performs a nontrivial computation for motion integration and eye movements.

Thus, the new findings of Li *et al.*[2] pave the way for a host of comparative experiments aimed at unraveling the computational mechanisms involved in complex motion integration. These studies will deepen our understanding of how species-specific and area-specific differences shape both neural computations and their behavioral outcomes. Resolving the ambiguity inherent in motion perception is a critical task shared across species. By exploring the convergences and divergences in visual processing, we will gain valuable insight into the fundamental principles of neural computation and how they inform behavior.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Evolution: Sexual selection and the origin of species

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https://doi.org/10.1016/j.cub.2025.01.021

Sexually selected traits, such as ornaments and colors, affect mating success and may also lead to reproductive isolation and species formation. A recent paper shows that genes underlying sexually selected differences between barn swallow subspecies do not pass across hybrid zones, implying that hybrids have low mating success.

Many species and subspecies differ from each other in traits thought to be subject to sexual selection[1], defined as differences in the mating success of different phenotypes[2]. Subspecies of barn swallow, *Hirundo rustica*, differ in the length of their tail streamers and the colour of their ventral underparts[3,4] (Figure 1). Elegant experiments have made an especially strong case for a role of sexual selection in generating these differences. First, darkening the underparts of males in subspecies with red underparts resulted in males gaining both more matings and more offspring[5,6]. Second, in subspecies with pale underparts, experimental lengthening of the tail streamers of male swallows resulted in males mating earlier in the season and gaining more offspring[6,7]. These are clear indications that both colour and tail streamer length are subject to sexual selection. A recent paper by Drew Schield and colleagues[3]

demonstrates an important role for these traits in speciation as well.

The three barn swallow subspecies (*H. r. rustica*, *H. r. tytleri*, *H. r. gutturalis*; Figure 1) breed across temperate regions of Asia. Where two subspecies come into contact, they interbreed, resulting in the formation of hybrid zones, which are defined as locations where different taxa meet, mate and form hybrids[8]. The zones are demarcated by gradients in colour or tail length over a relatively short distance, on the order of 100 kilometres. A limited spatial extent of hybrid zones is often attributed to low fitness of hybrids, in which case the hybrid zone is termed a 'tension zone'[8]. In tension zones the spatial limitation arises because an individual that enters the zone mates with an individual from a different (sub)species, producing few or infertile offspring[8].

If maintenance of a narrow hybrid zone results from low hybrid fitness, is there a role for sexual selection, which involves choice of mate? Theoretical models have questioned the importance of sexual selection in leading to reproductive isolation, especially if divergent populations come into contact before reproductive isolation is complete, as is the case when hybrid zones form. In such cases, sexually selected differences may be particularly prone to break down as preferences for one's own species cross the species barrier[9,10]. Consequently, while colouration and tail length have been the typical metrics used to identify swallow hybrid zones, it has not been clear that they play a large part in setting the narrow cline widths. Indeed, in these swallows, some hybrid zones are narrower than others, which has been related to migratory difficulties for hybrids formed in these zones[4] (these swallows winter in the tropics and subtropics).

In their new study, Schield and colleagues[3] apply genomics to settle the question. They show that a few genomic regions associated with streamer length and plumage colour are strongly differentiated among the three subspecies. These regions show signs of divergence driven by selection that is estimated to have happened within the past 10,000 years[3]. The authors then provide a detailed analysis that invokes a role for sexual selection against hybrids as a barrier to introgression.

