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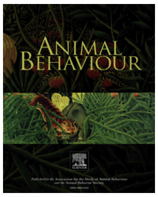

Territorial olive frogs display lower aggression towards neighbours than strangers based on individual vocal signatures

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Some territorial animals display a form of social recognition in which they direct low levels of aggression towards established neighbours, but maintain greater readiness to respond aggressively towards unfamiliar individuals. In many taxa, such as songbirds, this so-called 'dear enemy' effect involves discrimination between neighbours and strangers based on individually distinctive vocal signatures. Although most anuran amphibians (frogs and toads) are highly vocal, and many are also territorial, we know very little about neighbour–stranger discrimination in this group. In the present study of the olive frog, *Babina adenopleura* (Ranidae), we show that the vocal signals of males are individually distinct, and that territory holders use this information to direct lower levels of aggression towards their nearby neighbours. Analyses of individual variation in advertisement calls revealed many individually distinctive spectral and temporal acoustic properties, with spectral properties contributing most towards statistical discrimination among individuals. In a field playback experiment that simulated territorial intrusions, territorial males had higher thresholds for producing aggressive calls in response to the advertisement calls of their nearby neighbours compared with those of strangers. A simple model based on sound attenuation due to spherical spreading estimated that males responded aggressively to strangers at distances that were approximately twice as far away as for neighbours and that were similar to intermale distances recorded in the field. Together, results from this study indicate that territorial male olive frogs develop vocally mediated dear enemy relationships with their nearby neighbours. These results highlight the potential for convergence in social recognition systems across diverse taxa.

Animals discriminate among learned categories of conspecifics in a diversity of social contexts (Bee, 2006; Beer, 1970; Colgan, 1983; Sherman, Reeve, & Pfennig, 1997; Starks, 2004; Wiley, 2013). These categories may be broad and inclusive (e.g. familiar versus unfamiliar, kin versus nonkin), or they may correspond to specific individuals. A form of learned category discrimination common among territorial animals occurs when territory holders display relatively lower levels of aggression towards their established neighbours compared with unfamiliar strangers (Temeles, 1994). This so-called 'dear enemy' effect (Fisher, 1954) is hypothesized to function in allowing territory holders to avoid the costs of repeated aggressive interactions with the familiar occupants of nearby territories, which likely pose less of a threat to territory ownership than less familiar, nonterritorial individuals (Temeles, 1994). The ability to discriminate between neighbours and strangers has been studied most thoroughly in the acoustic modality in songbirds (Falls, 1982; Lambrechts & Dhondt, 1995; Stoddard, 1996), although it occurs in other sensory modalities and is taxonomically widespread, occurring in mammals (delBarco-Trillo, McPhee, & Johnston, 2009; Palphramand & White, 2007), lizards (Husak & Fox, 2003a, 2003b), amphibians (Davis, 1987; Jaeger, 1981), fish (Myrberg & Riggio, 1985; Sogawa, Ota, & Kohda, 2016), crustaceans (Booksmythe, Jennions, & Backwell, 2010) and insects (Langen, Tripet, & Nonacs, 2000).

Anuran amphibians (frogs and toads) represent a promising taxonomic group for elucidating social and ecological factors that promote the evolution of vocally mediated neighbour–stranger discrimination and its underlying causal mechanisms (Bee, in press; Bee, Reichert, & Tumulty, 2016). In addition to being highly

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vocal (Gerhardt & Huber, 2002), anurans exhibit remarkable diversity in their social and reproductive behaviours (Wells, 1977, 2007). Even within the same genus, different species exhibit this diversity, which can range from nonterritorial scramble competition, to lekking, to the aggressive defence of long-term territories that contain breeding resources (Wells, 1977, 2007). Territorial behaviour is common among male anurans and involves a suite of vocal and physical behaviours used in contests with intruders. The costs of contests in anurans can include reduced mate attraction, physical injury, and increased energy expenditure and predation risk (Dyson, Reichert, & Halliday, 2013). Hence, we might expect territorial individuals to direct reduced levels of aggression towards their established neighbours, and indeed they do in some species (Davis, 1987). However, only a few previous studies have tested the hypothesis that anurans exhibit dear enemy behaviour. Moreover, results from some of these studies are equivocal because of poor experimental designs, insufficient reporting of data, or inadequate consideration of the study species' natural history (reviewed in Bee, in press; Bee et al., 2016). Answering questions about the mechanisms and evolution of dear enemy behaviour in anurans demands additional investigation.

