

would not supply the needed sediment. Yet in more than half of the 93 sites with accretion data, marshes are building elevation faster than would be expected from the supply of sediment from rivers. Why?

Organic sediment accretion resulting from incomplete decomposition of vegetation can increase with RSLR, depending on the species and the preexisting marsh elevation. However, recent findings suggest that in at least some salt marshes, most of the carbon that accumulates long term is old carbon originating from elsewhere rather than produced in place (5). Ensign *et al.* additionally found that accounting for an average rate of organic accretion does not substantially change the fraction of marshes that are gaining elevation.

Recent work underscores the role of sediments from eroding coastlines or resuspended from the offshore seabed in helping marshes build elevation. For example, despite rapid RSLR and a 70% decline in riverine sediment, marshes in the Yangtze River delta in China are accreting rapidly, fed by resuspended material eroded from the delta front (6, 7). Worldwide, measured sediment accumulation rates in offshore deposits accelerated in the 20th century and are attributed to enhanced coastal and near-coastal erosion (8). Furthermore, RSLR may make this material more available to marshes. For the Plum Island Estuary in Massachusetts, USA, 0.5 m of RSLR has been estimated to produce 35% more resuspension of mud and 6.6% more sediment deposited on marshes (9).

Notably, the unexpected resilience of marshes reported by Ensign *et al.* is likely to be temporary under rapid RSLR. Tidal wetlands that build elevation mostly through organic accretion are widely regarded as less resilient than others because of susceptibility to waterlogging, sulfide toxicity, or species shifts (10, 11). Furthermore, RSLR promotes tidal channel deepening and ebb dominance (by which flows are faster and sediment loads higher on ebb tides than flood tides), leading to net export of sediment from the estuary (9). Ultimately, this process can lead to steepening of the continental shelf and more lateral marsh erosion by waves (6). Models project that resuspension of coastal sediment may have prolonged the persistence of marshes in the Yellow River delta in China by about a century and will likely prolong the existence of marshes in the Yangtze River delta by about

150 years (6). This process can explain why marshes seem to survive higher threshold rates of RSLR today compared with that in the stratigraphic record (for which temporal resolution is too poor to detect temporary resilience) (12). However, these collective findings suggest that without sufficient riverine sediment supply from inland, eventual losses are inevitable.

Coastal communities must proactively manage, or “choreograph,” sediment (13), exploiting relatively untapped sources, such as excavated sediment, construction waste, and dredged materials. However, these solutions are unlikely to match the magnitude of demand, requiring clear priorities and community objectives for coastal management. Site-specific models and planning that account for offshore hydrodynamics, changing seabed elevations, multiscale sediment feedbacks, and diverse sediment sources are needed to help identify where marshes would most benefit from augmentation and where sediments might be most strategically placed so that natural processes aid delivery to desired locations (see the figure). Pilot projects and experimentation are also needed to better understand how sediment augmentation practices might be refined and scaled up. End users of this science must also grapple with the inevitability of surprise. For decades, the observed changes to tidal marshes have differed from conceptualizations and model predictions. Large uncertainties remain regarding lateral sediment redistribution processes; dynamic bathymetry (seabed elevations); changes to sediment supply from watersheds as they adjust to more intense precipitation, changing vegetation cover, and increased fire frequency; and how marsh vegetation—sediment trappers—will respond to a range of stressors that include more frequent climate extremes and changing nutrient inputs. ■

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ECOLOGY

Human-wild bird cooperation

Honeyguides learn distinct signals made by honey hunters from different cultures

By William A. Searcy¹ and Stephen Nowicki²

Mutualisms in which humans cooperate with wild animals are exceedingly rare (1). One such system involves the greater honeyguide (*Indicator indicator*), a small African bird that leads humans to sources of honey, principally the nests of African honey bees (*Apis mellifera*). Once a nest is found, the human honey hunters break into it to obtain honey and bee larvae, and the birds benefit from consuming beeswax in the now-exposed honeycomb. Both the birds and the humans use specialized sounds to communicate their availability to participate in this cooperative interaction (2). On page 1155 of this issue, Spottiswoode and Wood (3) reveal a new layer of complexity in this remarkable mutualism, demonstrating that humans in two geographic areas use different sounds to communicate to the honeyguides, and that the birds respond preferentially to the signals used in their own local area. The coordination between signal and response suggests that cultural coevolution has occurred.

