

Are there any aspects of biology that you feel are neglected? I would say systematics. A field that clearly doesn't get the credit it deserves. Without having a firm understanding of species boundaries and how things are related to each other, doing comparative biology is impossible. Perhaps it stems from my fascination with 18–19th century zoology, but I find it a very interesting subject in its own right. Apart from working at the Max Planck, I am also a guest scientist at the Swedish Natural History Museum in Stockholm. Few things give me such pleasure (in science I should stress, I don't want to come across as a complete lunatic here) as sitting with a bucket full of unsorted insects from some obscure tropical location, sifting out the drosophilid nuggets.

Now and then you come across the most bizarre little critters that really make you wonder how on earth they evolved and what in their environment or ecology created such peculiar phenotypes. These odd ones serve as a strong reminder of the remarkable diversity of insects, and of how much is out there still left unexplored. For me personally it is also a sobering reminder of my own shortcomings as a taxonomist, since I mostly haven't got the foggiest idea what these things are. My fear is that as time passes by and we continue to neglect this fundamental area of biology, there won't be any people left able to identify these amazing insects.

What do you think are the big questions to be answered next in your field? The *Drosophila* toolbox, extensive as it is already, is continuously being updated with more and more sophisticated genetic techniques for controlling neuronal activity as well as for mapping neuronal circuits. These technical land-winnings will hopefully provide the means to pinpoint circuits and individual neurons underlying specific behaviors, such as courtship, innate attraction/repulsion and oviposition. We have already seen a number of beautiful papers on the flies' pheromone circuitry and more will surely follow. Exciting times ahead!

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Quick guide

Vocal mimicry

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What is vocal mimicry? Vocal mimicry occurs when an individual learns a sound from another species or the environment. It differs from other animal vocalisations such as bird song or human speech, as these are learned from members of the same species (conspecifics). Parrots are the most renowned mimics, with reports of their talents dating back at least to the early 1500s with Henry VIII of England's pet African grey parrot, *Psittacus erithacus*, which mimicked his servants' voices.

During the two hundred years and more since mimicry was first described in a scientific paper (by Barrington in 1773) showing that young linnets, *Acanthis cannabina*, learned the songs of other birds, mimicry has been documented in a multitude of songbird species: around 20% of bird species will copy sounds from sources other than conspecifics. The accuracy of the mimicry is often startling, especially when birds mimic sounds very unlike those of their own species. An example of both the accuracy of mimicry and diversity of sounds appeared on David Attenborough's Life of Birds television series, in which a male superb lyrebird, *Menura novaehollandiae*, mimicked the sounds of a car alarm, a chainsaw and the camera shutter of the film crew. The extent of mimicry, too, can be extraordinary: the average marsh warbler, *Acrocephalus palustris*, mimics 76 species, of which 40% are learned from their European breeding sites and 60% from their wintering sites in Africa.

It is not just birds that mimic other species. Vocal mimicry has also been heard occasionally from bottlenose dolphins (*Tursiops truncatus*), harbour seals (*Phoca vitulina*), killer whales (*Orcinus orca*), orangutans (*Pongo* spp.) and African savannah elephants (*Loxodonta africana*). In the 1970s, workers at an aquarium in Boston, America noticed that the vocalisations of one of their harbour seals sounded like a person talking: "Hoover" was able to mimic several short phrases, such as "get outta here" and "how are

you", all in a thick Bostonian accent. Such examples of mimicry of speech in non-human mammals are, however, vanishingly rare, probably, in part, because the vocal apparatus of other mammals differs significantly from that of humans and also because the sounds are relatively complex.

Why mimic sounds? Perhaps because mimicry can be so very accurate, it is often considered that it is produced 'for a reason'. For many species, however, this reason has been surprisingly difficult to confirm because of the paucity of data.

Perhaps the most common of the suggested explanations for vocal mimicry is that, as many male songbirds vocalise to attract females and/or repel rivals, mimicry may allow them to do this more effectively. In many songbird species, females seem to prefer males that sing multiple or varied songs. A male that can use mimicry to increase his repertoire may attract more females. Indeed, this appears to explain the use of mimicry by male satin bowerbirds, *Ptilonorhynchus violaceus*: males with larger mimetic repertoires mate with more females than do males with smaller repertoires. It also seems that females pay attention, not just to the diversity of sounds produced, but also to the accuracy of those productions: males that produce more accurate mimicry get to mate with more females than do males with less accurate mimicry.

Rather than attracting conspecific females, mimicry may be used to repel heterospecific competitors. For example, when great tits (*Parus major*) and blue tits (*P. caeruleus*) compete for food and nesting sites during the breeding season, great tits mimic blue tit song. As matching another individual's song is often used to signal aggression between conspecifics in many songbirds, it seems possible that the mimicking great tits are attempting to intimidate blue tits. Song sparrows, *Melospiza melodia*, may do something similar: their mimicry of white-crowned sparrow, *Zonotrichia leucophrys*, territorial song induces aggression in white-crowned sparrows although it is not clear to what effect.

