

## NEWS AND VIEWS

## PERSPECTIVE

## Increasing evidence of the role of gene flow in animal evolution: hybrid speciation in the yellow-rumped warbler complex

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In this issue of *Molecular Ecology*, Brelsford *et al.* (2011) present strong evidence for a case of hybrid speciation within the yellow-rumped warbler complex. Although homoploid hybrid speciation has now been documented in many animals (Mallet 2007), it seems rare in tetrapods (Mavárez & Linares 2008) and it has barely even been mentioned in birds (Price 2008). Brelsford and colleagues thus present the first detailed molecular evidence suggesting that hybrid speciation can occur in birds. Brelsford *et al.* (2011) posit that Audubon's warbler (*Dendroica auduboni*) constitutes a hybrid species originating from the admixture of two distinct parental lineages, represented today by myrtle warbler (*D. coronata*) and black-fronted warbler (*D. nigrifrons*). The authors present three major lines of molecular evidence suggesting that this is not simply a case of a hybrid swarm or limited introgression.

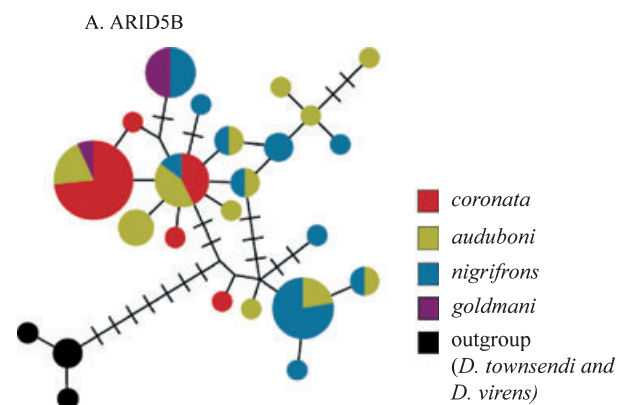
**Keywords:** admixture, *Dendroica auduboni*, homoploid hybrid speciation, hybrid species, introgression, recombinational speciation

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Brelsford *et al.* (2011) first present strong AFLP data showing substantial contributions of both parental lineages, especially in northern populations of *D. auduboni* (their Figs 2 and 3). Structure analysis of AFLP markers supported *nigrifrons* and *coronata* but not *auduboni* as distinct genetic clusters. The genetic make-up of *auduboni* varies across the range, from a nearly pure *nigrifrons* signature in the south to an increased admixture of the *nigrifrons* and *coronata* clusters as it approaches the contact zone with *coronata* in the northern Rocky Mountains (Brelsford & Irwin 2009). Second, analysis of mtDNA identified two major *auduboni* clades: one clade consisting of northern *auduboni* individuals as well as all sampled *coronata* individuals, and one clade consisting of southern *auduboni*

individuals and *nigrifrons*. (Brelsford & Irwin 2009 had previously interpreted the shallow mtDNA divergence between *coronata* and *auduboni* as evidence of just mitochondrial introgression and replacement.) A third line of evidence not emphasized by the authors comes from network analysis of the four nuclear loci sequenced for this study. Figure 1 shows one of these networks and illustrates a crucial point: the majority of *auduboni* alleles group either within *coronata*-dominated clusters or within *nigrifrons*-dominated clusters. There are few alleles unique to *auduboni*, except for some recently derived alleles that may have arisen since the recent split from the two suspected parental lineages. Importantly, very few of the sampled alleles are shared between *coronata* and *nigrifrons* except for a common, central ancestral allele that has likely been retained since the initial divergence of this complex. Finally, the authors state that *auduboni* displays a phenotype consistent with a hybrid origin. In overall appearance, Audubon's warbler is most similar to *nigrifrons* and *goldmani* (Fig. 2). However, by plotting three plumage traits along a distribution-wide transect, Brelsford *et al.* (2011), their Fig. 4) show that the plumage of *auduboni* generally is intermediate between that of *nigrifrons* and *coronata*, with some unique features not displayed in the extant populations of either putative parental lineage. Many other species of birds and other tetrapods are thought to have alleles derived from multiple lineages, but these all result from more simple processes, none of which results in an increase in species diversity, none of which is a cause of speciation.

