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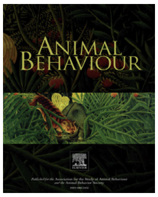

All signals are not equal: acoustic signalling of individuality, sex and breeding status in a cooperative breeder

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Repeated interactions between individuals in socially living animals select for the evolution of signals that convey information identifying individuals or categories of individuals, which may enable the discrimination of familiar versus unfamiliar individuals. Such information may help animals maximize their inclusive fitness by adjusting their own behaviour, allowing them to avoid conflict, preferentially direct help and/or ignore unreliable individuals. Acoustic signals in birds provide the potential to encode individual-specific information. We examined the degree to which individual identity, sex, breeding status, group membership and genetic relatedness were related to variability in six different call types, which occurred across a variety of different behavioural contexts in the apostlebird, *Struthidea cinerea*, a socially living and cooperatively breeding Australian passerine. We demonstrated that not all calls reflected the same extent of information. Of the six call types, call variation was related to individual identity in three call types, breeding status in two call types and sex and group relatedness in one call type. Finally, variation in two call types was not related to any of the measured variables. Our results suggest that some, but not all, acoustic signals in apostlebirds may be selected for individual distinctiveness between individuals and categories of individuals (male versus female, breeder versus nonbreeder), and these signals may be important in determining levels of cooperation and interaction between individuals in this cooperatively breeding society.

Animals interacting repeatedly within social groups may benefit from the ability to discriminate quickly and efficiently between other individuals or categories of individuals (e.g. familiar versus unfamiliar), with animals living in colonial or social groups having strong selection for recognition between individuals or classes of individuals (Beecher, 1988). Information on the attributes of other individuals may help animals maximize their inclusive fitness by adjusting their own behaviour, for example, allowing for conflict avoidance (Palombit, Cheney, & Seyfarth, 1999), preferentially directing aid (Russell & Hatchwell, 2001) and ignoring unreliable individuals with high false call rates (Hare & Atkins, 2001). Information on an individual's attributes may be encoded in visual, olfactory and acoustic signals (as reviewed in Tibbetts & Dale, 2007). However, in avian species, vocalizations are identified as the most commonly used recognition cues (Falls, 1982; Halpin, 1991; McDonald & Wright, 2011; Stoddard, 1996).

Some vocalizations may influence more than one receiver (e.g. alarm calls) or are subject to eavesdropping (Mathevon, Koralek, Weldele, Glickman, & Theunissen, 2010), or may be given by multiple individuals at the same time (Blumstein, Verneyre, & Daniel, 2004), particularly in a social species in which individuals are typically in acoustic contact with many others simultaneously. However, even in social species in which signals may have undergone selection to enable individual recognition, not all calls within a species' repertoire are expected to encode individual signatures to the same extent (Charrier, Jouventin, Mathevon, & Aubin, 2001). Indeed, some signals, such as alarm calls, are likely to have been selected to minimize individual differences to decrease any potential ambiguity of the main function (Falls, 1982; but see Fitch & Hauser, 1995).

Few studies have examined the information encoded in multiple call types within a species (Charrier et al., 2001; Colombelli-Negrel et al., 2012; Seddon, Tobias, & Alvarez, 2002; Sharp & Hatchwell, 2005). These studies demonstrate that within a species, there may be selection for a particular call type/behaviour to carry specific

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information about the caller. For example, social calls may be more likely to be individually distinct than calls used in less social contexts (e.g. Charrier et al., 2001), and calls used during separation may encode individual information whereas calls used in nonseparated contexts do not (Seddon et al., 2002). Furthermore, a recent study has highlighted the other potential types of socially important information that may underlie variation in a call type (such as sex, age, dominance; Mathevon et al., 2010). To date, no other study has examined multiple determinants of call variation in many different calls in an integrated way. Our study is important because a within-species approach examining variability in multiple call types across different contexts may elucidate the complexity and evolutionary drivers underlying acoustic variability in socially living species.

Apostlebirds, *Struthidea cinerea*, are extremely vocal cooperatively breeding birds that live in social groups that vary in size (Griesser et al., 2009; Woxvold & Magrath, 2004), sex ratio (Woxvold, 2004), number of breeders (Woxvold & Mulder, 2008), length of association (e.g. amount of time individuals have spent time in the same group; Griesser et al., 2009), and composition of related and unrelated members (Woxvold, 2004). Consequently, this complex social structure may promote the evolution of signals to discriminate between different classes or groups (e.g. breeder versus helper). Furthermore, vocalizations occur across a variety of different behaviours including during group foraging and movements, nest building and activities at the nest, and during intragroup and intergroup interactions (Baldwin, 1974). Although little is currently known about the information that might be encoded within these vocalizations, apostlebirds may use acoustic means to discriminate between individuals or classes of individuals. Therefore, examining the variation in call structure and the type of information driving variation within calls allows for a greater understanding of which factors are important to the evolution and maintenance of cooperative behaviour in this species.

