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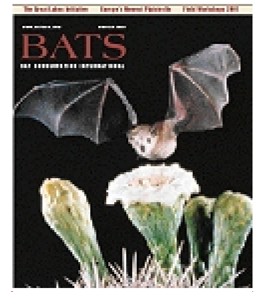

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Uncommon Discoveries about One of Europe's Most Common Bats
While studying echolocation, the author discovers a new and abundant species of pipistrelle. . .
Gareth Jones

Natural selection is a powerful force, shaping the appearance and behavior of animals in ways that allow efficient survival and reproduction. Because bats are nocturnal, many do not use visual signals to communicate, so natural selection does not always promote visual differences among them. For bats that echolocate, however, acoustic communication is of paramount importance, and natural selection can favor unique calls rather than visual differences. This is apparently what has happened in Europe’s most common bat, the pipistrelle. We now know that bats formerly known as Pipistrellus pipistrellus comprise two cryptic species (species that are difficult to distinguish visually). However, we can readily identify them by using a bat detector. They also use different “social calls” to communicate with one another.

Pipistrelles are widely distributed over Europe, and sometimes form maternity roosts that include more than 1,000 individuals. I began to suspect that there was more than meets the eye with pipistrelles in the early 1990s, when I was researching the ecology of bat echolocation at the University of Bristol. Scientists have long appreciated the fact that the echolocation calls of pipistrelles are highly variable. The calls are short (typically 5-7 thousandths of a second [ms]). They begin with a rapid downward frequency sweep, and end with a “tail” that is almost of constant frequency. This tail is used to detect flying insects, and is the part of the call that contains the most energy. To our ears, it is the loudest part of the call. Over much of Europe, pipistrelle calls tend to have constant frequency tails of either 45 kilohertz (kHz) or 55 kHz. The polarity of the two frequencies was first described by Swiss biologist Peter Zingg, who believed that pipistrelles simply used different calls in different habitats.

I personally believed that the distinction in call frequency was too sharp to be caused by habitat differences. In 1987 I recorded the calls from many bats exiting a maternity roost in western Wales. All the bats called with constant frequency tails close to 55 kHz, despite flying into a wide variety of habitats. This discovery prompted me to record bats from other maternity roosts. In 1992, I was joined in this venture by Sofie van Parijs, an undergraduate from Cambridge University who has since moved on to research the vocal behavior of seals. In every case, all bats exiting from a given roost emitted calls of either 45 kHz or 55 kHz. There was no mixing of the two “phonic types” within a roost. When I recorded pipistrelles of both types in a standard habitat, they still called at the frequency used by their roost mates. I was therefore able to conclusively reject the theory that differences in call frequency were due to differences in habitat use.

I then recorded foraging pipistrelles in a wide range of locations throughout Europe. Over much of Britain, colonies using these two phonic types could be found in the same area. In other parts of Europe, the situation was more complex. Only 55 kHz bats were found in much of Scandinavia and in several Mediterranean regions. The 45 kHz bats appeared to be more abundant in France, and were the only phonic type that I recorded in Holland. Other biologists recorded both types in Switzerland. There was no clear geographic pattern to the

distribution of the two types, except that 55 kHz bats appeared to be more widespread toward the edge of the pipistrelle's range. Because the two types occurred together in several countries, they were clearly not geographical races or "subspecies."

In the mid-1990s, Kate Barlow came to my lab to begin working on a Ph.D. on the ecological differences between the pipistrelle phonic types. (Kate is now researching the foraging behavior of penguins in the Antarctic!) It was soon apparent that the two pipistrelles filled quite different ecological niches. The 45 kHz bats mainly eat owl-midges, window-midges and dung flies, and bat detector surveys carried out by Nancy Vaughan at Bristol showed that they feed in a wide range of habitats. The 55 kHz bats eat mainly biting and non-biting midges, and are much more often associated with riparian (streamside) habitats. In southwestern England, bat detector surveys suggest that the two types are equally abundant, forming maternity roosts in modern buildings. The 55 kHz bats form larger maternity colonies, however, which sometimes contain more than 1,000 individuals. While a median roost size for 45 kHz maternity roosts was 76 bats before the young began to fly, it was 203 bats for 55 kHz roosts. The reasons the 55 kHz bats form larger colonies are not clear, but it could be associated with a greater dependence on unpredictable food resources and the colony's need to exchange information about the location of food patches.

