers in Asia (e.g. Irwin *et al.* 2008). While the level of reproductive isolation between the terminal forms of willow warbler is low compared to these other cases, willow warblers otherwise meet the definition of a ring species. In this context, the willow warbler ring is most welcome, as it provides another case in which variation in space can be used to reconstruct the causes of reproductive isolation between the terminal forms. It is likely that there are many such cases waiting to be discovered, and the Bensch *et al.* study serves as an example of the careful analyses of phenotypic and molecular variation needed to reveal them.

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