

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.

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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 unfamiliar 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.

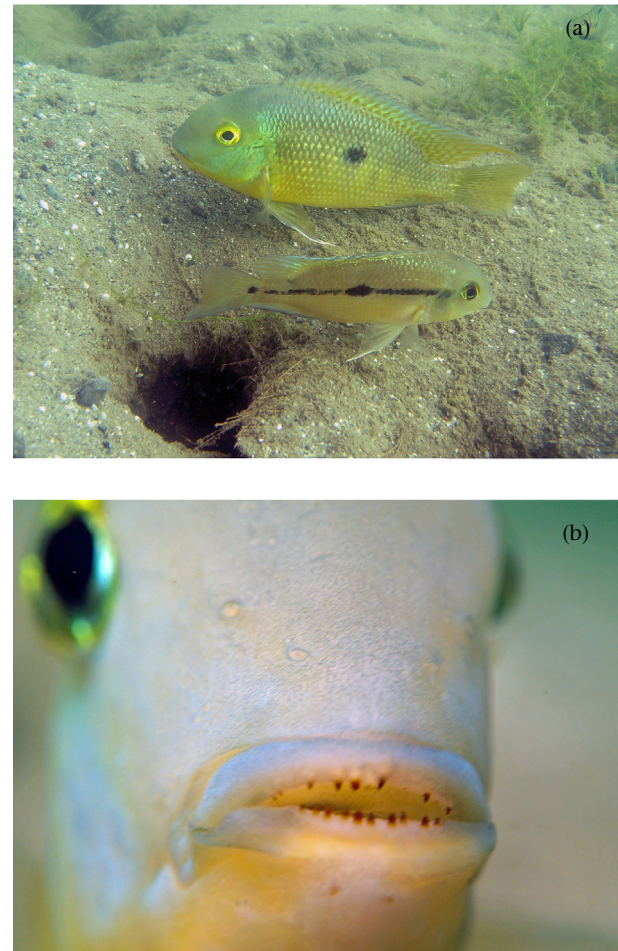


Figure 1. (a) A moga, *Hypsophrys nicaraguensis*, breeding pair in Lake Xiloá (Nicaragua), with the female in the foreground. (b) A close-up of an attacking male moga (Lake Xiloá).

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

borders (Lehtonen et al., 2015), we predicted that males might exhibit more flexibility in aggression than females.

METHODS

This field-based study was conducted in Crater Lake Xiloá (12°12.8'N; 86°19.0'W) in December 2011 (validation of fish models) and December 2013–January 2014 (aggression experiment). This relatively small Nicaraguan lake is home to more than 10, mostly biparental cichlid species that overlap extensively in their breeding sites and peak breeding seasons and, hence, compete intensively for territory space against both conspecific and heterospecific cichlid pairs (Lehtonen, McCrary, & Meyer, 2012; Lehtonen et al., 2015; McKaye, 1977a, 1986). In particular, aggression by mogas and their neighbouring cichlids is targeted towards both conspecific and heterospecific individuals that pose a risk as brood predators and/or competitors for territory space (i.e. territory take-overs; McKaye 1977a, 1977b; Lehtonen, 2014; Lehtonen et al., 2010, 2012). Such interactions with heterospecific individuals can be very frequent and even as common as (if not more so than) intraspecific aggression (Lehtonen et al., 2015; 2016), and can sometimes take place repeatedly towards specific individuals, if these are persistent or have their territories close by (Lehtonen et al., 2010; personal observations). When investigating adjustment of aggression in such an environment, it is important that the territorial responses are driven predominantly by the focal territory holder, as opposed to intruder behaviour (see Aires et al., 2015; Booksmythe, Jennions, & Backwell, 2010a). Thus, to explicitly control for confounding factors that might otherwise arise from differences in the behaviour of the stimulus animals, and to effectively decrease the possibility that any differences in behaviour are sexually motivated, we presented mogas with dummy models of sympatric, heterospecific cichlids. This approach also allowed us to test for responses to visual stimuli while controlling for other sensory modalities (e.g. smell). Hand-made dummy models have successfully been used for measuring ecologically relevant behaviours, both in the laboratory and field, in a wide range of fish taxa (Rowland, 1999). Indeed, such models have been particularly useful for measuring aggression in cichlids (Anderson, Jones, Moscicki, Clotfelter, & Earley, 2016; Cravchik & Pazo, 1990; Lehtonen, 2014; Ochi & Awata, 2009), including the moga (Lehtonen et al., 2015). The intruder models used in the current study were made by gluing a waterproof, photographic colour print of the lateral side of a live or freshly euthanized fish from Lake Xiloá (sex unknown or not noted) onto each lateral side of an elliptical floating plate (thickness = 6 mm), following Lehtonen (2014). The model was then attached to a small sinker with a thin, transparent fishing line, allowing it to float in a natural position approximately 15 cm above the substratum.

