

Evolution: Love thy Neighbour

Dispatch

Ken Kraaijeveld and Andrew Pomiankowski

Five neighbouring populations of a cichlid fish from Lake Malawi differ in male courtship colour. Females show strong mate preferences for male coloration from their own populations. This suggests that sexual selection is an important factor contributing to speciation in cichlids.

When Darwin [1] proposed his theory of sexual selection he was concerned mainly with explaining the widespread occurrence of exaggerated sexual ornaments and courtship displays, as these traits could not easily be explained by natural selection. He also noted that taxonomic groups with more pronounced sexual ornaments tended to have more species. This suggests that sexual selection may elevate the rate at which populations diversify and give rise to new species. A new study [2] of female mate preferences in five populations of an East African cichlid species strongly supports the connection between sexual selection and speciation.

With the surge of interest in sexual selection over the past few decades, the question of whether it can lead to speciation has also enjoyed renewed attention. A plethora of theoretical models have investigated the connection, and generally concluded that sexual selection can promote speciation (reviewed in [3]). The main evolutionary mechanism proposed invokes the rapid coevolution of female mate preferences and male courtship traits, leading to reproductive isolation between groups of individuals. However, empirical evidence in support of the idea is scarce.

An indirect way this idea has been tested involves looking across broad taxonomic groups for a link between the strength of sexual selection and species number. So far, the evidence from these studies has been conflicting. In birds for example, taxa with greater sexual differences in plumage colour — an indicator of sexual selection — have higher species numbers compared to sister taxa subject to weaker sexual selection [4,5]. However, surveys in other groups (butterflies, mammals and spiders) have failed to find such an association [6], and the positive result in birds has not been replicated in a recent reanalysis [7]. It seems premature to conclude from this that speciation is independent of sexual selection. One reason for the lack of a strong linkage is that sexual selection may promote extinction as well as speciation, if it leads to the evolution of traits maladaptive to male and female survival [7,8]. Another is that sexual selection can even retard speciation under certain conditions [9]. So in the long term, species numbers may only loosely be connected to sexual selection.

A more direct way of investigating the connection between sexual selection and speciation is to examine its action in closely related populations. In a recent paper, Knight and Turner [2] attempt such a test using populations of the cichlid fish *Pseudotropheus zebra* from Lake Malawi. The cichlid fishes of the East African lakes, in particular Lake Victoria and Lake Malawi, are renowned for rampant speciation over a very brief period of time — more than 1000 species have been generated in less than a million years [10]. Some of this diversity is due to ecological specialisation, facilitated by the 'key innovation' of the cichlid pharyngeal jaw [11]. But many closely related species show practically no differences except in male colour, suggesting that sexual selection may be an important additional mechanism of speciation.

Knight and Turner [2] conducted mating trials with five neighbouring but geographically separate (9–75 km) populations of *P. zebra* from the 'blue-black' complex. Male coloration differs in each population, varying in the number and intensity of dark stripes on a blue background and in the presence of orange highlights, mainly on the fins (Figure 1). Females were offered a choice of five males, one from each population. Males were confined to their own territories by plastic grids, which allowed the smaller females to swim around freely and mate with the male of their choice. Offspring were collected from all females that spawned and paternity was determined by microsatellite genotyping.

Females from each population were tested. For each female type, clutch paternity was predominantly assigned to males from the same population (mean 62%, range 45–81%, random expectation 20%) — most clutches were sired by a single male. Egg paternity showed a similar same population bias (mean 66%, range 39–92%, random expectation 20%). There was no evidence that between-population matings were less fertile or produced fewer offspring, indicating that post-mating effects like sperm–egg incompatibilities, differential sperm use or offspring mortality are unlikely to explain the excess of same population offspring. Knight and Turner [2] conclude that these patterns are due to female mate preferences that have coevolved with male sexual coloration within each population, making assortative mating the norm when populations are experimentally mixed.

This conclusion is supported by the two cases in which between-population matings were above random expectation. These involved females from Nkata Bay producing clutches (and eggs) at a high rate with males from Chizumulu, and the same in the reciprocal direction. The male colour patterns in these two populations are very similar, suggesting that females had problems telling them apart. As the Chizumulu population was the least closely related to the others used in the experiments [12], the similarity most likely reflects parallel coevolution of female mate preference and male sexual coloration in the two populations.

Why have female mate preferences diverged in different populations? One popular explanation evokes



Current Biology

Figure 1. Males of the *Pseudotropheus zebra* populations used in the study by Knight and Turner [2]. From top to bottom, these males are from populations at Nkhata Bay, Ruarwe, Chizumulu, Mara Rocks and Mphanga rocks. (Photographs by Ad Konings.)

