nature

NEWS & VIEWS

SENSORY ECOLOGY

In sight of speciation

Mark Kirkpatrick and Trevor Price

Adaptation of a fish's eyes to its visual environment can bias females to mate with different males according to their coloration. This sensory preference can contribute to the formation of new species.

How and why do barriers that prevent mating between species evolve? On page 620 of this issue, Seehausen *et al.*[1] present a rich and eclectic data set that suggests a key role for vision in African cichlid fishes. It has been shown in other fish that natural selection tunes eyes to their visual environment, so that individuals can best see not only what they eat and what eats them, but also members of their own species[2–4]. Seehausen *et al.* carry this story a step further with work on fish in which the males are either red or blue (Fig. 1), and which have genetic variation for visual sensitivity to those colours.

In some populations, females with blue-biased vision seem to mate only with blue males, whereas red-biased females mate only with red males. The inference is that natural selection acting on the visual system contributes to reproductive barriers and the formation of new species. In short, what you see determines what you get, and with whom you get it on. More controversially, the authors suggest that these barriers might arise within a population, and do not, as has previously been thought, require a phase in which red and blue populations evolve in geographical isolation.

The biological and ecological setting for this story is dramatic — the cichlid fish in the Great Lakes of Africa. These fish are the most rapidly speciating organisms on Earth, and this explosion of life has produced a panoply of colour, morphology and behaviour, a sampling of which can be seen at your local pet shop. The fish in Lake Victoria, where the present study[1] was done, show a fantastically high rate of speciation. More than 500 species inhabit the lake. They may have originated just a few hundred thousand years ago[5], and possibly went through a period of large-scale interbreeding 20,000 years ago[6].

The lake has diverse visual environments. Starting at the shore and descending along the lake bottom, red becomes increasingly dominant in the ambient visual spectrum. This spectral shift is rapid at some sites and more gradual at others. To study how the fish have adapted to these conditions, Seehausen *et al.* wanted to know what the fish see. They identified genetic variants (alleles) in one of the opsin genes responsible for tuning the fish's visual sensitivity to different colours. By expressing these genes *in vitro* and measuring the absorption properties of the resulting proteins, they found some variants that are red-biased in their sensitivity and others that are blue-biased. The red-biased variant is typically found in fish living at greater depths than the blue-biased one.

The numbers of males with red, blue and intermediate coloration vary between populations. At sites where the spectral shift is neither very rapid nor very gradual, notably Makobe island, blue males are confined to the shallows and red males to greater depths. At this site, the great majority of blue males carry the blue-biased opsin variant, whereas most red males carry the red-biased one. The two colour morphs also show differences in other genetic markers, suggesting that they are nascent species. At sites where the spectral shift is rapid, however, the colour forms interbreed, presumably because they encounter each other frequently.

Is beauty just in the eye of the beholder? In mate-choice experiments using fish from controlled crosses, Seehausen *et al.* find that the opsin variant alone does not strongly determine mating preference. Segregation of the colour morphs by depth in the lake must mean that the fish mainly encounter and hence mate with their own kind. It is not difficult to imagine that fish prefer to spend time in habitats in which they see best — that is, visual tuning could generate a type of habitat preference that

O. SEEHAUSEN & I. VAN DER SLUIJS

Figure 1 | Seeing red doesn't get you blue. These cichlid fish are examples of the colour morphs investigated by Seehausen *et al.*[1] in their study of visually determined mating preference.

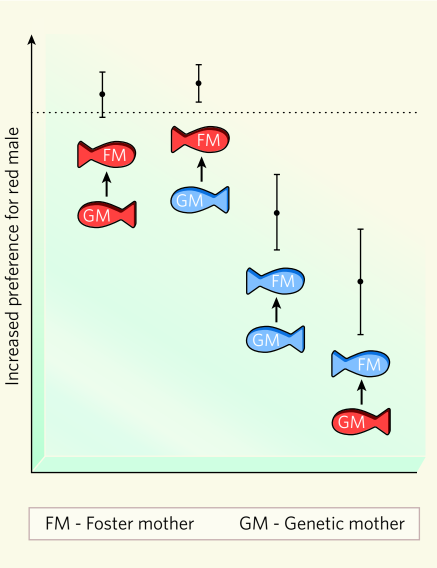

Figure 2 | The mother who raised you determines with whom you mate. In choice tests[7] with mouth-brooding cichlids, female fish raised by foster mothers belonging to different species from their genetic mothers preferred males of that different species. The stylized pictures are of males; females are dull and generally similarly coloured. The preference was measured by the difference in the number of approaches per male display when female fish are given a pairwise choice (with standard errors; dashed line indicates random choice). This evidence suggests that learning at a young age contributes to reproductive isolation in cichlids, in addition to other mechanisms such as the action of natural selection on vision described by Seehausen and colleagues[1]. (Modified from ref. 7.)

contributes to speciation above and beyond its effects on mate choice.