Validation of Fish Models

We first conducted a pilot study to validate that the reactions of the moga territory holders are in response to the specific fish models rather than a response to the mere presence of a foreign object appearing on their territory. For this purpose, the following two dummy types were used: intruder models of *Amphilophus* fish (*A. sagittae* or *A. xiloaensis*), which are sympatric to moga ($N = 18$; length mean \pm SE, range: 20 ± 0.8 cm, 16–24 cm) versus rectangular, elongated models that were white without any colour markings ($N = 8$; 19 ± 1.7 cm, 12–24 cm).

Each replicate ($N = 26$) was initiated by a SCUBA diver placing an intruder model approximately 40–50 cm from the centre of the focal territory (chosen as the first encountered territory in an area of a relatively high territory density). The diver then counted the

aggressive responses by both territory owners (male and female) towards the object for 5 min, giving the total rate of aggressive responses (Lehtonen, 2014). A different moga territory and intruder model were used in each replicate.

To assess the influences of sex of the focal territory holder (male versus female), and the model type ('*Amphilophus* model' versus 'inanimate object'), we used a generalized mixed model (glmmADMB package) with a negative binomial error distribution. To account for nonindependence of the actions of a male and female defending a territory, territory ID was added as a random effect. We used R 3.2.3 software (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) for all analyses.

Aggression Experiment

We used the following four model types, after Lehtonen et al. (2015): (1) *Amphilophus* (*A. sagittae* or *A. xiloaensis*) dark colour morph in dark grey/black breeding coloration, (2) *Amphilophus* dark colour morph in lighter greyish nonbreeding coloration with vertical darker colour bands, (3) *Amphilophus* gold colour morph (looks the same independent of the breeding phase), and (4) the jaguar cichlid, *Parachromis managuensis*. These particular intruder stimuli were chosen because they represent relevant heterospecific neighbours (Lehtonen et al., 2015; McKaye, 1977a) and the moga has a demonstrated ability to differentiate between these stimuli based on visual cues alone (Lehtonen et al., 2015). Furthermore, we are not aware of any interbreeding or courtship between moga and these heterogeneric species, either in the wild or in captivity. In the current study, we were not focusing on differential aggression towards the different types of models per se (for a study on that topic, see Lehtonen et al., 2015), but rather on adjustments of aggression to repeated heterospecific stimuli, as detailed below. All models were 16 cm long, being similar in size to a large moga male, as well as to typical *Amphilophus* territorial neighbours (Lehtonen et al., 2015; McKaye, 1977a, 1986), and allowing easy handling underwater. In this respect, we approximated total lengths of moga males assessed in this study to be 13–17 cm and those of females to be 6.5–10 cm. We had 10–11 different models of each of the four model types, with each model being based on a different photograph of an actual fish.

