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Males are quicker to adjust aggression towards heterospecific intruders in a cichlid fish

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To manage the costs of aggression, territory holders confronted by intruders commonly adjust their aggression according to the perceived level of threat. Yet, we currently know surprisingly little about heterospecific interactions or sex differences with regard to adjustment of aggression, particularly in the context of the 'dear enemy' phenomenon, in which familiar individuals are treated less aggressively than unfamiliar ones. To address these knowledge gaps, we experimentally manipulated territorial intrusions in a biparental cichlid fish, the moga, *Hypsophrys nicaraguensis*, in their natural habitat. We found that aggression by both females and males decreased quicker when the focal fish was sequentially presented with the same heterospecific intruder stimulus than when it was presented on each round with a different stimulus. We also found a significant sex difference: the decrease in aggression over subsequent encounters was quicker in males. Such patterns of adjustment in aggression can have important ecological implications by affecting the territory-holding success of the interacting individuals, and, in the case of heterospecific interactions, patterns of species coexistence at the community level.

Success in aggressive defence of a territory is an important requirement of reproduction in a wide range of animals. However, aggression or fighting can also be very costly due to, for example, increased predation risk (Brick, 1998; Jakobsson, Brick & Kullberg 1995), lost mating opportunities (Santangelo, Itzkowitz, Richter, & Haley, 2002), potential for injury (Neat, Taylor, & Huntingford, 1998; Wells, 1988), time loss (Marler & Moore, 1989), and energy expenditure (Briffa & Elwood, 2004; Riechert, 1988).

Owing to these costs, we should expect selection to favour the ability of individuals to adjust aggression according to the perceived threat level. For instance, it may be advantageous for a territory owner to use information it has gathered about resource-holding potential or fighting ability of individuals with which it is familiar, whereas the intentions of strangers are more likely to be uncertain, with strangers also often posing a higher risk of a territorial take-over (Getty, 1989; Temeles, 1994; Ydenberg, Giraldeau, & Falls, 1988). In this regard, a reduced level of aggression towards neighbours and other familiar individuals (that pose a lower threat) is commonly called the 'dear enemy' effect (Temeles, 1994). The phenomenon is widespread among different animal taxa, such as mammals (Palphramand & White, 2007; Rosell, Gundersen & Le Galliard 2008; Zenuto, 2010), birds (Briefer, Rybak, & Aubin, 2008; Hardouin, Tabel, & Bretagnolle, 2006; Lovell & Lein, 2004), reptiles (Carazo, Desfilis, & Beyond, 2008; Fox & Baird, 1992; Whiting, 1999), amphibians (Feng et al., 2009; Jaeger, 1981; Lesbarrères & Lodé, 2002), fish (Aires, Oliveira, Oliveira, Ros, & Oliveira, 2015; Leiser, 2003; Sogawa, Ota, & Kohda, 2016) and insects (Dimarco, Farji-Brener, & Premoli, 2010; Langen, Tripet & Nonacs, 2000; Pfennig & Reeve, 1989). Nevertheless, the precise mechanisms underpinning plasticity in aggression towards different opponents (such as that seen in the dear enemy phenomenon) are not well understood, and remain controversial. For instance, researchers have suggested that recognition of opponents with different threat statuses could be based on environmentally influenced recognition cues (such as scent), choice of territory sites based on genetic traits (resulting in genetic similarity among neighbours) or learned recognition (Dimarco et al., 2010; Langen et al., 2000; Peeke, 1984; Temeles, 1994).

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Indirect evidence suggests that a stimulus-specific decrease in frequency, or intensity, of response towards a repeated or constant stimulus may be the mechanism most commonly involved in a reduced responsiveness towards repeated (intruder) stimuli (Bee & Gerhardt, 2001; Langen et al., 2000; Owen & Perrill, 1998; Peeke, 1984). Hence, this type of rapid learning, often regarded as 'habituation' (sensu Groves & Thompson, 1970; Thompson & Spencer, 1966), can provide a simple, adaptive mechanism for adjusting the level of aggression to reduce the associated costs. To date, most studies assessing such moderation of aggressive signals have covered vocalizations in songbirds or anurans.

Studies investigating adjustment of aggression towards familiar versus nonfamiliar opponents have also tended to focus solely on conspecific intruders or signals (Temeles, 1994; Tibbetts & Dale, 2007). Indeed, the dear enemy effect is often defined as a phenomenon occurring among individuals of the same species, even though there is no a priori reason why adjustment of aggression towards heterospecific individuals could not be under similar selection pressures. Some species of ants, for example, react more aggressively to foreign or distantly located heterospecifics than to locals of the same species (Grangier, Le Breton, Dejean, & Orivel, 2007; Langen et al., 2000; Tanner & Adler, 2009). Having heterospecific neighbours may even be desirable, as they do not compete for mates.

Finally, the dear enemy effect, and adjustments of aggression in general, have been studied almost exclusively in the context of responses by a single sex (usually males). In the rare instances where both males and females have been tested, it has been difficult to directly compare their responses because different stimuli have been used (Gromov, Krasnov, & Shenbrot, 2001; Tierney, Andrews, Happer, & White, 2013). For example, Tierney et al. (2013) found that dominant female crayfish, *Procambarus clarkii*, presented with familiar and unfamiliar opponents preferred to fight the former, whereas dominant males responded similarly towards the different opponents. However, in that study, females were presented with female opponents and males were presented with male opponents. While such findings have provided a valuable starting point for studying sex differences in adjustment of aggression, we still know little about sex differences in plasticity of aggression towards stimuli that represent a comparable threat for both sexes.

