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Commentary

Kiwis to pewees: the value of studying bird calls

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Avian vocalizations are typically divided into two fundamental types: songs and calls. The dividing line between calls and songs is somewhat unclear, but researchers generally agree that songs are longer and more complex than calls, which tend to be brief and simple (Catchpole & Slater 2008). The literature on birdsong (particularly oscine passerine song) is extensive, encompassing the fields of behaviour, evolution, neuroscience, psychology and more (Slater 2003). Many fewer studies of avian vocalizations focus on the form and function of calls, but this is an area ripe for adding to our understanding of animal acoustic communication (Marler 2006).

Researchers can learn much from analyses of avian calls for a number of reasons. First, calls are produced by all species. Many species of birds, particularly those in basal lineages, are not known to sing. Some non-passerines do sing, but the majority of song research has been conducted on oscine passerine songbirds. Oscines are in part grouped together by their complex syringeal musculature and morphology that allows for the production of intricate song forms (Suthers & Zollinger 2006). However, it would be a mistake to assume that non-oscines, and even birds from basal lineages such as paleognath (ratites such as kiwis and ostriches), galliform and anseriform birds, do not exhibit complexity in the anatomy of their sound-producing structures or in their vocal repertoire. For example, ducks possess a range of fascinating syringeal morphologies (Livezey 1986, 1991); the relationship between the form of these structures and sound production remains to be studied. Basal birds can also produce a rich repertoire of vocalizations, as is seen in Wild Turkeys *Meleagris gallopavo*, which produce at least 28 different calls to help navigate their complex social world (Williams 1984). Both morphological and vocal complexity can hide undiscovered even in relatively well-studied species; in spite of decades of research into the vocal behavior of Greater Sage-grouse *Centrocercus urophasianus*, a ‘two-voiced’ system and a syringeal muscle found only in males were only recently described (Krakauer *et al.* 2009). Thus, while studies of song are necessarily taxonomically restricted, research into calls can take advantage of the rich diversity of morphology, ecology and behaviour found across all lineages of birds.

Ornithologists are interested not only in how birds make sounds, but also why such a dizzying array of acoustic signals has arisen. Many hypotheses postulate evolutionary benefits associated with particular features of calls or songs. Inter-individual, inter-sexual and inter-population differences in species with learned songs could result from the effects of learning. When the acoustic structure of an oscine song improves function, that outcome may be a result of cultural evolution. Calls, on the other hand, are generally thought to be innate, rather than learned (but this is not a universal rule, see Kroodsma & Baylis 1982, Zann 1985) (Catchpole & Slater 2008). Although they are innate, however, calls are not entirely fixed. The calls of many species show significant geographical and even inter-individual variation, as seen in the individual identity encoded in the harmonically rich calls of penguins (Aubin *et al.* 2000). Selection for communication functions has even led to adaptive variation within individuals. The calls of coucals, swans and tinamous vary with context or local environment, and the combination of vocal and visual displays in Red Junglefowl *Gallus gallus* has become a model system for understanding communication (Smith & Evans 2008, Geberzahn *et al.* 2009, Patel *et al.* 2010, Schuster *et al.* 2012). Thus, although calls are relatively fixed compared with songs, there is clearly individual variation and the potential for selection on these traits. When calls are unlearned, such selection would necessarily lead to biological evolution, allowing researchers to assess how vocal traits evolve in the absence of cultural influences.

Finally, calls are particularly useful in studies of inter-sexual interactions because across avian species they are generally produced by both males and females (Catchpole & Slater 2008). Many studies of song-learning and song variation have been conducted in species where only the male sings. Although there is a growing interest in and recognition of female song (used in solo song or song duets), studies of song continue to be male-biased (Langmore 1998, Garamszegi *et al.* 2007). In contrast, studies of call form and function often focus on the calls of both sexes. By studying call form, researchers can gain insights into the power of natural selection in shaping vocal communication in both sexes.

In an article published in this issue of *Ibis*, Digby *et al.* (2013) describe the calls of the Little Spotted Kiwi *Apteryx owenii*, providing an overview of call usage patterns and call structure. This article is one of only a

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handful describing kiwi vocalizations and it is the first to present data on the Little Spotted Kiwi. This species produces a range of call types, including grunts, snorts, sniffs, squeals and snarls, but their most often-used vocalization is a loud whistle call. The whistle calls of male and female Little Spotted Kiwis consist of a single syllable type repeated an average of approximately 30 times in 20–30 s (Digby *et al.* 2013). Female call fundamental frequencies are centred around 1500–2000 Hz, while male call fundamental frequencies are centred near 2500–3000 Hz. Males call more frequently than females, and the two sexes combine their calls to form duets. A description of these calls has conservation value, as acoustic monitoring is an important census technique for this nocturnal, near threatened species (IUCN Red List 2012). The study also has a great deal of scientific value. Kiwis are part of the most basal paleognath lineage of birds, and they have many unique ecological and behavioural features (Harshman *et al.* 2008). In general, paleognath calls are not well described, but some are known to show unusual features. Cassowaries (Casuariidae) produce very low frequency sounds (down to 23 Hz) (Mack & Jones 2003). Tinamous (Tinamidae) produce calls with a wide range of frequency characteristics (Bertelli & Tubaro 2002). Studies of the North Island Brown Kiwi *Apteryx mantelli* have revealed intersexual differences in call types and call usage patterns (Corfield *et al.* 2008). Digby *et al.* discuss call usage and explore three possible selective pressures promoting intersexual difference in call form in Little Spotted Kiwi: constraints due to body size, ecological selection and functional divergence.