The two areas studied by Spottiswoode and Wood are northern Mozambique, where the honey hunters are from the Yao cultural group, and northern Tanzania, where the honey hunters are from the Hadza culture. The Yao communicate with honeyguides using a trill followed by a grunt (“brrrr-hm”), whereas the Hadza use a melodic whistle. The authors show through field playback experiments that honeyguides in the Yao area are almost three times as likely to initiate guiding in response to the Yao’s brrrr-hm as to the Hadza’s whistle, whereas honeyguides in the Hadza area are more than three times as likely to respond to the Hadza’s whistle as to the Yao’s brrrr-hm. Thus, signal and response both vary geographically, with each species’ behavior

meshing with that of its local counterparts of the other species.

Which human signal is used where might be explained by environmental transmission, with hunters using a signal that transmits particularly well in the habitats in which they forage. Measurements of signal attenuation, however, do not support this idea, as the Hadza whistle attenuates less rapidly with distance than the Yao brrrr-hm in both geographic areas. Spottiswoode and Wood instead favor an economic explanation for the choice of signal. Hadza men, who typically hunt small game while foraging for honey, claim their whistles sound like birds, and therefore presumably are unlikely to scare away prey. The Yao do not hunt animals while foraging for honey, so scaring game is not an issue for them. The word-like signal they use in attracting honeyguides may instead identify them as humans and thereby help ward off dangerous animals such as buffalo and lions.

Spottiswoode and Wood propose that the geographic variation they have identified in this mutualism is the product of cultural coevolution. To qualify as cultural, the cooperative behaviors would have to be acquired through social learning from individuals of the same species. That proposition is noncontroversial on the human side, and indeed, Yao honey hunters report learning their honeyguide signal from their fathers (2). Social learning, however, is less of a given on the honeyguide side. The taxonomic order of birds to which honeyguides belong (*Piciformes*) is thought not to exhibit vocal production learning (4), meaning that birds in this order do not acquire the form of their vocal signals through experience with the signals of others. Learning geographic signal variants is not required of the honeyguides, however, as they use the same chatter vocalization to communicate to humans throughout their range (5, 6). Instead, what is required of honeyguides is another form of vocal learning—compre-



The greater honeyguide (*Indicator indicator*) leads humans to African honey bee (*Apis mellifera*) nests and consumes beeswax that is exposed when humans remove the honey.

hension learning—in which the meaning of a signal is learned (7). Comprehension learning is common in birds (8) and is the simplest explanation for how honeyguides in different areas come to respond to different signals. Whether social learning is involved, however, is not so obvious.

Honeyguides might learn to respond to the local honeyguide-directed signal by watching and copying the behavior of older honeyguides, but other explanations are possible. One possibility is that young honeyguides form an association between the human signal and the reward directly, through encountering honey hunters giving the signal and then consuming beeswax made available by the hunters' activities. For behavioral traditions in general, observations of geographic variation, even when coupled with detailed evidence of the behavior's development, are usually considered insufficient to demonstrate that social learning has occurred (9). Experiments will be necessary to establish conclusively whether the match of honeyguide response to human signal is maintained by social learning, for example, experiments that determine whether young honeyguides acquire different response patterns depend-

ing on which pattern is modeled for them by older birds.

The human-honeyguide interaction superficially gives the impression of idyllic benevolence: Honeyguides put in considerable effort helping their human partners find food and are faithfully rewarded by being given food in return. As is common for biological mutualisms (10), the details of the interaction turn out to be messier than this. In some human cultures, honey hunters purposefully leave out honeycomb to reward honeyeaters, but in others the hunters actively seek to deny the birds any reward, by collecting, burying, or burning any honeycomb exposed when they depredate a nest (5, 6). The rationale given for these acts is that keeping the birds hungry causes them to continue guiding. In cultures in which honey hunters purposefully leave honeycomb for the guiding birds, that resource may be exploited by a variety of other animals, including mammals such as honey badgers and birds

such as other, nonguiding species of honeyeaters (11). Exploiters also often include greater honeyguide individuals who themselves have not guided but are nevertheless able to scrounge beeswax exposed through the guiding efforts of others (12). A promising question for future research is whether geographic differences in human cultural preferences for rewarding or not rewarding honeyguides affect the preferences of individual birds for guiding versus exploiting the guiding of others. ■

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