What sounds do birds mimic? While the most startling sounds that birds mimic are made by us and by some of our implements, it is more usual that they mimic other animals. It is

also commonly the case that they mimic short, sharp calls — sounds that are often used as alarm calls. In some cases, such as when greater racket-tailed drongos, *Dicrurus paradiseus*, include mimicry of alarm and mobbing calls alongside their own alarm vocalisations, it looks as if it might be to enlist other species to the caller's aid. Appealing though this idea is, there is little evidence that it is actually the case, other than from a single experiment in which experimental playback of phainopeplas, *Phainopepla nitens*, mimicking heterospecific alarm calls alongside their own alarm calls did result in heterospecifics mobbing a predator decoy.

The mimicry by spotted bowerbirds, *Ptilonorhynchus maculatus*, of predators and of aggressive species points to another possibility, which is essentially that of Batesian mimicry. By pretending to be a predator, spotted bowerbirds may avoid being eaten. Alternatively, they may use this mimicry to frighten off competitors for resources such as food. An appealing idea again but one for which there is, as yet, little compelling support.

The explanation for vocal mimicry with the least immediate appeal is one suggested to explain the occurrence of mimicry in starlings, *Sturnus vulgaris*, which tend to mimic short, simple sounds that are abundant in their environment. It appears from their mimetic repertoire that they do not select particular sounds to learn, but rather learn environmental sounds that are frequent and similar to their own vocalisations, a repertoire that was best explained by a learning 'mistakes' model. This model is based on the well-accepted template model of song learning, whereby songbirds typically learn their species-specific songs by comparing the sounds they hear to a mental template and learn only the sounds that match their template. As species vary in the specificity of this template, some birds learn only sounds that fall within very narrow parameters (typically birds with few short, stereotyped songs), while others have more relaxed parameters (typically birds with many complex songs). The suggestion was that starlings have such a relaxed-parameter template and, therefore, acquire heterospecific songs by mistake. Although difficult to test directly, much of the mimicry data are more consistent with the

predictions of this hypothesis than with those produced from any of the functional hypotheses. There is also some experimental evidence that birds will mimic heterospecific sounds if those sounds are edited to fall within the remit of their template: song sparrows do not usually learn swamp sparrow, *Melospiza georgiana*, song but, if the syntax of swamp sparrow song is edited to resemble that of song sparrow song, then song sparrows will mimic the heterospecific.

Why is mimicry so common in captive animals? Under natural conditions, many animals use vocalisations to form and maintain social bonds with conspecifics (this is not strictly mimicry, as they do not copy heterospecifics). By copying each other's vocalisations, pairs or groups of individuals produce the same call or song, identifying them as part of that pair/group. This is most often the case for long-lived species living in dynamic societies where individuals frequently separate and reunite. When individuals of these species are isolated from conspecifics in captivity, they may copy sounds of other animals that they hear in the environment in an attempt to form social bonds, just as they would in the wild.

This is a plausible explanation for the observation that vocal mimicry has been heard in captivity by a number of species not heard to mimic in the wild, such as bottlenose dolphins, harbour seals and African elephants. Similarly, vocal mimicry in wild killer whales has been documented only in a juvenile that was separated from the natal pod. Separation from other members of their species may also explain why parrots in captivity are renowned for their mimicry, given that reports of parrots mimicking in the wild are rare. This is essentially a learning mistakes explanation: captive animals would learn conspecific vocalisations preferentially but in the absence of these they will copy heterospecifics.

What can we learn from mimics?

Language is often considered a peculiarly human skill and early efforts went into attempting to teach non-human primates to mimic human language so as to ask them questions in the way we would ask each other. It became clear, however, that Dr Dolittle approaches of trying to talk to animals were not going to work as non-human

primates lack the vocal apparatus to make appropriate sounds.

However, just as birds have more recently become useful models for addressing questions about episodic-like memory and tool manufacture and use, it was a bird that allowed Irene Pepperberg to use mimicry of human speech to examine 'complex' cognition in animals. At the time of his death, Alex, an African grey parrot, knew over 150 words and appeared to understand the meaning of these words rather than just repeating them verbatim, as often appears the case with much mimicry of human speech by parrots. He could recognise and label objects, colours and shapes and use these labels in conjunction with each other, as well as being able to use more abstract terms such as bigger, smaller, same and different. By demonstrating aspects of advanced arithmetic ability (such as being able to count up to six and understand the ordinality of these numbers), a trait that is generally considered to be a derivative of language and therefore unique to humans, Alex revealed more parallels between the cognitive capacity of humans and birds than was previously suspected. Part of his legacy can be seen in the considerable interest currently being shown in the cognitive capabilities of corvids that manufacture and use tools.

The ability to mimic might also be linked to another behaviour that we considered uniquely human, which is rhythm. Many animals that mimic also appear to move in time to a beat, an ability thus far only observed in vocal mimics. Although music is a ubiquitous cultural phenomenon in humans, the origins of music and dance are hotly debated. It may be that here, too, birds and their vocal mimicry skills may enable us to make progress.

Where can I find out more?

- Kelley, L.A., Coe, R.L., Madden, J.R., and Healy, S.D. (2008). Vocal mimicry in songbirds. *Anim. Behav.* 76, 521-528.
- Pepperberg, I.M. (1999). *The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots* (Cambridge, MA, USA: Harvard Univ Press).
- Schachner, A., Brady, T.F., Pepperberg, I.M. and Hauser, M.D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. *Curr. Biol.* 19, 831 – 836.

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