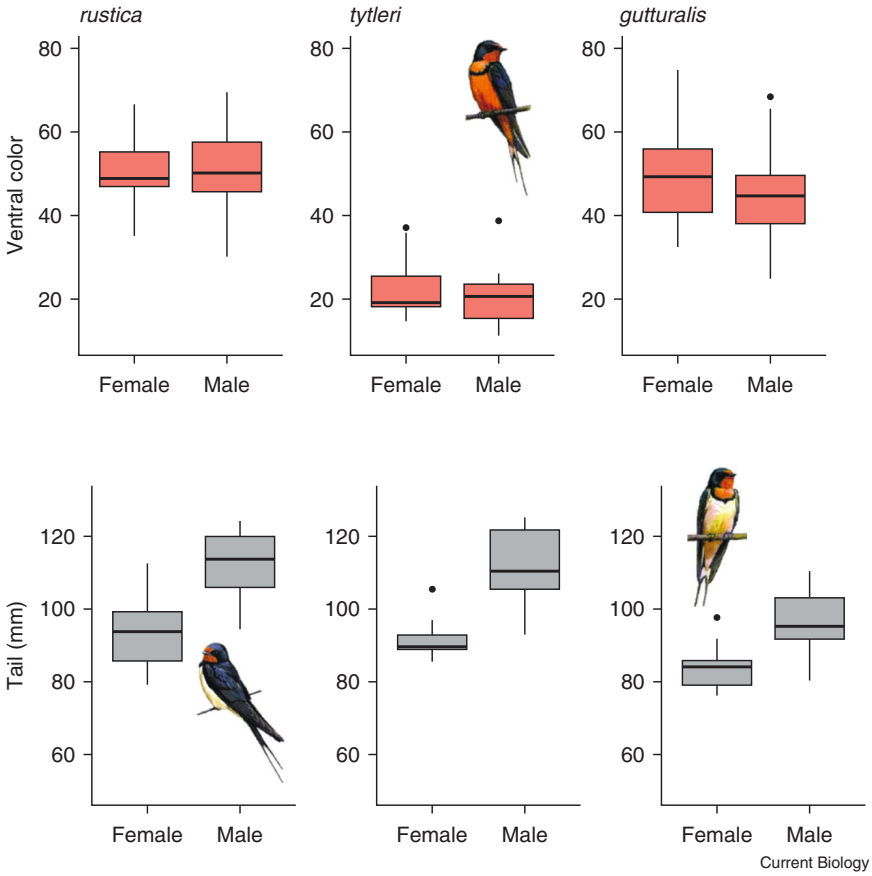

Figure 1. Sexually selected traits in three subspecies of swallow that breed in the temperate regions of Asia.
From left to right: *Hirundo rustica rustica, H. r. tytleri, H. r. gutturalis*. 'Ventral color' is a measure of reflectance. Note the relatively short tail streamers of *gutturalis* and the red underparts of *tytleri* (data from Schield *et al.*[3]; illustrations by Hilary Burn, used with permission).

First, genomic regions on two different chromosomes, associated with clear candidate genes, contribute to plumage colour differences. The subspecies *rustica* has white underparts while subspecies *tytleri* has red underparts. When an individual of one subspecies, say a male *rustica*, flies into the range of *tytleri*, it carries alleles on two chromosomes that cause white colours, designated here as w_{1a} and w_z (*w* for white, while the subscript indicates the associated chromosomes; *Z* is a sex chromosome and 1A is an autosome). If the male mates with a female *tytleri*, whose underparts are red, his offspring genotype would be w_{1a}/r_{1a} w_z/r_z (if a son) or w_{1a}/r_{1a} w_z (if a daughter, because the female only receives the Z chromosome from her father). When that hybrid reproduces, alleles at the two loci should recombine, and being on separate chromosomes, produce four different gametes in equal frequency. A male hybrid's sperm will thus carry one of four combinations: w_{1a} w_z, r_{1a} r_z, w_{1a} r_z, or r_{1a} w_z. The first two are the same gametes as are present in one or other subspecies. The second two are recombinants and appear only in hybrids. Without selection, these four combinations are expected to persist in equal frequencies. However, Schield and colleagues[3] show that in later generation hybrids, the recombinants are under-represented compared to markers from sites elsewhere in the genome. In other words, hybrids that differ from the parental forms in genes that affect colour have low fitness. Tail streamer length is controlled by several genes, with one region on a single chromosome standing out. As in the case of plumage colour, this genomic region shows a relatively steep change in frequency from genotypes typical of one form to those typical of the other across the hybrid zone. The steep

change again implicates selection against hybrid genotypes.

The study of Schield and colleagues[3] convincingly shows that colouration and tail streamer length contribute to low fitness of hybrids. Together with the earlier experimental studies that demonstrate an advantage to extreme tail and plumage traits in males, these genomic studies invoke a role for sexual selection in generating both trait divergence and reproductive isolation. One way this might happen is that preferences for exaggerated versions of a trait evolve along with the trait[11,12]. In that case, sexual selection favouring extreme streamer length in one parental form or dark colours in another means that hybrids have low fitness because they are less extreme. This mechanism is probably what is implied when researchers discuss the connection between sexual selection and speciation. However, an alternative mechanism is that sexual selection is just one, albeit powerful, form of selection that promotes trait divergence. Multiple traits are known to be used in species recognition, including those that have evolved under sexual selection, natural selection, and social selection outside of the breeding season. In the case of the swallow, both tail streamers and colours are present on young birds and carried throughout life. While tail streamers are sexually dimorphic, a characteristic signal of sexual selection, coloration is essentially sexually monomorphic (Figure 1), suggesting a role for social interactions outside the breeding season as having contributed to its evolution. Social interactions are frequent in these gregarious birds, which often occur in large flocks. Surely tails and colours (as well as other traits such as vocalizations) are employed in species recognition long before reproduction. In this case the low frequency of hybrids would result not as a side effect of sexual selection for extreme values within the parentals, but because hybrids are not recognized as belonging to either of the parental species.

Isolating the essential contributions of sexual selection to speciation is an important avenue for future research. Is sexual selection special because divergence in traits subject to such selection also generates divergence in mate preferences as a correlated effect[11,12] or is sexual selection simply a powerful mechanism of promoting divergence in traits that are subject to species recognition? The findings of Schield and colleagues[3] set the stage for disentangling exactly how sexual selection and speciation are linked and invite a return to the field.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Seabirds: Energy efficiency and foraging on the high seas

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https://doi.org/10.1016/j.cub.2025.01.030

The open ocean is a challenge for birds to traverse, forcing them to brave storms and navigate a featureless expanse. Modern tracking technology shows how shearwaters strategically balance energy costs against the need to reach a fixed goal: food or their home.

In 1588, the Duke of Medina Sidonia led the Spanish Armada toward the 'foraging grounds' of a weakened England, isolated by the Reformation and reeling from the loss of its last French possessions. However, the Armada faced formidable challenges, including severe headwinds and inadequate navigation strategies. After being driven north by English forces, many ships were wrecked along rocky coasts due to depleted supplies, unfavorable winds and navigational errors. The Armada's inability to efficiently balance the demands of energy (wind