Avian vocalizations are known to vary in form for a variety of reasons, including sexual selection, ecological selection and as a byproduct of morphology or physiology (Morton 1975, Gil & Gahr 2002, Podos *et al.* 2004). Taking these factors in reverse order, all three might affect call attributes in Little Spotted Kiwis. Comparisons show that larger avian species produce lower vocalization frequencies (Wallschläger 1980, Ryan & Brenowitz 1985). This pattern seems to be more common among non-passerines than among passerines, and is known to exist among tinamous, another paleognath group (Ryan & Brenowitz 1985, Bertelli & Tubaro 2002, Cardoso 2012). The same pattern may or may not be found on an individual level: within several species of non-passerines, including swans and owls, body size correlates negatively with vocal frequency (Hardouin *et al.* 2007, Patel *et al.* 2010). Researchers have suggested that calls are more likely than songs to reflect body size, making studies of call frequency particularly valuable (Patel *et al.* 2010). Despite finding some variation in male and female body size, Digby *et al.* found that sex differences in body size could not fully explain call frequency in Little Spotted Kiwis. Although the larger sex (female) has lower call frequencies, the frequency difference was much larger and more consistent than would be expected by allometry alone, leading the authors to conclude that this is more likely to be a result of individual ecology and sex roles than exclusively of morphology.

Kiwis are flightless, nocturnal forest dwellers, giving them an unusual avian ecological niche. Many birds call or sing from exposed perches high above the ground to broadcast their vocalizations. Ground-dwelling birds, and especially ground-dwelling forest birds, face particular challenges in producing sounds that can reach receivers (Morton 1975). Theory predicts that songs with fundamental frequencies of 1500–2500 Hz transmit best near the ground in cluttered habitat, with sounds at higher or lower frequencies suffering more transmission loss and degradation (Morton 1975). Digby *et al.* point out that Little Spotted Kiwi call fundamental frequencies fall within this range, allowing them to transmit relatively well. Male songs, in particular, are loud, often given and audible from long distances. As nocturnal animals, Little Spotted Kiwis are likely to rely on acoustic communication more than diurnal species do. Across nocturnal avian species, calls are used for a range of functions, including territory defence, mate attraction and maintaining contact with conspecifics (Farnsworth 2005, Delgado & Penteriani 2006, Odom & Mennill 2010). Kiwi calls serving any of these functions would benefit from the longer and more faithful transmission conferred by matching their calls to their environment.

Natural and sexual selection are predicted to shape vocalization form to match function (Gil & Gahr 2002, Catchpole & Slater 2008). Much remains to be learned about how Little Spotted Kiwis use calls during communication events, but Digby *et al.*'s analysis of call form provides an excellent starting point. They demonstrate that males call more often than females and surmise that male calls are optimized for long-distance transmission, while female calls are less audible at long distances. Future studies indicating that males benefit from long-range territory defence would provide evidence of a selective agent shaping the observed patterns. Digby *et al.* also note that the presence of duets and the particular frequency characteristics of male and female calls exemplify 'vocal cooperation' among the sexes. Whether this is the result of competition for acoustic space or cooperation (and if so, by which sex) may require additional investigation, but the result is that Little Spotted Kiwi male and female calls have frequency characteristics that do not interfere with each other but, rather, fit together like a lock and key. Male fundamental frequencies fall in a quiet space between female fundamental frequencies and higher harmonics, perhaps suggesting that the vocal tracts of females are somehow filtering out these key frequencies from the females' calls. In terms of the function of these coordinated calls, duets often occurred in the apparent context of territorial confrontations. Duet contributions with distinct frequency ranges would be beneficial in these situations because they would effectively convey duet participation by two partners to intruders and to the partners themselves (Hall 2009).

Digby *et al.* provide a much-needed description of the calls of a threatened bird species and present fascinating data regarding sexual call dimorphism in Little Spotted Kiwis. Their results will be useful for population monitoring, and also pose some intriguing questions about how calls evolve and function among species within basal avian lineages. Ecological habitat features seem to shape kiwi vocal traits in the same way that they shape learned song (Slabbekoorn & Smith 2002). Calls may also evolve to serve the same functions as song. Studies of the North Island Brown Kiwi suggest that they have calls with properties similar to those of the Little Spotted Kiwi. It remains to be seen if all five extant kiwi species share these vocal traits. Researchers might also ask if the social and ecological mechanisms shaping call features are common across paleognath species and beyond. By studying call form and function in a wide range of species, researchers may test hypotheses that were developed for song-learning birds in systems where vocalizations are innate. Teasing out separate effects of biological and cultural evolution can be very difficult among song-learning species. Among non-learners this problem is eliminated and we can have a clear view into the workings of biological evolution on acoustic signals.

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