In this study, we examined five types of information that are associated with individual attributes (individuality, sex, breeding status, group membership and genetic relatedness) that may drive variation in different calls of the apostlebirds. We also examined whether call features remained stable across the duration of the study (16 months). We analysed six different call types (out of 17 identified call types characterized in this species; Warrington, McDonald, Sager, & Griffith, 2014), across six different behavioural contexts that may (or may not) have been selected to also encode information on individual attributes. This study allowed us to examine the extent to which these six calls varied in the information that they might provide.

METHODS

Study Population and Vocalization Recordings

We recorded vocalizations of 60 free-living adult apostlebirds (19 breeding males, 17 nonbreeding males, 13 breeding females and 11 nonbreeding females) from 15 social groups at the University of New South Wales Arid Zone Research Station at Fowlers Gap (142°E, 31°S, New South Wales, Australia). Vocalizations were recorded in the spring from August to December in both 2010 and 2011 and also during the autumn in April and May 2011.

This study population was monitored between 2004 and 2012, and most birds (90%) were individually colour-ringed with a unique combination of three colours and a uniquely numbered metal service band supplied by the Australian Bird and Bat Banding Scheme. At the time of initial banding, blood samples were also collected for molecular analysis. Additionally, over the course of the study many of the birds in this population have become at least partially habituated to close human presence. As a result, most of the recordings were made within 5 m of the calling bird, allowing high signal to noise ratio recordings and accurate determination of the individual that was vocalizing within groups.

Vocalizations were recorded using a solid-state digital recorder (Marantz PMD670 or PMD660 model) using a cardioid directional microphone (Sennheiser ME66) with a K6 power module and preamplifier. Digital recordings were saved as uncompressed WAV files at a sample rate of 48 kHz with 16-bit resolution. Recordings were made during natural foraging, resting and nesting activities as well as during 34 focal sessions (of 20 min each) targeting individual birds. We randomly selected individual birds for focal sessions; however, not all individuals behaved naturally for a duration of 20 min, and as such, any focal sessions that showed signs of disturbance (birds flying and running ahead of the observer, repeatedly looking back, giving alarm calls) were terminated.

Voice dictation was recorded using a Sony ECM-77 lavalier condenser microphone (which was connected to a different audio channel on the same Marantz recorder), enabling commentary on individual identity or behaviour to be recorded simultaneously with vocalizations.

Description of Call Types

We examined call similarity within six different call types: (1) kweer, (2) chewa-reea, (3) nest pulses, (4) the piping call (eeuu variant), (5) kau and (6) charr (see Table 1). We also split the chewa-reea call into the three separate syllables (chewa-reea is the only call type here with more than one syllable) to examine whether different syllables encoded different types of information. The call features and contexts are described in detail in Warrington et al. (2014); however, the behavioural contexts of all calls in this study are as follows. The kweer call appeared to be a putative close contact call (hereafter referred to as ‘contact call’) given by individuals while foraging and when the caller was out of visual (but not auditory) contact with foraging group members even if the individual itself was not foraging. The chewa-reea call occurred in social contexts (hereafter ‘social call’) and was typically given when human observers first encountered a group, during interactions between different groups, when an adult was holding (but not eating) large food items, and at the nest during nest visits and the changing of shifts by adults during incubation. Nest pulses were given by individuals as they approached and left the nest area. The piping call was given by a caller on the nest (breeding season) and by individuals that had been separated from their group. Kau calls appeared to function as a putative group decision making/quorum call (hereafter ‘quorum call’) and were given after foraging or feeding and while the caller was standing or sitting with the group (callers were rarely actively moving). An increase in vocalization rate and number of calling individuals often resulted in the entire group flying off and leaving the area. The charr call was associated with aggression and agonistic interactions (hereafter ‘aggression call’). We chose these particular six calls (of the previously described 17 calls; Warrington et al., 2014) because (1) they represent six different behaviour contexts, and (2) they are the most common calls for which we were able to record enough calls per individual to do appropriate statistical analyses. For the six call types that were used, call variability ranged from audibly stereotypical nonvariable calls to highly variable calls (to human hearing, at least), and hence the calls differed in the extent to which they may act as signatures of individual or status.

Spectrographic Call Correlation (SPCC)

Call similarity was obtained in Raven Pro 1.4 using the batch cross-correlation tool (Charif, Strickman, & Waack, 2010).