



## Commentary

# Individual distinctiveness in avian vocalizations and the spatial monitoring of behaviour

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Advances in research on bird vocalizations often follow the development of new recording technologies and analytical techniques (Baptista & Gaunt 1994, Baker 2001). As recently as a decade ago, ornithologists recorded bird-song onto magnetic tape and analysed sounds with a Kay Elemetrics Sonograph. This rare and expensive computer allowed users to visualize sections of tape recordings and collect spectro-temporal measurements, although it lacked the ability to store sounds in memory or view long periods of recording. How far acoustic studies have progressed with the advent of digital sound recording and analysis! Portable digital recorders are widely available and memory for sound storage is increasingly affordable; thousands of hours of field recordings can now be stored on a single portable drive. Recordings can be visualized instantly and analysed on personal computers using a variety of powerful software packages. We have entered a new era of research on the incredible diversity of avian acoustic communication strategies, in which birds can be studied in unprecedented detail based on extended digital recordings of their vocalizations.

Digital recordings of bird vocalizations provide a tool for tracking individuals over space and time. Many birds produce loud, easily detected sounds throughout the year, usually with increased output during the breeding season. Vocalizations can provide information about a bird's behavioural state, quality or condition, and relationships with nearby animals (Catchpole & Slater 2008). Tracking birds through their sounds has many advantages over direct observations of individually marked individuals, radiotelemetry and other technologies. Acoustic monitoring can be used to study animals in environments in which direct observations might be difficult or impossible, such as animals in dense tropical forests (e.g. Mennill & Vehrencamp 2008) or animals that are active at night (e.g. Farnsworth & Russell 2007, Odom & Mennill 2010). Moreover, acoustic monitoring

is non-invasive, thereby minimizing the influence of the monitoring device on an animal's behaviour or movements (McGregor *et al.* 1997). Providing that a bird's vocalizations have some individually distinctive signature, they can be used to track particular individuals, whether for studies of territorial and mating behaviour, survival and site fidelity, population dynamics or habitat use patterns.

In this issue of *Ibis*, Kirschel *et al.* (2011) describe a study of digital sound recordings and spatial monitoring of a population of the Mexican Ant-thrush *Formicarius moniliger*. Based on digital recordings of birds in a neotropical rainforest, Kirschel *et al.* provide a compelling demonstration that bird songs can be used to track individuals over space and time. They employ the latest sound recording technologies (including handheld digital recorders and arrays of stationary microphones) combined with modern sound analysis techniques (including discriminant analysis based on automated measurements of song structure). From recordings collected over nine field expeditions spread over four years, they demonstrate that Mexican Ant-thrush songs are individually distinctive and that spatial monitoring based on recordings of these songs can provide reliable estimations of ant-thrush territories.

The maps of Mexican Ant-thrush territories presented in Kirschel *et al.*'s Figure 3 are remarkable. The upper map shows bird territories generated through sound recordings, where birds were distinguished on the basis of individually distinctive features of their songs. The lower map shows territories based on an independent dataset of locations where individually marked birds were observed by the researchers. The correspondence between the two maps provides compelling evidence that acoustic monitoring yields data that match conventional observation-based monitoring. Moreover, acoustic monitoring yielded more information than the observational monitoring; the acoustic approach detected more of these secretive birds and provided more data per territory (although more time may have been devoted to recordings than visual observations). These data verify the utility of acoustic monitoring for tracking wild birds and provide a clear demonstration of the acoustic approach's advantages, particularly for species that are difficult to observe due to their secretive behaviour, dense habitat, or, as with Kirschel *et al.*'s Ant-thrushes, both.

The use of microphone arrays to monitor the position of free-living birds is an important component of Kirschel *et al.*'s study. Microphone arrays collect simultaneous recordings from multiple microphones and allow the researcher to triangulate the positions of animals based on their sounds (McGregor *et al.* 1997, Mennill *et al.* 2006, Collier *et al.* 2010). This technique has been used to study avian countersinging behaviour (e.g. Burt & Vehrencamp 2005, Fitzsimmons *et al.*

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2008b), duetting behaviour (e.g. Mennill & Vehrencamp 2008), sound directionality (Patricelli *et al.* 2008) and population density (Dawson & Efford 2009). Kirschel *et al.*'s study complements previous findings by demonstrating that microphone array recordings are a useful technique for passive monitoring of territories. In the recent past, microphone arrays have been logistically challenging to operate and expensive to manufacture. Today ornithologists can purchase wireless microphone arrays at relatively low cost so that acoustic monitoring is a widely accessible technology, although the analysis of extensive amounts of spatio-temporal data remains a challenge.

Can any species of bird be tracked with acoustic monitoring? There are at least three prerequisites. (i) The birds must be sufficiently vocal that the positions of their vocalizations provide information about their movement patterns. (ii) The birds must have individually distinctive features in their vocalizations. (iii) The individually distinctive features must persist over time. Kirschel *et al.* use discriminant analysis to show that Ant-thrush songs can be assigned to the singer through sound measurements, and that these distinctive measurements remain stable over extended time-periods. The technique of discriminant analysis involves plotting numerous variables in multi-dimensional space (in this study, 18 automated measurements of the time and frequency components of Ant-thrush songs) and finding combinations of those variables that best distinguish between user-specified groups (in this study, singer identity). It is important to avoid circular inferences in this type of analysis; given that the analyst specifies the grouping variable in the analysis (here, singer identity), a training dataset should be used to construct the discriminant analysis, and a separate dataset should be used to evaluate the efficacy of the discrimination. Kirschel *et al.* use this cross-validation approach to show that two years of training data yield reasonable estimations of individual identity in a third year of recordings, supporting the idea that Ant-thrush songs have individually distinctive features that are stable over time.

