

Bird speciation in the Gulf of Guinea, West Africa

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The Gulf of Guinea island system is a spectacular centre of endemism mysteriously forgotten by most biologists. It comprises three oceanic islands (Príncipe, São Tomé, and Annobón), one land-bridge island (Bioko) and one ecological island (Mt. Cameroon), all part of the Cameroon line of volcanoes (Fig. 1). Birds are one of the groups for which endemism levels are truly impressive. The

independent Endemic Bird Area (EBA), whereas Bioko and Mount Cameroon are part of the Cameroon mountains EBA that, with another 29 endemic species, is the third most important in Africa. São Tomé and Príncipe are in the world top 25% EBAs, a unique feat for small oceanic islands.

Despite these levels of endemism and the presence of some peculiar species – for

case for very isolated islands. Interspecific competition may have been important from early on, preventing radiations from occurring. This has resulted in endemism being spread across different families rather than being concentrated in species-rich genera, which has the advantage of offering more phylogenetically independent replicates to test evolutionary hypotheses.

Below: The four 'aberrant' white-eyes of the Gulf of Guinea, making the genus *Speirops* (left), facing the 'typical' white-eyes of the region, from the genus *Zosterops*. A molecular phylogeny showed that aberrant patterns evolved twice in the history of the group, *Speirops* being an invalid genus.



three oceanic islands with a total area of about 1000km² support at least 29 endemic species, with up to five endemic genera. For comparison, the Galapagos archipelago with 13 islands totalising ca. 8,000km² holds 22 endemic species. Each of the oceanic islands is listed by BirdLife International as an

example, the world's largest sunbird and largest weaver and the smallest ibis – researchers have overlooked this region probably because no spectacular bird radiation occurred here. The moderate distances to mainland allowed colonisation by a wider array of species than is normally the

An expedition to the region took place from November 2003 to February 2004, with the support of a Genetics Society field grant. This was the second expedition to continue investigations into the processes promoting bird speciation in the Gulf of Guinea. Its objectives were:

- 1 to complete sampling for phylogenetic and phylogeographic analyses aimed at describing the diversification patterns of different groups (thrushes, sunbirds, white-eyes, seedeaters);
- 2 to collect phenotypic, genetic and behavioural data at the population level for the Príncipe seedeater (*Serinus rufobrunneus*), the model species chosen to investigate the factors driving the divergence of small allopatric populations.

Regional diversification patterns

Taxon sampling for the phylogenetic analyses was successfully carried in the four islands, Mt. Cameroon, and mainland. The highlight was the capture of the extremely rare São Tomé grosbeak (*Neospiza concolor*), a passerine of uncertain affinities last captured 113 years ago, and only observed five times since then. Having handled the bird, the hypothesis that it is a true finch closely related to the Príncipe seedeater with which it co-occurs seems the most plausible.

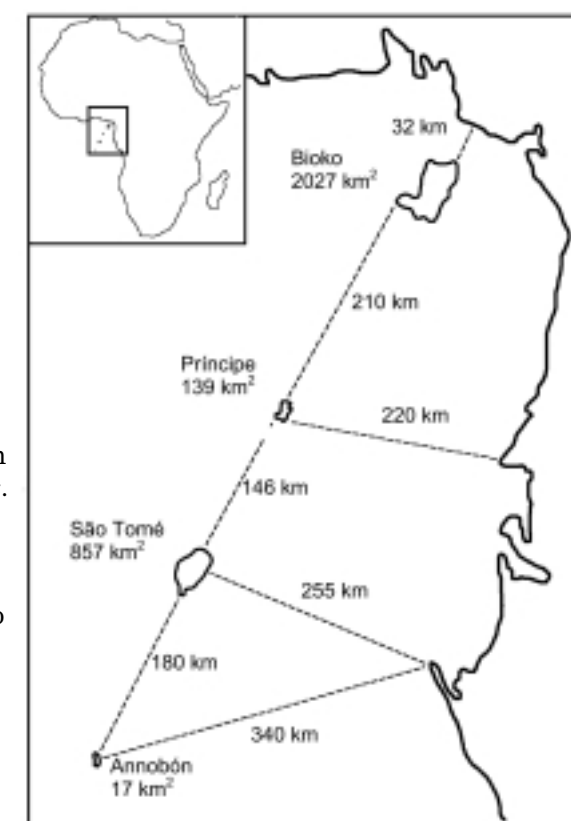
Direct sequencing of mitochondrial and nuclear DNA sequences is currently being carried out to build genealogies for the different bird groups. The results will allow us to infer the speciation modes, geographic origin of taxa, colonisation routes and

timing of colonisation events, allowing the identification of any major regional factor(s) responsible for the high levels of endemism. This will establish the basis for any subsequent testing of process-oriented hypotheses.

Preliminary results are available for the white-eyes (*Zosteropidae*), passerines known for their ability to disperse to islands and speciate once there. The Gulf of Guinea is no exception, with 8 endemic taxa present. In the four instances where two species co-occur (São Tomé, Príncipe, Bioko, Mount Cameroon), one of the species differentiated dramatically from the typical white-eye phenotype. These 'aberrant' white-eyes have been placed in a genus of their own: *Speirops*. Curiously the molecular phylogeny shows that the aberrant white-eyes do not form a monophyletic group, so that *Speirops* must be an invalid genus. The Gulf of Guinea white-eyes are separated in a 'mainland' clade (which includes Bioko) and an 'oceanic island' clade. This suggests that inter-island dispersal was more common than mainland-island dispersal in the history of the group. The two mainland *Speirops* species are basal to the tree, probably being relicts from the last glacial period, whereas the two youngest species are the two oceanic islands *Speirops*. This contrasting pattern suggests that the evolution of the aberrant pattern was not

necessarily due to the same causes. It is nevertheless puzzling why such a pattern has evolved only in the Gulf of Guinea.

