



Intraspecific variation in audience effects during outgroup conflict in a cooperatively breeding fish

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Conspecific audiences have frequently been shown to affect behaviour during competitive interactions. However, research on audience effects has focused almost exclusively on how individual observers influence dyadic contests. Few studies have investigated more complex social scenarios, such as when groups defending a collective territory against outsiders can be monitored by neighbours. We used groups of the cooperatively breeding cichlid fish *Neolamprologus pulcher* to test experimentally how the presence of neighbours influences group and individual level defence behaviour towards a female intruder, as well as associated within-group interactions. In the presence of neighbours, groups performed more defensive acts and spent more time defending their territory, but the nature of the response to neighbour presence differed between group members. Dominant females attacked intruders more, while subordinate females produced aggressive displays of longer mean duration; dominant males also tended to increase mean display duration. Despite the significant audience effects on defence behaviour, neighbour presence did not lead to any discernible changes in within-group aggression, affiliation or submission during the intrusions. Our study expands the small current literature on audience effects in group-living species and thus contributes to a fuller understanding of within- and between-group social dynamics.

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In nature, animals live in interconnected networks of conspecifics such that social interactions rarely take place in isolation (Matos & Schlupp, 2005; Zuberbühler, 2008). Third-party individuals (also referred to as audiences (Matos & Schlupp, 2005), spectators (Barve et al., 2020) or bystanders (Bertucci et al., 2014)) are often in close enough visual or auditory proximity to eavesdrop on interactions between others, without taking part in them. Eavesdropping can provide valuable information about, for example, the quality (Mennill et al., 2002), competitive ability (Oliveira et al., 1998; Toth et al., 2012) and leadership potential (Thomsen et al., 2021) of those engaged in the interaction, as well as the social environment more broadly (Barve et al., 2020). Because information gathered through eavesdropping can be used to inform the future behaviour of audience members (Mennill et al., 2002; Oliveira et al., 1998), the presence of an audience may in turn cause the observed individuals to adjust their behaviour, a phenomenon known as an 'audience effect' (McGregor & Peake, 2000). While audience effects have been documented in a variety of contexts, including when

assessing potential mating opportunities (Baltz & Clark, 1997; Overduin-de Vries et al., 2012), making reproductive investment decisions (Nöbel & Witte, 2013) and caring for offspring (Keddy Hector et al., 1989), experimental studies have overwhelmingly focused on competitive interactions between rivals (e.g. Matos & McGregor, 2002; Montroy et al., 2016).

In line with theoretical predictions (Johnstone, 2001), the presence of an audience has been shown to induce increased aggression during contests in several taxa (crustaceans: Darden et al., 2019; dos Santos et al., 2017; insects: Fitzsimmons & Bertram, 2013; Montroy et al., 2016; fish: Matos & McGregor, 2002). These audience effects can be modulated by factors relating to both the audience, such as their sex (dos Santos et al., 2017; Dziewczynski et al., 2012; Montroy et al., 2016) and prior knowledge (Bertucci et al., 2014), and the contest participants, such as their familiarity with the opponent (Dziewczynski et al., 2012; Oliveira et al., 1998) and previous exposure to an audience (Cruz & Oliveira, 2015; Darden et al., 2019; Matos et al., 2003). For instance, the presence of a male observer induces heightened aggression between male Siamese fighting fish, *Betta splendens* (Matos & McGregor, 2002), likely because eavesdroppers extract information from the interactions that inform future behaviour: eavesdroppers are slower to attack males that

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they have observed previously winning a contest (Oliveira et al., 1998). However, when the audience is female, males engage with opponents for longer but attack less, possibly because excessive aggression drives females away during courtship (Matos & McGregor, 2002). While extensive, research on contest-related audience effects has focused primarily on dyadic interactions observed by single individuals, and thus has mostly been conducted on solitary territorial species (dos Santos et al., 2017; Matos & McGregor, 2002) or those that form temporary, unstructured aggregations (Cruz & Oliveira, 2015; Montroy et al., 2016). Audience effects have rarely been studied in species with stable, structured groups (Hellmann & Hamilton, 2014), but identifying their influence on competitive outgroup interactions and associated within-group behaviour is important for our understanding of broader social dynamics and evolution.