Each territory-holding moga pair (Fig. 1) tested in this study ($N = 48$) was presented with either a different stimulus type in each of the four rounds ('different stimuli' treatment) or the same intruder stimulus four times ('repeated stimulus' treatment). A significantly quicker decrease in aggression in the latter case should imply a habituation to the repeated (i.e. familiar) intruder stimulus (see Peeke, 1984). Each replicate of the 'different stimuli' treatment ($N = 24$) was initiated by a SCUBA diver placing an intruder model approximately 40–50 cm from the centre of the focal territory (chosen as the first encountered territory in an area of high territory density). The diver then counted the aggressive responses by both territory owners (male and female) towards the model for 5 min, giving the total rate of aggressive responses (Lehtonen, 2014). After a 5 min resting period (with all models out of sight), the procedure was then repeated with another model type, so that, one after the other, all four types of models were presented to the focal moga pair. We used a 5 min resting period between presentations to minimize temporal changes in both abiotic (e.g. lighting) and biotic (e.g. other fish moving in and out of the area) conditions. A 5 min interval is also ecologically relevant since territory holders commonly encounter a range of different species within a span of a few minutes (Lehtonen et al., 2012). Every possible order of presenting the four different model types ($N = 24$ different combinations) was used once. The 'repeated stimulus' treatment was

otherwise identical to the 'different stimuli' treatment, except that the same model (i.e. based on the same image) was presented on each of the four rounds. In the former, six different intruder models of each of the four stimulus types were used in total, with a different territory ($N = 24$) being sampled each time. In one of the 24 replicates, the data for the fourth presentation were missing because the pair started to relocate their juveniles before the end of the replicate. After each replicate, the territory was marked with a numbered piece of ceramic tile to avoid sampling the same territory more than once. The different model types ('repeated stimulus' treatment) and combinations of model types ('different stimuli' treatment) were run in a random order. As far as possible, the same number of replicates (usually one or two) of each treatment was run on each day that data were collected.

To assess the influences of sex of the focal territory holder (male versus female), the round of presentations (from first to fourth presentation) and the treatment ('different stimuli' versus 'repeated stimulus'), we first considered applying a generalized mixed model with a Poisson distribution. However, we found that the data were overdispersed (Zuur, Hilbe, & Ieno, 2013), and we therefore switched to a negative binomial error distribution, as appropriate for overdispersed count data (Zuur et al., 2013), using the `glmmPQL` function of the packages 'nlme' and 'MASS'. To account for the repeated design of the experiment, nonindependence of the actions of a territory-holding male and female and the potential aggression biases towards each intruder model, we added fish ID, territory ID and model ID as random effects (as per Pinheiro & Bates, 2000). This approach involved using *t* tests to assess the effects from the simplified models.

To further examine any sex differences in adjustment of aggression, and to facilitate comparisons to previous studies (see Dijkstra & Groothuis, 2011; Lehtonen, 2014), we also analysed males and females separately. Here, the two mixed models, one per sex, were similar to the model above, except that we only had two fixed effects (the round of presentations and the treatment) and two random effects (fish ID and model ID). In all cases, we then assessed whether the model could be refitted without the least significant term of the highest remaining order, using $P = 0.10$ as the cutoff point (Crawley, 2007).

Ethical Note

Work carried out in this study was approved by MARENA, Nicaragua (permit no. 013–276102013) and adheres to the ASAB/ABS guidelines for the use of animals in research. We observed a total of 74 moga territories during this study, with the observer being careful to minimize the disturbance to these and any neighbouring fish territories. Because the photographs used for model constructions were taken in the context of previous studies and no new photographs needed to be taken for this study, the current study included no potentially harmful manipulations, invasive samples, trapping, tags or radiotransmitters, and it resulted in no pain to any of the subjects. The staged territorial intrusions by model intruders may have caused mild distress, but only of a kind that the study subjects are constantly exposed to in their densely populated breeding environment.

