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Male hyraxes increase countersinging as strangers become 'nasty neighbours'

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Many territorial animals interact less aggressively with neighbours than with strangers, a phenomenon known as the 'dear enemy' effect, although some species show the opposite behaviour. Rock hyraxes, *Procavia capensis*, are social mammals that communicate via a rich acoustic repertoire. Male hyraxes produce elaborate advertisement calls (i.e. songs) both spontaneously and in response to occasional attention-grabbing events (e.g. pup screams, agonistic interaction), as well as to conspecific male songs. When replying to conspecific songs, male hyraxes tend to respond more to familiar males than to strangers, reflecting the 'nasty neighbour' effect. Our study relates to the general question of why some species respond aggressively towards neighbours, while others are more aggressive towards strangers. We hypothesized that male hyraxes eventually familiarize themselves with a stranger, subsequently perceiving its intentions as highly threatening and deserving of a vocal response. To simulate the presence of a stranger in the area we exposed wild hyrax groups to playbacks of natural songs of unfamiliar hyraxes. Male rock hyraxes became more likely to reply to a stranger's song over time, but this was independent of the number of times they heard the song. This suggests that either (1) the threat presented by a stranger increases when it is no longer perceived as transient or (2) because listeners do not physically encounter the stranger, they perceive replying aggressively as a low-risk response. Our work implies that species may demonstrate a range of condition-dependent behaviours instead of a dichotomy between the 'nasty neighbour' and 'dear enemy' strategies.

Territorial animals generally respond less aggressively to neighbours than to strangers, a phenomenon termed the 'dear enemy' effect (Getty, 1987). In accordance with this effect, selection favours a set of one or several strategies that fit game theory (e.g. limited war strategy; Smith & Price, 1973), wherein a territory owner can learn to recognize and respect the territory of others (Parker, 1974). Gains and losses from interactions may predict the intensity of a territory owner's responses to neighbours and strangers. Territorial competitors' interactions are commonly explained by two hypotheses: (1) the familiarity hypothesis and (2) the threat level hypothesis. The familiarity hypothesis argues that familiar neighbours reduce aggression towards each other to enable better management of time and energy, and thus decrease the risk of injury (Catchpole & Slater, 2008). According to the 'asymmetric law of attrition' model, as the opponents come to know one another better, errors in identity and purpose become less likely, and the intensity of aggression decreases (Ydenberg, Giraldeau, & Falls, 1988). Alternatively, the 'fighting to learn' model asserts that animals engage in fighting to learn about their opponents and therefore familiar neighbours fight very little because they have little to learn about each other (Getty, 1989).

In accordance with the threat level hypothesis, the relative threat presented by neighbours and strangers influences the intensity of a territory owner's aggressive response (Temeles, 1994). Thus, a consideration of the relative threats presented by neighbours versus strangers may explain why, in some species, territory owners may increase aggression towards familiar neighbours (Müller & Manser, 2007; Temeles, 1990). This 'nasty neighbour' effect has been demonstrated when neighbours compete intensely and residents outnumber strangers. For example, banded mongooses, *Mungos mungo* (Müller & Manser, 2007) and song sparrows, *Melospiza melodia* (Moser-Purdy, MacDougall-Shackleton, & Mennill, 2017) respond more strongly to neighbouring groups than to strangers, as neighbours threaten the

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owner's territory, compete for mates and participate in lethal fights. A tit-for-tat conditional strategy may also lead to increased aggression towards neighbours. For example, male red-winged blackbirds, *Agelaius phoeniceus* (Olendorf, Getty, Scribner, & Robinson, 2004) and hooded warblers, *Wilsonia citrina* (Godard, 1993) tend to increase aggression towards familiar individuals that intrude upon their territories.

The rock hyrax, *Procavia capensis*, is a social mammal that lives in mixed-sex groups. In our study area (Ein Gedi, Israel) a hyrax group comprises several males (one mature immigrant resident and several young, local late dispersers) and 3–20 females with their pups (1–3 pups/female; Bar Ziv, et al., 2016). Males reach puberty at the age of 17–24 months, and, soon after, voluntarily and gradually leave their birthplace, or occasionally are forced to disperse by the resident male (Hoeck, 1989; Koren, 2000). Breeding is seasonal and synchronized (Mendelssohn, 1965), and females mate with multiple males, possibly to mask paternity (Bar Ziv, et al., 2016; Koren & Geffen, 2009). Bachelors live mostly solitarily on the periphery of colonies and in rare cases may congregate into bachelor groups (Koren, Mokady, & Geffen, 2006). Bachelors interact with the mixed-sex groups mainly for mating and during feeding (Koren, Mokady, & Geffen, 2008).