The best-known examples of genetic admixture in animals are cases in which there is introgression of mitochon-



**Fig. 1** Haplotype network for a nuclear locus at which *auduboni* shares several common haplotypes with both *coronata* and *nigrifrons*. Adapted from Fig. S1A (Supporting information) Brelsford *et al.* (2011).



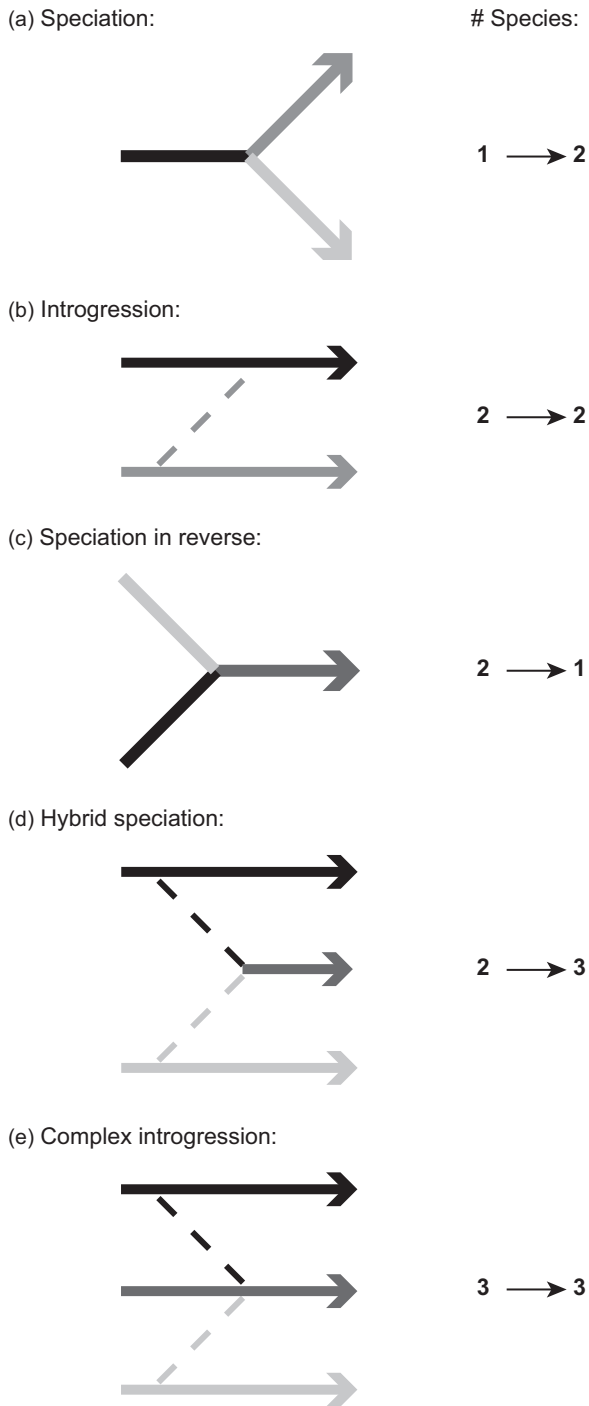
**Fig. 2** Four members of the yellow-rumped warbler complex (*Dendroica coronata* spp.). Images display diagnostic adult male characteristics of *auduboni* (top left), *coronata* (top right), *nigrifrons* (bottom left), and *goldmani* (bottom right). (Photos Alan Brelsford and Borja Mila).

drial DNA (mtDNA). Mitochondrial introgression results in incongruence between mitochondrial DNA and species boundaries based on other characteristics (Funk & Omland 2003), or incongruence between mitochondrial and nuclear gene phylogenies (e.g. Tosi *et al.* 2003; Linnen & Farrell 2007). Even in the case of complete mitochondrial capture and replacement (Tegelström 1987; Irwin *et al.* 2009), it would be simplistic to consider the resulting lineage to be a 'hybrid species' if only the mtDNA and/or a small fraction of the nuclear genome introgressed (but see Arnold 2006). Such limited introgression has no net effect on species diversity (Fig. 3b). Furthermore, one would not want to use the term hybrid speciation for two formerly isolated lineages that came into contact and remerged (Mallet 2007). Several examples of such 'speciation in reverse' or 'despeciation' have been documented in recent years (e.g. Dabrowski *et al.* 2005; Taylor *et al.* 2006; Webb *et al.* 2011), and the result is a decrease in species diversity (Fig. 3c).