RESULTS

Validation of Fish Models

The rate of male aggression towards *Amphilophus* models was 6.1 ± 1.0 responses/min and towards the inanimate object 0.2 ± 0.2 responses/min. For females, these aggression rates were 3.9 ± 0.7 and 0.0 ± 0.0 , respectively. This implies that males showed

a higher overall rate of aggression than females (mixed model, sex effect: $z = 3.05$, $P = 0.002$) and fish models were treated more aggressively than inanimate objects (treatment effect: $z = 6.92$, $P < 0.001$).

Aggression Experiment

When we applied a generalized mixed model to assess the effects of sex of the focal territory holder, progress of presentation and stimulus treatment, we found a significant interaction between sex and round of presentation after model simplification. Specifically, there was already a marginally nonsignificant round effect difference in male versus female aggression in the second round of presentations (second presentation*sex interaction: $t_{378} = 1.869$, $P = 0.062$; Fig. 2) and, by the third round, males had decreased their aggression significantly more than females (third presentation*sex interaction: $t_{378} = 3.360$, $P < 0.001$; Fig. 2), a sex difference that became even stronger on the fourth round of presentations (fourth presentation*sex interaction: $t_{378} = 5.011$, $P < 0.001$; Fig. 2). We also found that the level of aggression had decreased significantly more in the 'repeated stimulus' treatment than the 'different stimuli' treatment by the third (third presentation*treatment interaction: $t_{378} = 1.972$, $P = 0.049$; Fig. 2) and especially fourth presentation (fourth presentation*treatment interaction: $t_{378} = 3.081$, $P = 0.002$; Fig. 2), whereas the difference was in the

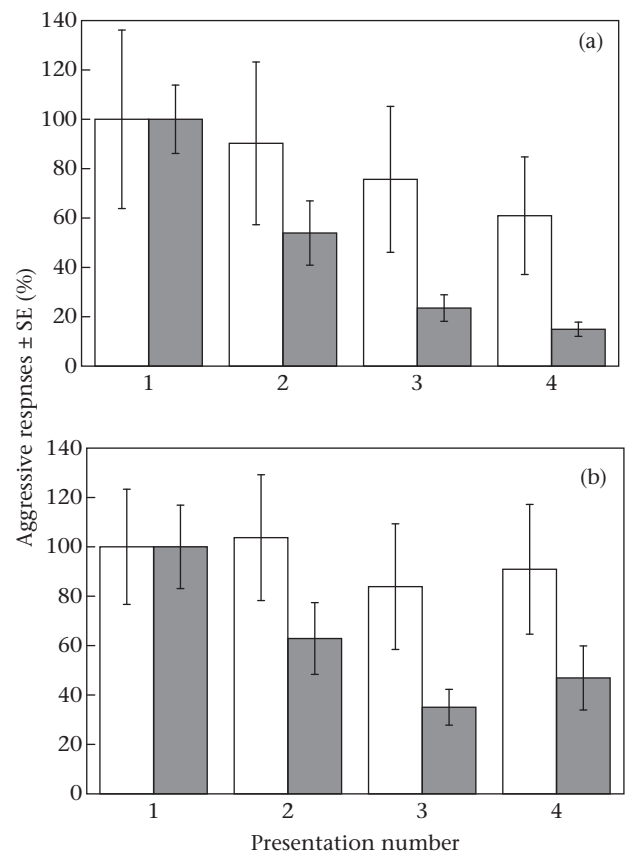


Figure 2. The change in the rate of aggression by female (white columns) and male (grey columns) mogas during the first, second, third and fourth rounds of intruder presentations. The rate of aggression has been scaled (as a percentage) relative to the responses of females and males during the first presentation (females: 9.4 responses/min; males: 21.3 responses/min). (a) Responses towards the same intruder stimulus repeated four times. (b) Responses when a different intruder stimulus was presented on each round. The number of territories sampled: fourth presentation $N = 23$; all other presentations $N = 24$.

same direction, albeit nonsignificantly so, in the second round of presentations ($t_{378} = 1.095$, $P = 0.27$; Fig. 2).