We investigated vocally mediated neighbour–stranger discrimination in the olive frog, *Babina adenopleura* (Ranidae; formerly *Rana adenopleura*). The olive frog is a common species throughout Southeast Asia and is abundant in Taiwan, where this study was conducted. The olive frog mating system is resource defence polygyny (Chuang, Bee, & Kam, 2013). Males use a combination of distinct vocalizations and physical combat to defend small territories that function as oviposition sites. Males occupy and defend their territories for an average of 8.4 consecutive days, although some individuals have been observed to defend the same territory for up to 43 days (Chuang et al., 2013). The vocal repertoire of the male olive frog consists of several different call types (Chuang, Kam, & Bee, 2016). Advertisement calls are by far the most common call produced by males (Fig. 1a). As in other frogs, this call type almost certainly functions both in attracting mates and repelling rival males (Wells, 1977, 2007). Males also produce two acoustically distinct types of calls in aggressive contexts that involve close-range vocal and physical interactions between competing males (Chuang et al., 2013, 2016). Following convention (e.g. Toledo et al., 2014; Wells, 2007), these have been termed territorial calls (Fig. 1b) and encounter calls (Fig. 1c) (Chuang et al., 2016). Territorial calls appear to function early in contest escalation, whereas encounter calls are used in more highly escalated contests.

The present study had two aims. First, we tested the hypothesis that advertisement calls are individually distinct and could function as identity signals. Our predictions were that acoustic properties of this signal would be more variable among individuals than within individuals, and that this pattern of individual variation would allow calls to be assigned to the correct individual above chance levels in multivariate statistical analyses. Second, we tested the hypothesis that territorial males behaviourally discriminate between the advertisement calls of neighbours and strangers. We measured ‘aggressive thresholds’ in response to calls representing these two social categories in a field playback experiment. The aggressive threshold was operationally defined as the lowest stimulus amplitude that elicited aggressive vocalizations (Brenowitz & Rose, 1994; Marshall, Humfeld, & Bee, 2003; Robertson, 1984; Rose & Brenowitz, 1991). According to a dear enemy hypothesis, we predicted aggressive thresholds would be relatively lower (i.e. males would be more aggressive) in response to the calls of a stranger.

METHODS

Study Sites

This study was conducted at the Lien-Hua-Chih Research Centre, Taiwan. We made acoustic recordings of actively calling males between June and September in 2007, 2008 and 2009. These recordings were made either in a natural forest (120°52′59.5″E, 23°55′8.9″N) or in a nearby palm farm where areca nuts were grown (*Areca catechu*; also known as betel nuts; 120°53′12″E, 23°55′01″N). The two sites were located approximately 600 m apart. In the natural forest, males established territories around the perimeter of a permanent pond (5×10 m, maximum depth of approximately 1 m; see Figure 1 in Chuang et al., 2013). The site at the palm farm consisted of numerous shallow (<30 cm depth), flooded areas where males established territories. This site was also used for conducting playback experiments in 2009. Territorial male olive frogs were abundant at both sites, where they invariably called while floating on the surface of the water, similar to some North American ranids (e.g. Howard, 1978; Wells, 1978).

Sound Recordings

Advertisement calls were used for acoustic analyses of individual distinctiveness and as stimuli in playback tests. Calls were only recorded from males that were not interacting with other conspecifics at the time recordings were made. Upon selecting a focal male for recording, we placed a directional microphone (Sennheiser ME67) mounted on a tripod approximately 0.5 m away from the male. We recorded calls (44.1 kHz sampling rate, 16-bit resolution) onto a digital recorder (Marantz PMD670). After completing a recording, we captured the focal male, measured its body length (snout–vent length (SVL) to the nearest 0.01 mm) using callipers (Mitutoyo 505-666 dial calliper and Mitutoyo 500-672 digital calliper) and its mass (to the nearest 0.05 g) using a portable electronic balance (Hiroda MT-300). Measurements of SVL and mass were used to compute an index of physical condition (i.e. length-independent mass) following Baker (1992). We also recorded the water temperature to the nearest 0.1 °C at the male's calling site using a Tecpel DTM-3108 digital thermometer.

We used a Tecpel DSL-332 sound level meter to record the sound pressure level (SPL re 20 μPa, fast RMS, C-weighted) of the calls of 11 males. We positioned the microphone of the sound level meter at a distance of 1 m from the frog and recorded the maximum SPL of between 4 and 10 calls for each individual. We computed the minimum, median and maximum SPLs of the sample of 11 males based on using individual median values computed over the sample of calls recorded from each individual.

Individual Vocal Distinctiveness

We tested the hypothesis that advertisement calls are individually distinct by analysing patterns of individual variation in their acoustic properties. A quantitative description of the call is provided elsewhere (Chuang et al., 2016). We used Raven Pro 1.4 (Charif, Waack, & Strickman, 2010) to analyse 70 acoustic properties of 899 advertisement calls recorded from 45 males in 2008 (20 calls for each of 44 males and 19 calls for one male). Supplementary Table S1 provides a full description of all 70 acoustic properties, which we summarize briefly here. We analysed four temporal properties using the entire call as our unit of measurement (Fig. 2), including call period (Fig. 2b), call duration (Fig. 2c), the number of notes per call (Fig. 2c) and note rate. Twenty-two additional