But is even this enough? Other findings point to an additional mechanism that complements reproductive isolation via vision. The females of these remarkable fish brood their eggs in their mouths, then guard the young fry after they hatch. In experiments reported last year, Verzijden and ten Cate[7] swapped eggs between the mouths of red morph and blue morph mothers. Females raised from the experimental broods strongly preferred males from their foster morph over those of their own morph (Fig. 2). As females of the two species look very similar, it is unclear whether the offspring preference is based on colour or some other correlated cue such as odour. Regardless of that, learning at a young age (sexual imprinting) apparently contributes to reproductive isolation in these cichlids, as it does in other groups such as birds[8]. The implication is that assortative mating — the tendency of like to mate with like — can arise whenever male characteristics diverge in response to differences in the environment, which might happen even without divergence in the opsin pigments. It remains to be seen if imprinting, vision and perhaps other mechanisms have been sufficient to generate new species without geographical isolation.

An intriguing observation mentioned by Seehausen *et al.*[1] is that the red- and blue-biased opsin alleles are evolutionarily much older than the species studied here. Red and blue colour morphs are found in other species of cichlid[9], suggesting that the colour polymorphism may also be ancient. Perhaps one key to the spectacular species radiation of African cichlids is that they inherited from distant ancestors a trove of genetic variation for sensory systems and male signals, possibly contributed during the inferred episode of interbreeding 20,000 years ago. This variation is entrained again and again in speciation events. To systematists, these events represent independent nodes on the evolutionary tree. From the fish's point of view, however, they are perhaps more like an evolutionary play that is re-enacted, night after night, with the same genetic cast. ■

Mark Kirkpatrick is in the Section of Integrative Biology, University of Texas, Austin, Texas 78712, USA. Trevor Price is in the Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637, USA.
e-mails: kirkp@mail.utexas.edu; pricet@uchicago.edu

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CLIMATE CHANGE

When did the icehouse cometh?

Stephen F. Pekar

The concentration of atmospheric carbon dioxide decreased between 45 million and 25 million years ago, a trend accompanied by glaciation at the poles. Modelling results suggest when and where the ice closed in.

As atmospheric carbon dioxide is predicted to rise to concentrations not seen in perhaps 25 million years (Myr)[1], scientists are working to understand the impact on Earth's climate and ice sheets. This requires a shift in perspective: geologists typically use the present as a key to the past, but in this case the past might well be the key to predicting how climate will change in the future.

The concentration of CO_2 in the atmosphere is predicted to increase to between 500 and 900 parts per million (p.p.m.) by the end of this century. Geochemical proxies indicate that the last time CO_2 levels were that high was about 45 to 25 Myr ago[1]. This was when Earth changed from a generally ice-free 'greenhouse world' to a more heavily glaciated 'icehouse world'[2,3], with atmospheric CO_2 gradually decreasing from more than 1,000 p.p.m. to near pre-industrial levels (280 p.p.m.)[1]. So how did the falling atmospheric CO_2 concentrations affect ice-sheet development during this period? On page 652 of this issue, DeConto *et al.*[4] use numerical modelling to constrain the timing of the initiation of glaciation in relation to decreasing levels of CO_2. Their results not only address a long-standing geological debate, but are also relevant to today's discussion about climate change.

Given the current interest in the effects of CO_2 on climate, it may be surprising to learn that there is a great deal of uncertainty about the extent of ice sheets, and the causal factors in their development, during the last period when atmospheric CO_2 concentrations reached levels as high as those predicted for the end of this century. Some information can be gleaned by studying the remains of shells from foraminifers — single-celled marine organisms — of that period. The ratio of oxygen isotopes in the shells depends on both the temperature and the isotopic composition of the water in which the foraminifers lived. The isotopic composition, in turn, was controlled by the ice volume at the poles, and by the evaporation–precipitation history of the water when it was near the ocean's surface. By contrast, the ratio of magnesium to calcium in the shells is controlled mainly by the seawater temperature alone. By measuring the two ratios, the isotopic composition of sea water can be calculated and used to constrain the polar ice volume for the period in which the foraminifers were alive.

The data suggest[5,6] that the ice volume was much larger than could be reasonably placed on the Antarctic continent. These high ice-volume estimates, combined with evidence of ice-rafted debris off the coast of Greenland, raise the possibility that glaciation in the Northern Hemisphere might have developed about 40 Myr earlier than was previously thought (that is, up to 44 Myr ago, rather than 3 Myr ago).

DeConto *et al.*[4] cast fresh light on this issue. They developed a model of global climate and of ice-sheet formation that incorporates the decreasing levels of atmospheric CO_2 found