We then considered females and males in separate generalized mixed models. The results followed the above pattern. In particular, in males, the level of aggression had decreased significantly more in the 'repeated stimulus' than 'different stimuli' treatment by the fourth presentation (fourth presentation*treatment interaction: $t_{187} = 2.251$, $P = 0.026$; Fig. 2), whereas the interaction was not significant in the second or the third round of presentations ($P > 0.10$; Fig. 2). The pattern was the same for females, with a significantly faster decrease in aggression in the 'repeated stimulus' than 'different stimuli' treatment by the fourth presentation (fourth presentation*treatment interaction: $t_{187} = 2.150$, $P = 0.033$; Fig. 2), but not before it ($P > 0.10$; Fig. 2).

DISCUSSION

The results of this study show that, when presented with visual cues of heterospecific intruders, the rate of aggressive responses by moga territory holders in their natural habitat decreased quicker when the same intruder stimulus was presented repeatedly than when the territory holders encountered a different intruder stimulus each time. Interestingly, male and female moga differed in their responses, with males not only having a higher overall level of aggression, but also adjusting their aggression quicker than females.

Our results, in this regard, are among only a handful of studies to focus on sex differences in adjustments of aggression or the dear enemy effect. Previous studies assessing sex differences within the dear enemy context have tended to do so by comparing the patterns of between-male aggression to between-female aggression (see Gromov et al., 2001; Tierney et al., 2013). In addition, although the ability to discriminate between familiar and unfamiliar conspecifics of the opposite sex has sometimes been considered in the context of the dear enemy effect (Gherardi, Aquiloni, & Tricarico, 2012; Van der Velden, Zheng, Patullo, & Macmillan, 2008), these studies have not compared responses of the two sexes. Indeed, territory holders may consider conspecific intruders of the opposite sex not only as a territorial threat, but also as potential mating partners/competitors, which can cause uncontrolled behavioural biases that are not related to sex differences in adjustment of aggression or the dear enemy effect per se. Accordingly, for the territory intruder to pose a similar threat (or opportunity) for both sexes, we used heterospecific intruder stimuli, thus allowing us to rule out the possibility that any differences in aggression may be driven by reproductive motivations. By so doing, we found that, following a stronger initial response, males show a stronger adjustment of aggression over repeated encounters than females. This sex difference may relate to the different roles of the sexes in territory defence and parental care, with females being more focused on tending the fry and males being more focused on guarding territory borders (Lehtonen et al., 2015, 2016). This sex-based difference in specialization of roles may also lead to sex-specific motivational differences towards intruders in general, although we cannot exclude the existence of sex-specific cognitive biases.

To date, such adjustments of aggression have been considered surprisingly rarely in the context of heterospecific opponents. This may be because the dear enemy literature has been dominated by studies of male bird vocalizations in the conspecific context. However, the competitive regime and species composition in the community are likely to be relevant in determining the importance of heterospecific interactions in territorial aggression. For example, Leiser (2003) found no dear enemy effect in the pupfish *Cyprinodon variegatus* when the intruders were heterospecific striped killifish,

Fundulus majalis, which posed no risk of a territory take-over. In contrast, sensitivity to heterospecific intruders is more important, for example, in species of ants that habituate to heterospecific individuals from close-by colonies (Langen et al., 2000; Tanner & Adler, 2009) and in fiddler crabs, *Uca* spp., that have been found to even cooperate with their heterospecific neighbours in territory defence (Booksmythe, Jennions, & Backwell, 2010b). In cichlids, individuals of the cichlid *Neolamprologus mustax* were subject to higher levels of aggression by another species, *Variabilichromis moorii*, when the former were displaced by the researchers further away from their own territories to face unfamiliar *V. moorii* territory holders, than when displaced locally within the ranges of familiar *V. moorii* territory holders. One explanation for this finding is that *V. moorii* are less aggressive towards familiar than unfamiliar *N. mustax* individuals (Ochi et al., 2012). Furthermore, recent results also suggest that in the moga (Lehtonen et al., 2015), territory holders are able to assess the threat status of different individuals of another species and act accordingly. Hence, in combination with these recent findings, the current results suggest that familiarity effects towards heterospecific individuals could be relatively widespread and should, therefore, be considered in the context of territorial neighbours and other relevant types of adjustments of aggression more regularly than has thus far been the case.

