

EVOLUTIONARY BIOLOGY

Communication and speciation

Manuel Leal and Jonathan B. Losos

An electrifying evolutionary radiation has evidently occurred among elephant fish in Africa's Ivindo basin. An implication is that open niches for communication can result in species diversification.

Groups of organisms that have diversified to produce species adapted to a variety of ecological niches have attracted increasing attention in recent years^{1–4}. A widely held view is that such adaptive radiation is triggered by the availability of under-exploited resources or the absence of predators, as may occur after colonization of an island or a mass extinction^{1,5,6}. Such ecological opportunity allows organisms to explore new ecological niches, the result being the evolutionary flowering seen in radiations such as those of Darwin's finches, Hawaiian honeycreepers, rift-lake cichlid fish and Caribbean anole lizards. However, adaptive radiation involves not only ecological divergence, but also divergence into different species. Ecological opportunity is widely implicated as the prompt for speciation, as well as for ecological divergence, but this explanation does not account for species-rich groups that exhibit little ecological differentiation. How exceptional species diversity is produced in such cases has long been discussed^{1,7}.

Writing in *The American Naturalist*, Arnegard *et al.*⁸ propose that, in a situation analogous to ecological opportunity, groups that communicate using a signal modality that is not used by other species, and is not detected by predators, may diversify in the signals used to communicate species identity. They may thus speciate to a much greater extent than species that have to contend with a more occupied signal space and more attuned predators.

Arnegard and colleagues investigated the evolutionary radiation of African mormyrid fishes, commonly known as elephant fish because of their proboscis-like snouts (Fig. 1). To a casual observer, elephant fish seem bland — they have no flashy colours, a mysterious life history and little morphological diversity. However, like many weakly electric fish, elephant fish have for decades intrigued neuroethologists because of their ability to communicate by sending and receiving electric-organ discharges (EODs); distortions of their self-generated EODs are also used to locate prey and to navigate their murky habitat. These signals are part of courtship displays, and the fish can modulate the frequency of the EOD during social interactions. Moreover, EOD waveforms



C. HOPKINS

Figure 1 | The elephant fish *Campylomormyrus rhynchophorus*. Mormyrid species such as this were the subject of Arnegard and colleagues' study⁸. The length of the specimen is about 14 cm.

differ greatly among species, allowing the use of EODs as species-recognition signals.

The Ivindo basin in west-central Africa is known for its rich diversity of elephant fish; up to 20 species may be found at a single locality. Such high diversity raises the question of what factors promote species diversity, particularly when most of the species are ecologically and morphologically very similar. Arnegard *et al.* tackled this question by combining decades of research on the evolution of EODs with state-of-the-art phylogenetic comparative methods, which allowed them to infer the contributions of ecology, morphology and signal modality to the formation of species assemblages.

This window onto the past revealed two unexpected results. First, species-specific EODs have evolved at a faster rate than have morphology, size and feeding ecology. Second, EODs diverged during early stages of the radiation, whereas morphological and ecological traits diverged later. The authors' interpretation of the results is that the ability of the fish to enter an open communication niche triggered species diversification, which was followed by a lesser degree of ecological and morphological divergence. Furthermore, they conclude that the empty communication niche allowed for species-specific signal divergence to occur in the absence of morphological or ecological divergence, resulting in species assemblages in which communication is the major axis of diversification.

But why does diversification in signal structure occur? A popular hypothesis invokes

ecological speciation, in which adaptation to different ecological niches produces, directly or indirectly, divergence in species-recognition signals, leading to reproductive isolation and, hence, speciation. Arnegard *et al.* suggest that this is unlikely for species inhabiting the Ivindo because there is no evidence of divergence in EOD waveform as a result of ecological conditions. A second possibility is that genetic drift has occurred — perhaps populations randomly diverged in signal structure, eventually becoming so different that they no longer recognize each other. Although possible in principle, this hypothesis is difficult to test and currently not in fashion.

A third explanation is that sexual selection is responsible for waveform divergence. The authors favour this view on the basis of the fact that, within species, individual differences in components of EODs are used for mate discrimination^{9,10}. How intraspecific sexual selection would produce speciation is not clear, however. Presumably it would involve different populations evolving, for some reason, differences in mate choice. The result would be divergence in sexual signals that incidentally led to reproductive isolation between populations. Differences in mate preference, mediated by differences in male mating calls, among populations of the Amazonian frog *Physalaemus petersi* may provide one such example¹¹.

