What drives song variation in tropical birds? A study across habitats and populations in Cameroon and Uganda

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Black-headed Gonolek in the savanna at Queen Elizabeth National Park, Uganda

Animals communicate vocally with one another in order to deliver important messages. Birds sing so that other birds of the same species know that they are there. Male birds put a lot of energy into their songs to attract females and to defend territories from rival males. Tropical rainforests contain the highest levels of biodiversity, and birds that sing in rainforests need to compete with a plethora of other vocal animals in order to transmit their signals to their intended receivers. Singing at the same time and in the same frequency range as other vocal animals can result in songs being masked and not heard by other individuals of the same species. If a male bird's song is not heard, it is unlikely to attract a mate and pass its genes on to the next generation.

I study how the songs of birds in tropical rainforests can be affected by differences in ecology between populations. My work in Africa centers on the songs of common species and how their songs are influenced by regular and continuous background noise. Cicadas, crickets and other vocal insects cause much of this noise, and differences in the respective insect assemblages at different locations lead to much variation in ambient noise. Many insects are tied to certain habitat types so different insects can be found between rainforests and more open, drier habitats.

Previous work by Center for Tropical Research (CTR) biologists found that songs of the little greenbul (Andropadus virens) varied between closed rainforests and the transitional forest, or ecotone, and between the rainforest and savanna in Cameroon. The songs of the little greenbul were not found to vary between isolated sites within each habitat type, and analyses of ambient noise suggested that the birds' songs have been adapted to their sound environment in each habitat. Such song variation between habitats could drive divergence between populations to the extent that one population does not recognize the song of another population. If the birds did not recognize songs, were these populations to



Little greenbul singing from dense cover within the rainforest understory

come together, they could potentially fail to recognize each other as the same species and not interbreed. The two populations would thus be regarded as separate species. Such processes are thought to have led to the high levels of biodiversity we find in the tropics. A competing school of thought purports that isolation for long periods within the same habitat is more important in generating biodiversity. My research aims to test these hypotheses experimentally.



Alex Kirschel recording little greenbuls in the rainforest in Zoebefam, Cameroon

I recorded songs of the little greenbul at rainforest sites in Uganda and Cameroon during the summers of 2004 and 2005, respectively. I added songs recorded in the ecotone of Cameroon by Dr. Hans Slabbekoorn (a CTR Senior Research Fellow) of Leiden University, and prepared stimuli for song playback experiments. The idea behind the experiment is that if little greenbuls from populations in the forests of Cameroon respond more to songs from the Cameroon ecotone than the Uganda rainforest, this would suggest that songs in Uganda are more different and less recognized as belonging to the same species. We would infer then that isolation alone for a long period of time has led to the song variation. Conversely, if the birds in the Cameroon forest respond less to the Cameroon ecotone song than the Ugandan rainforest song, then we infer they do not recognize the song from the

adjacent ecotone and that differences in ecology have driven this perceptual song divergence. I conducted playback experiments at Ndibi, Nkwouak, and Zoebefam in the Cameroon rainforest during summer 2005, and the results indicate that little greenbuls from the Cameroon rainforest do not detect any difference between songs from the Cameroon forest and the Uganda forest, but respond significantly less to Cameroon ecotone song. The results imply that little greenbuls do indeed fail to recognize songs (or the threat from the singer) from different habitats to a much greater degree than songs from populations over a thousand miles away in the same habitat.

I plan to return to Uganda and Cameroon during the breeding season in the ecotone and record little greenbul songs in the gallery forests there. I will conduct playback experiments there to determine whether differences in ecology affect perceptual song recognition in the same way as in the rainforests.

Back in the lab at the University of California, Los Angeles we also analyze the little greenbul songs that I recorded and examine how the songs vary per population in relation to continuous bands of ambient noise. I have worked with undergraduate student Rachel Cohen on this project, testing whether song frequencies are correlated with ambient noise frequencies. Analyses on little greenbul and green hylia (*Hylia prasina*) songs from Uganda imply that they are, providing evidence for the role of ecology in driving song divergence between populations.



Crowned hornbill in Kibale National Park, Uganda



Yellowbill, a member of the cuckoo family, in Ndibi, Cameroon