We found that by the fourth round of stimulus presentations at the latest, the level of aggression in both sexes had decreased more when they saw the same stimulus repeatedly than when they encountered a new heterospecific stimulus on each round. Similar approaches in other studies, indicating a more intense response towards a novel (rather than repeated) stimulus, have earlier been used to differentiate between habituation versus fatigue or sensitization to stimulus presentations (Aires et al., 2015; Humfeld, Marshall, & Bee, 2009; Peeke, 1984). Some researchers have also made a distinction between short-term and long-term habituation (Bee & Schachtman, 2000), such that the former is detected over a single observation session, whereas the latter is measured over days or weeks (Peeke, 1984). In this regard, it has been suggested that long-term habituation is necessary for habituation to function as the proximate mechanisms in the dear enemy effect (Bee & Schachtman, 2000). However, processes also akin to short-term habituation can allow individuals to interact with neighbours using an appropriate level of aggression, especially in dynamic social environments (Humfeld et al., 2009). In this respect, future studies may wish to modify the timeframe of intruder presentations and the level of similarity among the stimuli, or to compare responses towards a single individual versus different individuals of a certain species, to test how these factors might affect the adjustment of aggressive responses. Interestingly, a seemingly lower level of aggression directed by moga territory holders towards established convict cichlid pairs nesting near the mogas' territories (Lehtonen, 2008), suggests that mogas are capable of individual level recognition of heterospecific intruders, at least when all relevant sensory cues are available.

We note that the territory holders may have actively collected information about the fighting ability of the model intruders which never expressed aggression after 'invading' the territory. In other words, the territory holders may initially have been uncertain about the intruder's fighting ability and intentions, but with each round of encountering the same intruder, it might have become increasingly apparent to the territory holders that the specific intruder was not posing a high threat, resulting in a gradual decrease in the aggressive response (Arnott & Elwood, 2009; Enquist & Leimar, 1983; Heap, Stuart-Fox, & Byrne, 2012). Hence, the changes in the responses to a repeated intruder stimulus over successive presentations may reflect an active correction to an

initially uncertain response. Importantly, whether or not active information gathering is involved, moderation of aggression towards an increasingly familiar intruder can be adaptive. In particular, familiar individuals can not only be more predictable, but in the case of lacustrine cichlids, also less likely to predate upon the territory holder's offspring, especially if they are also territory holders themselves (Lehtonen et al., 2010, 2015). For example, besides moga (Lehtonen, 2008), territory-holding pairs in another crater lake-dwelling cichlid, *Amphilophus astorquii*, are also more aggressive towards visiting or floating nonbreeding individuals than towards neighbouring (i.e. more familiar) breeders (Lehtonen et al., 2010).

To conclude, while the dear enemy phenomenon has been studied most extensively in the context of bird vocalizations, comparable mechanisms can be important also in species that rely on other sensory modalities. In this context, our findings are concordant with recent studies showing that visual input alone can be sufficient for identification of familiar versus unfamiliar individuals (Aires et al., 2015; Kohda et al., 2015; Van Dyk & Evans 2007) and for neighbour recognition (Detto, Backwell, Hemmi, & Zeil, 2006). Importantly, the current results also show that such adjustments are relevant towards heterospecific intruders and can differ between the sexes. More generally, adjustments of aggression can provide important insights into species interactions and even community level processes, especially when expressed by key species in the community. Therefore, as our study highlights, greater attention should be paid to the role of heterospecific interactions and sex differences when assessing habituation, familiarity effects, dear enemy and other relevant patterns of plastic expression of aggression.

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