One particularly promising species for assessing adjustments of aggression is a freshwater fish, the moga, *Hypsophrys nicaraguensis* (also known as the butterfly cichlid, macaw cichlid, Nicaragua cichlid and parrot cichlid). The male and female of a breeding pair claim a territory on the lake (or river) bottom (Fig. 1), and then aggressively defend the area within which the eggs will be laid and fry will later be herded (Lehtonen, 2008; Lehtonen, Sowersby, & Wong, 2015; McKaye, 1977a). When the fry have had time to develop into sufficiently strong swimmers, longer parent-led excursions, or even territory relocations, are possible, with the juveniles being ready to become independent of their parents a month after they have started to swim (McKaye, 1977a; personal observations). Moga pairs compete intensively with both conspecifics and heterospecifics for territory sites (Lehtonen, 2008; Lehtonen et al., 2015; McKaye, 1977a). Therefore, success in aggressive territory defence against would-be usurpers and offspring predators plays a key role in parental fitness. In Crater Lake Xiloá, where this study was conducted, the moga is also a key territorial neighbour of other cichlid species, such as the poor man's tropheus, *Hypsophrys nematopus* (McKaye, 1977b), the convict cichlid, *Amatitlania siquia* (Lehtonen, 2008), and the colour polymorphic *Amphilophus sagittae* (Lehtonen et al., 2015). Previous studies and observations provide strong indirect evidence for the dear enemy phenomenon in the context of interactions between the moga and other species.

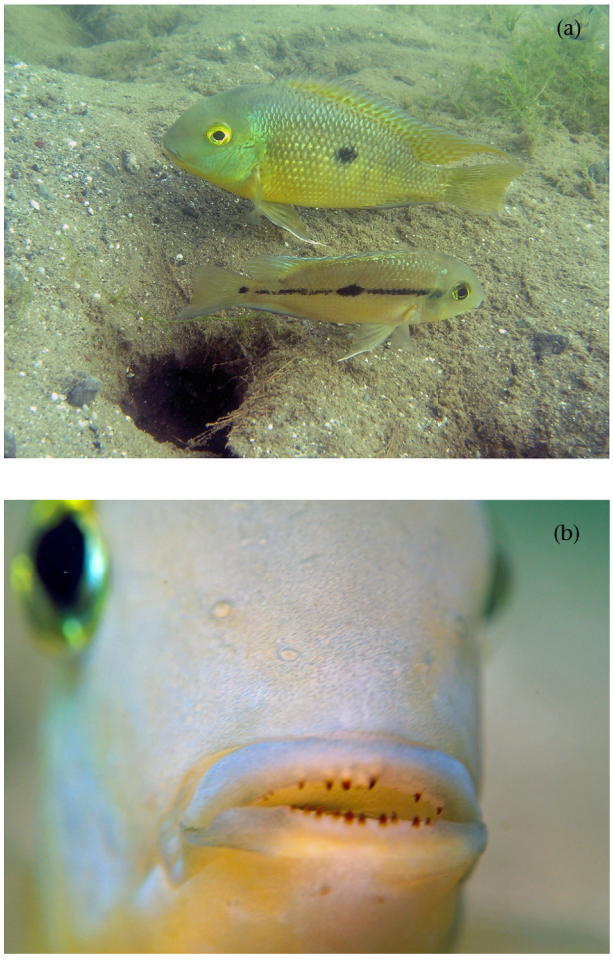

Figure 1. (a) A moga, *Hypsophrys nicaraguensis*, breeding pair in Lake Xiloá (Nicaragua), with the female in the foreground. (b) A close-up of an attacking male moga (Lake Xiloá).

Specifically, moga territory holders appear to be less aggressive towards their established convict cichlid neighbours than non-neighbour convict floaters (Lehtonen, 2008), suggesting that the dear enemy effect exists among heterospecifics. Similarly, in another species with a similar breeding system to that of moga, territory holders were found to be more aggressive towards visiting nonbreeding individuals than neighbouring breeders of the same size (Lehtonen, McCrary, & Meyer, 2010). The consequences of these interactions have the potential to impact the reproductive success of other species that co-occur with the moga (Lehtonen, 2008; Lehtonen et al., 2015; McKaye, 1977b) and, in so doing, the local community as a whole.

We set out to investigate whether male and female moga differ in adjustment of aggression in heterospecific interactions when presented repeatedly with either an identical or a different set of visual signals. We predicted that even when only visual heterospecific intruder stimuli are available, mogas will decrease the intensity of their aggressive response to a repeated intruder stimulus quicker than when they are presented with novel (i.e. unfamiliar) stimuli. Given evidence that males and females may differ in their rate of habituation to certain tasks in other species (e.g. humans: Tighe & Powlison, 1978), we also tested for sex differences in such adjustments of aggression. Owing to the pronounced sexual size dimorphism (with male mogas being larger: McKaye, 1977a, 1986), and the more pronounced role males play in defending the territory