Fisher's runaway process of sexual selection [13]. In this model, females have preferences for arbitrary male traits, and there can be a quick turnover in female preference and male courtship traits, especially if mate discrimination carries a small cost in time or energy [14,15]. Separate populations are thus expected to diverge as random factors and small selective differences become magnified as changes in female attraction and male coloration [14,15]. A genetic mechanism that may underlie this diversity in cichlids lies in the finding that new male colours can be generated through alternative splicing of mRNAs from a pigmentation gene [16].

Alternatively, male sexual traits may reveal important aspects of male quality — the so called 'handicap' hypothesis of sexual selection [17]. In this case, divergence is not predicted, unless the populations are under very different natural selection pressures — predation rates, for example — and this is reflected by the diverged sexual traits. As yet there is little evidence for this in *P. zebra* cichlids. Finally, it is possible that local environmental conditions (such as water turbidity) vary between populations, and this has selected for different traits to maximize visibility. This is unlikely, as there was no evidence that males with the brightest coloration had a mating advantage under standard laboratory conditions. Rather, females showed specific preferences for male coloration from their own population.

The patterns revealed in *P. zebra* suggest that sexual selection is intimately involved in speciation. If these cichlid populations were to come into secondary contact, the divergence in female mate preferences and male sexual traits would to some extent prevent interbreeding and keep gene pools distinct. On its own, this is unlikely to lead to speciation, as even a little gene flow will tend to homogenise populations. Cichlid fish are known, not only for their variation in colour, but also for their diversity in feeding strategies and morphological adaptation. Ecological specialization probably needs to go hand in hand with divergence through sexual selection in the creation of new species that can coexist in the same environment. But maybe ecological specialization only happened after sexual selection created distinct reproductive groups. It is too early to know just how important sexual selection was in the adaptive radiation of cichlid fishes in the African lakes, or if the link between sexual selection and speciation holds in other groups. Nevertheless, the work of Knight and Turner [2] provides an important step forward that is likely to encourage further investigation.

References

1. Darwin, C.R. (1871). *The Descent of Man and Selection in Relation to Sex*. (London: John Murray).
2. Knight, M.E., and Turner, G.F. (2004). Laboratory mating trials indicate incipient speciation by sexual selection among populations of the cichlid fish *Pseudotropheus zebra* from Lake Malawi. *Proc. R. Soc. Lond. B* 271, 675-680.
3. Turelli, M., Barton, N.H., and Coyne, J.A. (2001). Theory and speciation. *Trends Ecol. Evol.* 16, 330-343.
4. Barraclough, T.G., Harvey, P.H., and Nee, S. (1995). Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond. B* 259, 211-215.
5. Owens, I.P.F., Bennett, P.M., and Harvey, P.H. (1999). Species richness among birds: body size, life history, sexual selection or ecology? *Proc. R. Soc. Lond. B* 266, 933-939.

6. Gage, M.J.G., Parker, G.A., Nylin, S., and Wiklund, C. (2002). Sexual selection and speciation in mammals, butterflies and spiders. *Proc. R. Soc. Lond. B* 269, 2309-2316.
7. Morrow, E.H., Pitcher T.E., and Arnqvist, G. (2003). No evidence that sexual selection is an 'engine of speciation' in birds. *Ecol. Letters* 6, 228-234.
8. Tanaka, Y. (1996). Sexual selection enhances population extinction in a changing environment. *J. Theor. Biol.* 180, 197-206.
9. Parker, G.A., and Partridge, L. (1998). Sexual conflict and speciation. *Phil. Trans. R. Soc. Lond. B* 353, 261-274.
10. Fryer, G., and Iles, T.D. (1972). *The Cichlid fishes of the Great Lakes of Africa: Their Biology and Evolution*. (Edinburgh: Oliver and Boyd).
11. Galis, F., and Drucker, E.G. (1996). Pharyngeal biting mechanisms in centrarchid and cichlid fishes: insights into a key evolutionary innovation. *J. Evol. Biol.* 9, 641-670.
12. Allender, C.J., Seehausen, O., Knight, M.E., Turner, G.F., and Maclean, N. (2003). Divergent selection during speciation of Lake Malawi cichlid fishes inferred from parallel radiations in nuptial coloration. *Proc. Nat. Acad. Sci. USA* 100, 14074-14079.
13. Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proc. Nat. Acad. Sci. USA* 78, 3721-3725.
14. Iwasa, Y., and Pomiankowski, A. (1995). Continual change in mating preferences. *Nature* 377, 420-422.
15. Pomiankowski, A., and Iwasa, Y. (1998). Runaway ornament diversity caused by Fisherian sexual selection. *Proc. Nat. Acad. Sci. USA* 95, 5106-5111.
16. Terai, Y., Morikawa, N., Kawakami, K., and Okada, N. (2003). The complexity of alternative splicing of hageromo mRNAs is increased in an explosively speciated lineage in east African cichlids. *Proc. Nat. Acad. Sci. USA* 100, 12798-12803.
17. Iwasa, Y., and Pomiankowski, A. (1994). The evolution of mate preferences for multiple sexual ornaments. *Evolution* 48, 853-867.