Evolutionary biology

# Is speciation no accident?

Roger K. Butlin and Tom Tregenza

New species arise when previously conspecific populations no longer interbreed successfully, even when they are living in the same place. This reproductive isolation can often be explained as an incidental by-product of other evolutionary changes[1]. But whether natural selection ever acts directly to increase isolation has been a controversial question ever since Dobzhansky[2] championed the idea in 1937. The proposal is straightforward — when populations have diverged genetically to the extent that the offspring of within-population matings are more fit than hybrid offspring, selection favours an increase in assortative mating (non-random mating resulting from a preference for similar partners). Assortative mating increases reproductive isolation, reducing the exchange of genes between the populations.

Despite the undoubted appeal of taking some of the chance out of the origin of species, this mechanism — known as reinforcement — has been challenged theoretically[3], and it has never been supported by fully convincing examples. However, the idea has recently been undergoing something of a renaissance, and it will be boosted by a new study from Sætre *et al.*[4], published on page 589 of this issue, which makes a case for reinforcement in European flycatchers.

A standard test for reinforcement is to study mating signals or mate choice in an area where the ranges of two populations overlap (sympatry), and to compare these with the mating behaviour of each population where it occurs alone (allopatry). Reinforcement should result in greater divergence, or stronger assortative mating, in the area of overlap. Unfortunately, there are other possible explanations for this pattern[3], so a convincing example must also show that the pattern evolved *in situ*, in the face of gene exchange, and that it reduces the frequency of unfit hybrids. Sætre and his co-workers have come closer to this than any previous study, with their work on the European *Ficedula* flycatchers.

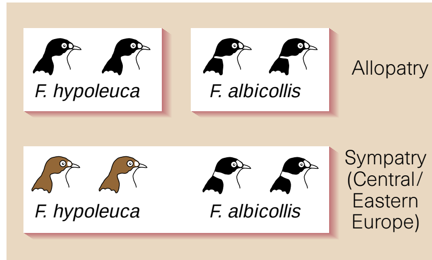


Figure 1 **An increase in assortative mating can lead to the development of a new species, in a process known as reinforcement. Sætre *et al.*[4] now provide a convincing example of this with their study of two species of European flycatcher. The ranges of *Ficedula hypoleuca* and *F. albicollis* are mainly separate (allopatry), and males have a similar black-and-white plumage. But in Central and Eastern Europe, where the ranges overlap (sympatry), the two species appear much more distinct.**

The principal players are the pied flycatcher (*F. hypoleuca*) and the collared flycatcher (*F. albicollis*). The two species are allopatric over much of their distribution, and males have similar black-and-white plumage. However, where their ranges overlap in Central and Eastern Europe, the pied males are brown rather than black, and the collared males have extended areas of white, making the two forms much more distinct (Fig. 1).

Sætre *et al.* argue that this divergence is due to reinforcement, by demonstrating four points. First, between-species (heterospecific) matings are rarer than expected, and the hybrids generated do have reduced fitness (roughly 30% of parental). However, they produce enough offspring through matings with parental types to allow regular gene exchange. Second, a phylogeny that is based on mitochondrial DNA sequences indicates that the divergent plumage of the sympatric population is a separately derived character in each species, strengthening the inference that it evolved *in situ*. Third, females from sympatric populations choose to mate with males of their own species, and they do so much more reliably when the plumage colour of the males is of the more distinct, sympatric type. Finally, when given a choice between two males of their own species, females from sympatric populations prefer males that have the sympatric colouring over those with the allopatric colouring. This is especially remarkable for the pied females — their preference for dull, brown, sympatric males over the more striking black-and-white allopatric males (Fig. 2) is the opposite to the preference for conspicuous males shown in most populations, which is thought to be based on sexual selection for male quality[5].

The last two points show that the combination of plumage traits and female preferences is enough to explain the reduced production of hybrids. At present, both the phylogeny and the data on mate choice are based on limited sampling. The case for reinforcement will be more secure when the generality of the preferences has been established, and when a more complete picture of the biogeographic history of the flycatchers is available.

The new study is more satisfying than another proposed example of reinforcement, in *Drosophila*[6], because the signal traits involved have been identified. More fundamentally, the studies differ in the levels of gene exchange that are observed between the two species in each case. Although there is hybridization between the two species of *Drosophila* (*D. pseudoobscura* and *D. persimilis*), it is so rare — and hybrid fitness is so low — that the two genomes can remain distinct in sympatry. This weakens one of the main theoretical objections to reinforcement: namely, that recombination can break down associations between the genes that are involved in mate choice and those contributing to selection against hybrids, removing the advantage to assortative mating. If isolation is already strong, as in the *Drosophila* example, the reduction in recombination between

