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Can common cuckoos discriminate between neighbours and strangers by their calls?

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Common cuckoos, *Cuculus canorus*, are brood parasites: they lay their eggs in the nests of other bird species, and let these hosts incubate their eggs and feed and rear the nestlings. Although cuckoos do not show parental care, they demonstrate complex social interactions, including territorial behaviours and male–male aggression. Cuckoos have a well-known and simple two-phrase call ('cu' and 'coo'), uttered by males during their breeding season. Previous studies suggested that the 'cu-coo' call of males is individually unique, potentially allowing discrimination between different classes of males. Using playback experiments in a dense population of radiotagged cuckoos, we tested whether neighbouring males are tolerated more than unfamiliar intruders: the classic 'dear enemy' phenomenon. Focal birds responded more aggressively to the calls of unfamiliar simulated intruders (strangers) than to the calls of conspecifics with whom they shared territorial boundaries (familiar neighbours). Cuckoos responded quickly, within, on average, less than half a minute; they often approached the loudspeaker to within 5–10 m, even from up to 80 m away, and used their 'cu-coo' calls in response. Our results showed that cuckoos used their simple call for the discrimination of familiar versus unfamiliar individuals, and did so specifically to defend their own territories. In turn, cuckoos showed tolerance to nearby conspecifics, for example neighbours with overlapping territories, and did not respond to control playbacks. Finally, as typically more than one cuckoo was interested in the playbacks, this study confirmed the opportunity for brood-parasitic birds to socialize during the breeding season.

In territorial behaviour, the so-called 'dear enemy phenomenon' (Fisher, 1954) is defined as territory owners tolerating familiar neighbours living on adjacent territories more than unfamiliar intruders that represent a potential source of territorial threat. In this way the residents reduce interindividual aggression and unnecessary conflicts. This phenomenon has already been shown in a wide range of animals, and territorial bird species provide the most common and best-known examples (Searcy, Akcay, Nowicki, & Beecher, 2014; Temeles, 1994). Irrespective of the function and mechanism, including sensory modality, of the dear enemy phenomenon, these processes include an ability to discriminate between familiar and unfamiliar individuals. For example, songbirds with a large repertoire may share some of their song types with neighbours, which helps them recognize one another (Briefer, Aubin, Lehongre, & Rybak, 2008; Stoddard, 1996). Songbirds with a small repertoire may use unique frequency characteristics for discrimination and recognition (Osiejuk, 2014). There is also an increasing number of studies on nonoscine birds, which do not learn their songs, where the dear enemy phenomenon has also been detected (e.g. Budka & Osiejuk, 2013; Hardouin, Tabel, & Bretagnolle, 2006; Mackin, 2005). However, neighbour–stranger discrimination sometimes reveals equal aggression toward neighbours and strangers when they show equal threat (Bard, Hau, Wikelski, & Wingfield, 2002; Battison, Wilson, Graham, Kovach, & Mennill, 2015), or even works in reverse (Brunton, Evans, Cope, & Ji, 2008).

Common cuckoos, *Cuculus canorus*, (hereafter cuckoos) are well-known brood parasites (Davies, 2000; Schulze-Hagen, Stokke, & Birkhead, 2009) that lay eggs in the nests of other avian species

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(hosts), and leave these hosts to incubate the eggs and rear their offspring (Wyllie, 1981). The cuckoo hatchling evicts all eggs and other hatchlings from the nest (Honza, Voslajerová, & Moskát, 2007), and consequently it monopolizes all food delivered by the foster-parents (Anderson et al., 2009). Host nests serve as resources for reproduction by female cuckoos, whereas males can be observed spatially aggregating near females. A female cuckoo lays every second day, altogether ca. 20 eggs (up to 25) in a breeding season (Wyllie, 1981), so their reproductive strategy could be characterized by an extended laying cycle. Consequently, females primarily protect resources (host nests), while males protect females directly or areas used by females. For this reason, we predict an evolved territorial signalling and protection system in cuckoos. We hypothesized that individually distinctive calls could enable neighbour–stranger discrimination, which could have a territorial function in cuckoos. Territorial behaviour, including defence and interannual use of the same sites, has also been detected in several other brood-parasitic species, including Horsfield's bronze-cuckoos, *Chalcites basalis*, in Australia (Langmore, Adcock, & Kilner, 2007) and brown-headed cowbirds, *Molothrus ater*, in North America (Hauber, Strausberger, Feldheim, Lock, & Cassey, 2012). Furthermore, cuckoos seem to be polygamous (Marchetti, Nakamura, & Gibbs, 1998), and this may explain why male cuckoos defend partly overlapping or shared territories. In contrast, in the Horsfield's bronze-cuckoo, genetic parentage analysis revealed that females were monogamous and that males were also monogamous, or sequentially monogamous (Langmore et al., 2007). The breeding system may also have implications for the type of territoriality exhibited by different brood-parasitic taxa.