Rather, to be considered a case of hybrid speciation, there should be evidence of major genetic contributions from two lineages in forming a third independent lineage (e.g. Schwarz *et al.* 2005). The most straightforward case of hybrid speciation would involve individuals from two allopatric populations moving into a third geographic range where they interbreed. Such a scenario has been suggested in birds for the extinct Mariana Islands mallard (*Anas oustaleti*) (Madge & Burn 1988). Mallet (2007), his Fig. 1 emphasizes the likely importance of a vacant adaptive peak, which would be the case for a distinct oceanic island, or an isolated continental sky island (e.g. Gompert *et al.* 2006). Import-

tantly, the two parental lineages should persist, thus resulting in a net increase in diversity from two species to three (Fig. 3d). Although 'hybrid speciation' and 'speciation in reverse' have the opposite effects on species diversity, both are facilitated by lack of strong reproductive isolation, and both result in a species with a combination of two genomes.

Recent use of more pluralistic species criteria (de Queiroz 2007), instead of the exclusive use of strict reproductive isolation, provides an opportunity for evolutionary biologists to investigate this full range of processes that occur when there is gene flow between phenotypically distinct forms (Arnold 2006). Such research will likely uncover additional cases of hybrid speciation and enhance our understanding of the role of interspecific gene flow in influencing animal evolution (Arnold 2006). Eventually, we are likely to find evidence of a continuum of processes connecting all the idealized types of reticulation events (Fig. 3). Indeed, in many cases, evolutionary history may be so complex that multiple scenarios will be consistent with the available data. Frequently, we assume some simple time in the past when there were well-defined reciprocally monophyletic groups. However, we know that today gene lineages are paraphyletic for large percentage of extant species (Funk & Omland 2003); paraphyly and complex patterns of allele sharing were probably common among ancestral species as well. Such complexity in the past may make it hard to reconstruct the history of speciation in many cases. Consider what the evidence of speciation would look like 100 000 years in the future if one of these warbler species began allopatric speciation today.



**Fig. 3** Five idealized evolutionary scenarios illustrating several effects of gene flow on species diversity: (a) one ancestral species splits resulting in a gain in species diversity, (b) introgression between two species that remain intact resulting in no change in species diversity, (c) two species merge resulting in a loss in species diversity, (d) admixture from two parental species resulting in hybrid speciation and a gain in species diversity, and (e) extensive introgression among three species resulting in no change in species diversity.

Brelsford *et al.* conclude: '...our results suggest that Audubon's warbler likely originated through hybridization'. What further evidence would provide additional support for this hypothesis? What data could further elucidate how, when, and where these evolutionary events may have occurred? The existing data and analyses have not rejected the possibility of other more complex scenarios (Fig. 3e). More thorough geographic sampling will provide many opportunities for new insight. For example, sequencing mtDNA throughout the ranges of all three species will help researchers further evaluate how current mitochondrial diversity fits with different scenarios and different time estimates. The current relatively small sample suggests that the second most common haplotype in *D. auduboni* is not found in *D. coronata*, which could be expected if the admixture occurred long ago. Also, within each of the two main mitochondrial clades, there should generally be lower or similar nucleotide diversity in *auduboni* compared to *coronata* or *nigrifrons*. But the most important next step will be to analyse multilocus sequence data using coalescent methods to test a range of explicit a priori scenarios ('statistical phylogeography', Knowles & Maddison 2002; Knowles 2009; Hey 2010). This important paper by Brelsford *et al.* (2011) will cause researchers to look for evidence of hybrid speciation in other groups of birds, and the yellow-rumped warbler complex will present many further opportunities to study the role that gene flow plays in animal evolution.

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