Variation in bird vocalizations may arise due to differences between individuals, or differences within individuals over time. The relative importance of these two sources of variation is not often studied (Ellis 2008). A recent study of Black-capped Chickadees *Poecile atricapillus* (Wilson & Mennill 2010) showed that recordings collected on multiple occasions from one individual exhibit more variation than recordings collected in a single recording, but that variation between individuals is much greater than the variation within individuals. Playback revealed that animals conceptually group together recordings of the same individual sampled on different occasions (Wilson & Mennill 2010). Kirschehl *et al.*'s Ant-thrush research adds to a growing number of studies that reveal that individual distinctiveness persists over time. Studies of birds from many different orders

show patterns of multi-year stability, including owls (e.g. Rognan *et al.* 2009), cranes (e.g. Klenova *et al.* 2009) and divers (e.g. Walcott *et al.* 2006; although diver call structure can change with changes in territories, reinforcing the importance of confirming acoustic identities with direct observations). One of the most powerful components of Kirschel *et al.*'s study is that animals were sampled repeatedly over multiple recording sessions and multiple years.

Ant-thrushes are suboscine songbirds. One crucial distinction between oscine and suboscine songbirds is that oscines have an important learned component to song development, whereas suboscines are thought to develop songs without learning (Kroodsma & Konishi 1991). Given that the learning process may lead to copying errors, we can predict that song-learning birds will have more individual-level variation and higher potential for individual distinctiveness in their vocalizations than non-learning birds. Yet individual distinctiveness appears to be common in both song-learning and non-learning birds; many detailed studies have found individually distinctive vocalizations in oscine passerines (e.g. Christie *et al.* 2004, Nelson & Poesel 2007), suboscine passerines (e.g. Lovell & Lein 2004, Fitzsimmons *et al.* 2008a, 2008b), and non-passerines (e.g. Aubin *et al.* 2000; Cortopassi & Bradbury 2006). Kirschel *et al.*'s research confirms the individual distinctiveness in the songs of another suboscine species, in spite of the superficial similarity in their songs (e.g. Figure S1 in Kirschel *et al.* 2011). Acoustic monitoring may actually be better suited to studying non-song-learning animals versus song-learning animals, since the latter often have song repertoires. Birds with song repertoires or other forms of individual-level variation may require a more extensive period of sampling to create a catalogue of each individual's repertoire. Advances in techniques that classify new and unknown individuals (e.g. Fox 2008) may create opportunities for classification of complex song repertoires in the future.

The work of Kirschel *et al.* is one of the first comprehensive studies to use digital recordings of birds to map territories and study spatial behaviour. Several of the techniques and conclusions in this pioneering work should be refined and clarified through further study. One important area for refinement is the use of kerneling methods in territory estimation. Many authors consider kerneling to be a preferable alternative to convex polygons (see Barg *et al.* 2005, Anich *et al.* 2009). This point is nicely demonstrated by the bird 'YYG' in Kirschel *et al.*'s Figure 3; in both the acoustic analyses (Figure 3a) and the direct observations (Figure 3b) this bird's activity is concentrated in two distinct regions, one near the northwestern edge of its territory, the other along the southern edge of its territory. The minimum convex polygon produces an estimated territory that encompasses a large area between the two clusters where

the bird was never detected. The kerneling approach, in contrast, would estimate territory boundaries weighted towards the locations where the bird was most often detected. Kerneling may produce territory estimates that are a truer reflection of the animal's activity space.

Some of the conclusions tentatively drawn in Kirschel *et al.*'s study should be tested more rigorously in future work, such as the suggestion that female song and female territoriality are convergent on male song and territoriality. Female song is rare in the temperate zone, but relatively common in the tropics (Langmore 1998). To provide compelling support for the idea of sex role convergence in territorial behaviour, it is important to conduct a direct comparison of male and female singing behaviour and territorial behaviour, and carefully to consider sex differences in song output. A recent microphone-array study of neotropical Rufous-and-white Wren *Thryophilus rufalbus*, for example, includes quantitative comparisons of male versus female territories, and shows that the sexes have statistically indistinguishable territory sizes with congruent shapes (Osmun & Mennill 2011). Similarly, the conclusions that male territory boundaries do not change and that females act as floaters in this population require more empirical support and further study.

In 1993, Baptista and Gaunt wrote: 'today digital technology is proving as revolutionary in bioacoustics studies as the advent of the magnetic tape recorder both in digital sound recording and computer technology for sound synthesis, manipulation and analysis.' Kirschel *et al.*'s study of Mexican Ant-thrushes is a case in point. Their use of digital sound recordings and analytical techniques demonstrate that these secretive subspecies have individually distinctive songs that are stable over time, and that their songs can be used to create reliable bioacoustic maps of the birds' positions in thick neotropical forest.

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