Fig. 1. The Gulf of Guinea island system



What drives the divergence of allopatric populations?

Príncipe seedeater individuals were sampled on the three islands where they occur and in two different habitats (cocoa plantations and primary forest). Populations in each sampling site will be characterised for a) neutral

genetic diversity, b) adaptive morphometric traits, c) male songs, and d) plumage colour. Divergence in these traits between all populations will be measured in order to determine the relative importance of isolation (drift) versus ecology (selection) in the divergence of allopatric populations. The degree of gene flow between and within islands will be inferred from microsatellite variation data. The target of sampling 20 birds per site was achieved in three sites out of six. In the next field season sampling will be completed and extended to more plantation-forest replicates.

For the analysis of morphological divergence individuals still need to be sexed following a genetic based protocol. The pooled morphological data suggest that isolation is more important in promoting divergence in this species than habitat-type: there are significant between-island but not between-habitat differences. Song repertoire also differed between islands, with no single song type shared between populations. The relevance of this song divergence for the evolution of reproductive isolation will be tested by means of playback experiments.

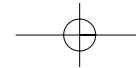
By gaining a better understanding of the phylogenetic relationships and of the factors promoting divergence of birds in this system we hope to contribute to



a wider awareness among evolutionary and conservation biologists of the significance of this neglected evolutionary and biodiversity hotspot. This hotspot is still in an enviable state of conservation, though this may change with the increasing development pressures it faces since the discovery of deep-sea oil reserves.

This research is part of a PhD project primarily funded by the Fundação para a Ciência e a Tecnologia, Portugal. Fieldwork was carried with the support from the following institutions: Annobón and Bioko: Universidad Nacional de Guinea Ecuatorial. Cameroon: Cameroon Biodiversity Project; Limbe Botanic and Zoological Gardens. São Tomé and Príncipe, and Gabon: ECOFAC

Príncipe; Annobón; Bioko; São Tomé; Annobón Príncipe



INVESTIGATING HYBRIDISATION BETWEEN ANADROMOUS AND FRESHWATER THREE SPINED STICKLEBACKS

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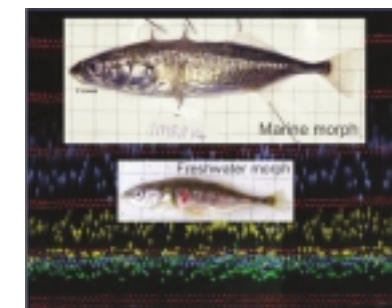
Three-spine sticklebacks (*Gasterosteus aculeatus*) have become a model for the study of fish speciation due to the work of Schluter and colleagues on species pairs in four Canadian lakes. Less widely appreciated is the fact that throughout their distribution in estuarine environments divergent 'freshwater' and 'anadromous' morphs of the three-spine stickleback reproduce sympatrically. It is likely that there is incipient speciation in nearly every major river system, giving replication of the process on a very large scale (McKinnon 2002).

Migratory anadromous and freshwater-resident sticklebacks typically differ in morphometric traits such as size, armour plating and spine length, and show differences in mating preferences, life history and allele frequencies. Nevertheless, intermediate morphs are common in most sympatric populations, and their genetic status and fate

has not been studied. However, circumstantial evidence suggests that both natural and sexual selection act on hybrid morphs to maintain reproductive isolation (McKinnon 2002). Within-river population processes such as migration, microhabitat preference, natal homing, and population density are likely to have a major effect on hybrid survival and thus the evolution of reproductive isolation.

At the start of 2003 a field grant from the Genetics Society was used to launch a year-long field study of the River Tyne, Dunbar (Scotland), where anadromous and freshwater sticklebacks breed sympatrically. Specific aims of this research included:

- investigating the effect of factors such as population size and the scale within-stream movement on the extent of hybridisation between the two morphs,
- determining the nature of selection on hybrids by investigating temporal changes in morphology and genotypes,
- a QTL association study investigating whether the divergence between marine and freshwater forms involve selection of the same genes in different places.



Photos: © Felicity Jones



The field work involved monthly collection of morphological data from each of eight sites within the river. In addition, over this year-long period approximately 3500 fish were tagged, sampled for genetic analysis, and released back into the river for mark-recapture purposes.

Preliminary results suggest that pre-zygotic isolation is not strong between the morphs and that hybridisation and introgression occurs readily. Sticklebacks in the River Tyne show strong site fidelity with little or no movement between sites. Mark-recapture results indicate little difference between mortality rates of freshwater, hybrid and anadromous young of the year. Interestingly, weirs within the river appear to act as significant barriers to the upstream migration of anadromous sticklebacks having large repercussions on the extent of introgression and gene flow within the river. Further analyses will investigate the maintenance of the two genetically and morphologically distinct stickleback types by looking at the factors affecting hybrid survival.

I would like to take this opportunity to thank the Genetics Society for the Field Work Grant from which many interesting results have emerged. Research carried out in this report has received additional funding from the Royal Society.

McKinnon, J. and Rundle, H. (2002) Speciation in nature: the threespine stickleback model systems. *Trends in Ecology and Evolution*, 17(10) 480-488.