Several studies have linked sexual selection and rates of speciation. But just because a trait is subject to sexual selection within a species, it does not necessarily follow that interspecific

differences arose through this process. Rather, we have known since the time of the early naturalists that many signals are used to allow an organism to distinguish individuals of different species from those of the same species. Such signals can arise in many ways that do not involve competition among members of one sex for reproductive success, unless one is willing to broaden the definition of sexual selection to encompass all mating decisions, including those involving individuals of other species. Reinforcement and reproductive character displacement, in which selection favours individuals that mate preferentially with members of the same species, are two well-established ideas about how the ability to recognize a member of a different species may arise to prevent interspecific mating without the operation of sexual selection (Arnegard *et al.*⁸ do acknowledge this possibility).

Regardless of whether signal evolution was driven by sexual selection or by selection for species recognition, Arnegard and colleagues' general point is an excellent one. Evolutionary radiation, whether adaptive or non-adaptive, requires speciation. It is certainly plausible that taxonomic groups with a greater ability to diversify in species-recognition signals, and that are thus more likely to speciate, may be those that diversify to the greatest extent.

Technological advances are opening a window onto many hitherto little-appreciated communication channels. For example, frogs can communicate using ultrasonic calls¹², and polarized light is used for mate recognition in butterflies¹³. Findings such as those of Arnegard *et al.* provide fertile ground to further explore the contribution of using a previously empty communication niche in evolutionary radiations. The constraining effect of eavesdropping predators also remains to be determined. The observation^{14,15} that weakly electric fishes in South America exhibit a great diversity of species and EODs, even though they have evolved in the presence of predators that can perceive electric discharges¹⁶, suggests that partitioning of signal space along the communication axis is the more potent evolutionary force. Examples from other sensory modalities are needed to test the generality of this hypothesis. ■

Manuel Leal is in the Department of Biology, Duke University, Durham, North Carolina 27708, USA. Jonathan B. Losos is in the Museum of Comparative Zoology, and the Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA.

e-mails: mleal@duke.edu;
jlosos@oeb.harvard.edu

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CLIMATE CHANGE

A glacial test of timing

Martin P. Kirkbride

Meticulous reconstruction of the former extent of a glacier high in the mountains of New Zealand will help in interpreting global-scale climatic adjustments that occurred at the end of the last glaciation.

Both the Northern and Southern Hemispheres experienced phases of cooler climate that interrupted the general warming of Earth during late-glacial time, as ice sheets on the northern continents decayed. One of these cool phases, the Younger Dryas stadial (12,900 to 11,700 years ago), was triggered by huge volumes of cold, fresh meltwater entering the North Atlantic Ocean¹. The result was a slowing-down of ocean circulation and a reduction of regional temperatures by up to 15 °C. In the south, the Younger Dryas was preceded by the Antarctic cold reversal (14,500 to 12,900 years ago), recorded in Antarctic ice cores².

Understanding how far each cooling event propagated to lower latitudes is important for understanding how oceans distribute heat (and cold) across the planet. This can be achieved by dating the physical manifestations of such climate changes using preserved marine microfossils, plant pollen, insect faunas — or,

as Kaplan *et al.* demonstrate (page 194 of this issue³), the bouldery moraine ridges deposited by former glaciers.

One problem is that terrestrial evidence of oceanographic change is fragmentary, linked to regional-scale climate and difficult to date with sufficient precision. Kaplan and colleagues' study from the Southern Alps of New Zealand is noteworthy in providing a well-constrained case study of a contemporary glacier advance. They have combined rigorous field investigations and state-of-the-art geochronology to resolve a long-standing debate^{4,5}.

Kaplan *et al.*³ exploit the fact that small alpine glaciers are beautifully simple physical systems that respond sensitively to climate variability. The delicate balance between winter snow accumulation and summer melting determines the size and distribution of glaciers in a mountain range. Having reconstructed the location and topography of the former glacier



Figure 1 | Evidence of glacial action: a view of the mountain basin studied by Kaplan *et al.*³. The authors dated moraine ridges, including the prominent moraine in this photo, to reconstruct the topography of the glacier that once occupied the basin.

A. PUTNAM