Cuckoos belong to an avian lineage which does not learn its songs (Brenowitz, 1991). This reduces the presence of individual differences due to cultural transmission. Neighbour–stranger discrimination is a case of familiarity recognition; it must be based on distinguishable characteristics of familiar versus unfamiliar individuals, for example in song frequency, duration or repertoire, and the ability of the receiver to recognize these differences (Tibbetts & Dale, 2007). The receiver must also memorize the familiar, known song types (Kiefer, Scharff, Hultsch, & Kipper, 2014; Marler, 1997). In songbird species with a small song repertoire, neighbour–stranger discrimination is typically based on differences in the frequency of shared song types (Osiejuk, 2014). In contrast, oscines with large song repertoires often learn syllable sequences from each other (Briefer et al., 2008). However, acoustic neighbour–stranger discrimination is less studied in nonsongbirds, although there are some confirmatory results even in species using simple calls. For example, a playback study revealed that the nocturnal species, the corncrake, *Crex crex*, uses simple calls for neighbour–stranger discrimination (Budka & Osiejuk, 2013). In the little owl, *Athene noctua*, territory owners responded more aggressively to neighbours' calls played at an unexpected part of their territory than to the correctly positioned neighbours' calls (Hardouin et al., 2006).

Common cuckoos have a very simple two-tone advertising call (Lei, Zhao, Wang, Yin, & Payne, 2005), the well-known 'cu-coo' call. These calls are produced by males during the breeding season (Jung, Lee, & Yoo, 2014). In a previous study, we showed that this simple call type contains sufficient diversity for it to vary distinctively between different cuckoo individuals. Using sound analysis tools, it is possible to discriminate different cuckoo individuals with high precision by their 'cu-coo' calls (Zsebök, Moskát, & Bán, 2017). We hypothesized that these small differences in calls could be used to discriminate between individuals in cuckoos, which may help the development of neighbour–stranger discrimination in this species. We predicted that cuckoos would be more aggressive towards simulated stranger intruders than towards territorial neighbours. If the alternative hypothesis was true, i.e. cuckoos cannot use their simple calls for neighbour–stranger discrimination, we predicted similar aggression towards each male cuckoo. A second, alternative hypothesis is that the dear enemy phenomenon works in reverse in parasitic cuckoos, especially if male cuckoos' main competitors for females are in fact their immediate neighbours. If this was correct, we predicted that cuckoos should be more aggressive towards neighbours than towards strangers. Here we tested neighbour–stranger discrimination in cuckoos, in a study site where the only known host species is the great reed warbler, *Acrocephalus arundinaceus*, the cuckoo parasitism rate is unusually high (around 50% of host nests; Zölei, Bán, & Moskát, 2015) and the different phenotypes of cuckoo eggs suggest that different female cuckoos lay eggs in the same nests (Moskát et al., 2009; see also Moksnes et al., 2008). Consequently, the laying areas of some of the female cuckoos may overlap. Multiple male cuckoos can also be located along short sections of irrigation channels. The dynamics of this unusually dense host–brood parasite interaction thus set the stage for us to study neighbour–stranger discrimination in cuckoos. As far as we know, there is no previous study on this type of cognitive skills in avian brood parasites.

METHODS

Study Site

The experiments were carried out around Apaj (47°6′53.9″N, 19°5′21.2″E) and Kunpeszér (47°3′40.1″N, 19°16′31.3″E), ca. 40–60 km southeast of Budapest, Hungary. We also recorded calls of unfamiliar (stranger) cuckoos in the surrounding areas (ca. 20 km). The study was conducted 7 May to 30 May 2016. The laying season of cuckoos follows the availability of host, great reed warbler, nests and lasts about 60–70 days (Moskát, Barta, Hauber, & Honza, 2006) in our study area. This laying season starts in the first half of May and ends in mid-July in Hungary (Moskát & Honza, 2000), and can be divided into three periods of similar length. In the first period, the availability of host nests is high, in the second period it is much lower and in the third period it is very low. As the phase of the breeding season may affect vocal responses of birds to playback (Courvoisier, Camacho-Schlenker, & Aubin, 2014), we conducted our fieldwork within the first 3 weeks of the breeding season (just after cuckoo territories have been established), when the availability of host nests for parasitism is typically high (Moskát et al., 2006).

In our study area cuckoos parasitize great reed warblers at a high rate (ca. 50%; Moskát & Honza, 2002; Zölei et al., 2015). Great reed warblers breed in reed beds grown on both sides of small channels. Typically, cuckoos can be observed in channel-side tree lines, in small woodland patches or sitting on poles and wires. This predominantly linear habitat is especially suitable for studying cuckoos' territorial and related behaviour as channels form a network in the area, and cuckoos' distribution along them can be regarded as one-dimensional (Fig. 1a). Because of the dense host population and the high parasitism rate (see above), this dynamic host–brood parasite system is characterized by a high frequency of multiple parasitism (ca. 24–52% of parasitized nests, Zölei et al., 2015) and overlapping cuckoo territories (Fig. 1).

Sound Recordings

Cuckoo calls were recorded using a Marantz PMD-620 MKII recorder (D&M Holdings Inc., Tokyo, Japan), connected to a Telinga Universal Parabola (Telinga Co., Tobo, Sweden) with a Sennheiser ME 62 microphone and a K6 powering module (Sennheiser Electronic GmbH & Co., Wedemark, Germany). As cuckoo calls in our