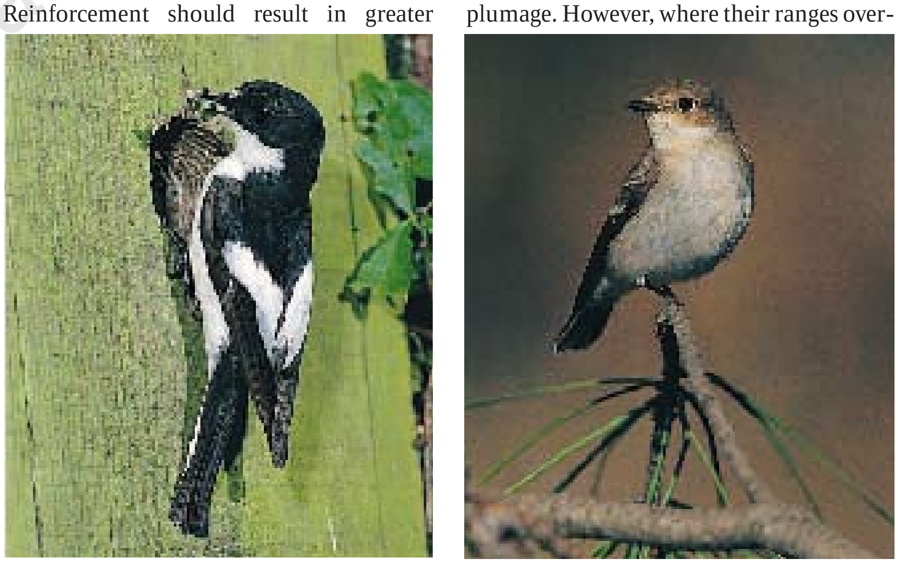
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Figure 2 **Birds of a feather. The plumage of the pied flycatcher (*Ficedula hypoleuca*) is black and white in areas where the birds are allopatric (for example, in Wales; left panel), but dull brown where the birds exist in sympatric populations with the collared flycatcher (*F. albicollis*) (for example, in Central Europe; right panel).**

species may make reinforcement much more likely[7]. The flycatcher case is different because 2.6% of matings produce hybrids, and their fitness (around 30%) allows plenty of opportunity for gene exchange. Of course, if reinforcement has occurred it must have initially operated against much higher levels of interbreeding, and it would be interesting to measure the extent of mixing of neutral alleles between the sympatric flycatcher populations.

Comparative studies that show much stronger behavioural isolation between pairs of sympatric *Drosophila* species than between allopatric pairs[8,9] also support the reinforcement hypothesis. More recent models[7,10] tend to show higher probabilities of reinforcement than do older models, mainly due to more realistic views of the operation of mate choice[7] and the genetics of hybrid dysfunction[10]. We may not be returning to Dobzhansky's whole-hearted enthusiasm for the idea, but it does seem to be much more plausible now than it was only a few years ago. □

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Archaeology

# Husbandry at the oldest henge

Elizabeth Aveling

Henges are ancient circular monuments formed by an outer mound and an inner ditch, generally dating from the late Neolithic (3000–2000 BC). As possible sites of ritual activity, they replaced the causewayed camps of the early Neolithic (4000–3000 BC). Causewayed camps, which are usually associated with long barrows (earthen burial mounds), were also circular constructions, with concentric ditches segmented by several causeways, whereas henges are continuous earthworks except at their entrances. Henge monuments, with one or two exceptions, are specific to the British Isles, and there are several hundred of them. A henge in northern England has now been shown to pre-date Stonehenge by some 800 years[1]. Its unusual shape could shed new light on the origin and significance of these enigmatic structures.

The purpose of henge monuments is unknown. Were they open-air temples for the worship of astronomical bodies? The site of markets for the exchange of goods and cattle? A ritual meeting place where people could come together to find marriage partners? Or a combination of these?

The Coupland enclosure in the Milfield Basin, Northumberland, has been known from aerial photographs for several decades (Fig. 1), but recent excavation of the site, by Clive Waddington and his team from Newcastle and Durham universities, has thrown up a few surprises. The site is described in a new booklet[1].

Henge monuments are not unusual in the archaeologically rich Milfield Basin[2], but the Coupland enclosure is unique in several ways. Its first unusual feature is its sheer size: with a diameter of approximately 110 metres, the area enclosed by the mound and ditch is more than 19 times greater than other henge sites in the area, which are all about 25 m across. Two carbon-14 measurements of charcoal[3] date the site to between 3800 and 4000 BC. This places the site in the early Neolithic, and makes it the earliest henge-like enclosure[2].

The most exciting discovery, however, is a double-ditched linear feature, bisecting the enclosure between its two opposed entrances, and continuing for 1.7 km to a ford on the River Till. This 'droveway', as it has been called, has no parallels at other henge sites. Pottery found along it shows that it is broadly contemporary with the henge. Post holes to either side of the ditches at the entrance to the enclosure are all that remain of a gateway to the henge. The depth of these holes indicates that the gate was a chest-high affair, of similar dimensions to a modern farm gate. There is also evidence that the section of droveway closest to this entrance was fenced with wooden planks standing to a similar height[4]. On the basis of this evidence, Waddington has interpreted the Coupland enclosure as a cattle kraal for the over-wintering of livestock. We know that cattle grazed the uplands in summer but were driven into the valley for winter — what better place to drive them to than a ditched kraal in the middle of the settlement belt? Phosphate analysis of soil samples taken from the droveway, apparently unaffected by later activity, are currently being undertaken at Bradford University by my colleagues; high phosphate levels would imply an accumulation of organic material.

The cattle kraal theory is a nice, neat, sensible one. The work at the site has been thorough, involving intensive field walking, aerial photography, geophysical surveying, phosphate and pollen analyses, and so far the evidence seems to imply that the henge really was used for the management of stock. Cattle could have been brought down from the uplands that flank the basin to the west, south and northeast, and driven into either end of the enclosure. There is no recorded evidence for stock kraaling at other henge sites — but it has never been looked for before. And although causewayed camps contemporary with the Coupland henge have evidence for the killing and eating of cattle, they have never been considered as stock kraals either. ▶

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Figure 1 **For farming or festivals? The Coupland enclosure in northern England is the oldest-known henge monument, nearly 6,000 years old, and a unique 'droveway' runs between its two entrances. It was probably used to keep cattle.**