Hyrax males are typically not territorial and do not monopolize food resources (Bar Ziv, et al., 2016). However, when resident males reside with a group of females they display aggressive behaviour and dominate bachelors that approach the group females (which can also occur outside of the breeding season; Koren et al., 2008). Moreover, during the mating season only the resident males are observed mate guarding the older and experienced females, and displaying aggression towards any bachelor males that attempt to court and mate with those females that were mothers in previous years (Bar Ziv, et al., 2016). Accordingly, emphasizing the defence of females as a resource (i.e. rather than defending space), a territory may be defined as 'floating' or 'moving': a spatiotemporal area that a group occupies and that remains centred on the group as it moves (Kaufmann, 1983). Thus, we view the hyrax social group as a moving area that is kept free of bachelor males by the resident's aggressiveness towards them.

Rock hyraxes employ a rich vocal repertoire as an important means of information transfer (Fourie, 1977). Adult males communicate using long-distance vocalization signals that we term 'songs' (Koren & Geffen, 2009): these are variable, complex signals that express individuality and are likely to make the caller familiar to the listeners (defined as song by Spector, 1994). Song conveys information communicated via acoustic characteristics through parallel pathways: body size, weight, condition, social status, identity and hormonal profile of the singer are encoded in the song (Koren & Geffen, 2009, 2011). Male hyraxes perform complex songs throughout most of the year and singing gradually increases during March–April (with an average number ±SD of 3.815 ± 2.76 singing events per day), peaks in July (7.9 ± 7.45) and decreases in frequency shortly after. Both resident and bachelor males sing when they are spatially separated and have no physical contact with other males (Koren et al., 2008). In our study area, individual males sing naturally every day and male-to-male countersinging comprises about 25% of overall songs performed (Demartsev, Ilany, et al., 2016; Ilany, Barocas, Koren, Kam, & Geffen, 2011). During countersinging, songs are more elaborate than songs that males perform spontaneously or without any observable external trigger (Demartsev et al., 2014). Resident males tend to reply at a high rate to bachelors whereas bachelors reply at a low rate to residents, while other factors such as body weight and tenure on site have no effect on listeners' reply rate (Demartsev, Ilany, et al., 2016). In many species, singers may countersing with conspecifics to signal aggression (Hyman, 2003), suggesting that hyrax countersinging probably constitutes an escalated mutual signalling between males, enabling them to advertise their relative social and physical traits without the need for actual fighting (Demartsev, Ilany, et al., 2016; Koren & Geffen, 2009).

Recently, Demartsev, Ilany, et al. (2016) demonstrated that male hyraxes reply more readily to familiar males than to strangers (Wald $\chi^2_1 = 4.3$, $P = 0.038$; Fig. 1), contrary to the 'dear enemy' effect. Here we investigated the 'nasty neighbour' effect further by conducting playback experiments simulating the arrival of a stranger into the area. The stranger hyrax's songs were played for several consecutive days/weeks, and the rate of response by local male hyraxes was recorded. Following the observations of Demartsev, Ilany, et al. (2016) and the 'nasty neighbour' hypothesis, we posited that once the local males had become familiar with the signal (i.e. song) of a stranger, they would reply to it, probably because they perceived the stranger either as a new threat with the intention of settling in the area or as a potential audience. We expected that a greater number of playbacks would facilitate the extraction of information and make the stranger more familiar to the listeners (the familiarization hypothesis). However, because, playbacks over a longer time are indicative of settling in the area, this could therefore also be interpreted as a high threat (the threat level hypothesis). Thus, we predicted that the reply levels of individual local male hyraxes would rise both over time and with frequency of playback, and would be higher in response to a song of a stranger that had been a resident (i.e. residing with a group of females) before.

METHODS

Ethical Note

This study was conducted under a permit from the Israeli Nature and Parks Authority. The annual permit numbers are 2011/38061, 2012/38400, 2013/38803, 2014/40185, 2015/40768, and 2016/41174. Throughout the 18-year field study, no long-term stress or interference effects were detected in individual animals or in the overall population. Both population numbers and the integrity of the specific social groups in the research area remained stable.

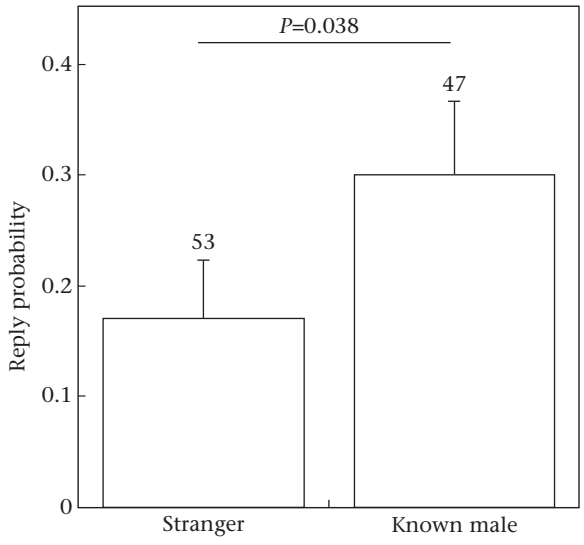

Figure 1. The probability (± SE) of replying to a playback of a local male (i.e. known individual) or a stranger. Values above bars denote number of playbacks. Data taken from Demartsev, Ilany, et al. (2016).