On a cool summer's evening in Britain, people often become aware of foraging bats by hearing high-pitched squeaks. These squeaks are not echolocation calls, but social calls that pipistrelles use in communication. The squeaks usually contain the most energy between 16 and 23 kHz. Because many humans can hear sounds up to 18-20 kHz, the social calls of pipistrelles are often quite obvious.

Kate Barlow and I also studied social calls in pipistrelles. To determine the function of these calls, we recorded the rate of social calling while simultaneously measuring insect abundance with a suction trap. The rate of social calling increased when insects were more scarce. Why then do pipistrelles make more social calls when prey are scarce? Are they trying to call in others of the same species to help track down patches of insect prey in the same way that cliff swallows do during the day? Or, are they warning other bats to stay away from their own patch of precious insects? We determined the function of the calls by performing playback experiments in the field. Playback experiments with bats are tricky to conduct. First, because we were working in the dark, it was not easy to see how the animals responded. We therefore determined how many bats were in the area by recording their echolocation calls. Second, because the playbacks were largely ultrasonic, we were unable to hear them, and so had to check frequently to ensure that the equipment was working properly.

We already knew that the social calls of the 45 kHz and 55 kHz pipistrelles were subtly different. The social calls of 45 kHz pipistrelles usually have four components, and are slightly lower in frequency than the social calls of 55 kHz pipistrelles, which usually have three components. When Kate made playbacks of the social calls of 45 kHz bats, the activity of 45 kHz bats in the immediate area dropped significantly. The 55 kHz bats showed no such reduction in activity in response to playbacks of 45 kHz bat social calls, but they did reduce activity in response to playbacks of social calls from 55 kHz bats.

Thus, the social calls of pipistrelles clearly function in defending feeding patches. Because social calls cause other bats to leave the area, they are perhaps better termed "anti-social calls!" In addition, bats respond to the social calls of only their own phonic type. This suggests that competition between phonic types may be minimal, perhaps because of their

differing diets.

In the fall, male bats repeat very similar social calls in a “song-flight.” The function of the calls now seems to change from one of repulsion to one of attraction. Males use the song-flight to defend roost sites to which females are attracted. The mating system of pipistrelles is termed “resource defense polygyny.” Resource defense refers to males defending roost sites; polygyny refers to males mating with several females.

In Europe, males defend roosts, which are often in manmade bat houses. Bat houses normally contain a single sexually active male and one to three females. In collaboration with Kirsty Park and John Altringham of the University of Leeds, we showed that these mating groups always contain bats of just one phonic type, suggesting that the phonic types are reproductively isolated. Because reproductive isolation is one of the criteria for species designation, it seemed likely that the phonic types were two distinct species.

In order to prove that the echolocating types were indeed distinct species, I joined forces with Elisabeth Barratt of the Institute of Zoology in London and Paul Racey of the University of Aberdeen. We sequenced the DNA and discovered that the two phonic types were genetically distinct, despite being strikingly similar in appearance. The genetic sequence differed by more than 11 percent, which is a greater divergence than is seen in many bat species that look very different.

Discovering that one of Europe’s most abundant bats is really two species has been one of the highlights of my academic career. I have suggested to the International Commission on Zoological Nomenclature that the 45 kHz phonic type remain the common pipistrelle, and the 55 kHz type become the soprano pipistrelle (Pipistrellus pygmaeus), since it was first discovered through its high-pitched voice.

Most new species that are described are obscure or rare. I’ve been privileged to discover a common one. I believe that many additional bat species will be described from acoustic characteristics in the future. In Malaysia, for example, Tigga Kingston recently found a previously undiscovered leaf-nosed bat (family Hipposideridae, not yet named) that is almost identical to the bicolored roundleaf bat (*Hipposideros bicolor*), but which calls at a frequency difference of almost 10 kHz. In conservation terms, these findings are important because they suggest that considerable biodiversity may be hidden. Many bat species probably remain undiscovered because of our biased sensory perception of the world. Because sound is more important than vision for bats, we need to pay more attention to their acoustic world. By doing so we will paint a clearer picture of the diversity of life on earth.

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