In many social species, groups and their members face numerous threats from conspecific outsiders seeking to capture fitness-limiting resources such as territory or reproductive opportunities (Arseneau-Robar et al., 2016; Radford, 2008a; Ridley, 2012; Thompson et al., 2017). Empirical research on outgroup conflict (that arising with one or more outsiders; we use 'intergroup' conflict to refer to conflict between rival groups specifically) has traditionally focused on the interactions between rivals during contests, including which individuals participate and how much they contribute (Kitchen & Beehner, 2007; Meunier et al., 2012; Radford, 2003). Contributions can vary greatly and depend partly on the personal risks and opportunities that individual conflicts present; for instance, outsiders that pose a threat to all group members may face defensive actions from the whole group (Isbell et al., 1990), while those posing a threat to specific individuals may elicit heightened responses from only a subset of group members (Desjardins, Stiver, et al., 2008; Ligocki et al., 2015; Mares et al., 2012). More recently, there has been increasing research into how within-group interactions change both during (Arseneau-Robar et al., 2016; Braga Goncalves & Radford, 2019) and in the aftermath (Braga Goncalves & Radford, 2019; Mirville et al., 2020; Radford et al., 2016) of outgroup contests. For instance, female vervet monkeys, *Chlorocebus aethiops pygerythrus*, use both affiliation and aggression during intergroup contests to incentivize male group-mates to participate (Arseneau-Robar et al., 2016), while increases in within-group affiliation are seen following outgroup contests in green woodhoopoes, *Phoeniculus purpureus* (Radford, 2008b), and in the daffodil cichlid, *Neolamprologus pulcher* (Bruintjes et al., 2016). Although neighbours in territorial species are well placed to eavesdrop on contests between nearby conspecifics, studies of outgroup conflict have generally not considered the wider social environment (but see Barve et al., 2020; Hellmann & Hamilton, 2019). As a result, audience effects arising from the presence of third-party outgroup individuals on the dynamics of outgroup contests and associated within-group interactions are largely unexplored.

Neolamprologus pulcher, a highly social cichlid fish from Lake Tanganyika, is an ideal species in which to assess outgroup audience effects during territorial intrusions. It is a cooperatively breeding species that lives in groups comprising a dominant breeding pair and 1–15 subordinates of both sexes (Balshine et al., 2001). Subordinates contribute to several cooperative tasks including aggressive defence against conspecific rivals (Bergmüller & Taborsky, 2005; Taborsky, 1984). The very small substrate-based territories defended by groups (range 0.08–1.01 m², Balshine et al., 2001) are often clustered together, meaning that they share borders with those of multiple neighbours (Balshine-Earn et al., 1998; Stiver et al., 2007) and that there is the opportunity for monitoring of the wider social environment. Dominants and subordinates of both sexes frequently leave their territories to visit other groups (range 0.5–16 m away,

Bergmüller et al., 2005; range 0.2–7.7 m away, Jungwirth et al., 2015), intruding on other territories in search of opportunities for sneaky matings (Hellmann et al., 2015), the take-over of breeding positions (Balshine et al., 2001; Balshine-Earn et al., 1998; Stiver et al., 2004) or dispersal (Balshine et al., 2001; Bergmüller et al., 2005). Regular extraterritorial forays appear to be advantageous as breeding positions are filled quickly after becoming available (Balshine-Earn et al., 1998), even though outsiders – territorial intruders and neighbours at shared borders – can be met with substantial aggression by all residents (Balshine et al., 2001; Jungwirth et al., 2015; Ligocki et al., 2015). Previous studies have shown that outgroup conflict in the daffodil cichlid can have immediate (Braga Goncalves & Radford, 2019) and delayed (Bruintjes et al., 2016) impacts on within-group interactions. Furthermore, the presence of neighbours influences both within-group interactions (Hellmann & Hamilton, 2019) and interactions with heterospecific individuals: subordinates contribute more to antipredator defence when neighbours are within sight (Hellmann & Hamilton, 2014). There are thus good reasons to expect responses to conspecific outsiders also to be influenced by the presence of neighbours.

To test experimentally the effect of a third-party outgroup audience (i.e. a neighbouring group) on contributions to outgroup contests and associated within-group interactions, we simulated territorial intrusions by single, large unfamiliar females into group territories when familiar neighbours were either present or out of sight (Fig. 1). We predicted that focal groups would be more aggressive towards an intruder when their neighbours were visible, to signal resource-holding potential and group cohesion and to seek reputational benefits (Johnstone, 2001) (prediction 1). Comparing different categories of individual, we predicted that subordinates would display a greater relative increase in defensive efforts than dominants in the presence of neighbours as a means of advertising their cooperative skills (prediction 2). Subordinates are less tolerated by dominant individuals when neighbours are present, likely because neighbouring groups provide potential dispersal opportunities to subordinates as well as a source of new (more helpful) helpers (Hellmann & Hamilton, 2019). Therefore, by increasing their defensive effort, subordinates may concurrently appease their own groupmates (Bergmüller & Taborsky, 2005) and signal their cooperative value to neighbours to ease a potential future dispersal attempt (Bergmüller et al., 2005). In addition, as defensive behaviours can be classified as high-intensity attacks and low-intensity aggressive displays – which represent markedly different levels of conflict escalation and of associated energetic costs (Ros et al., 2006) – we predicted that individual categories may vary in their specific defensive actions in response to the presence of an audience during outgroup conflict (prediction 3). In terms of within-group behaviour, we predicted that dominants would direct significantly more aggression at the subordinates during intrusions when the neighbours were visible for two reasons. First, previous work has shown that dominants target subordinates during intrusions by large female rivals possibly as an incentive for subordinates to increase their defensive efforts (Braga Goncalves & Radford, 2019); the need for increased subordinate defence may be higher in the presence of neighbours to end the conflict faster and as a display of group strength. Second, lower dominant tolerance of subordinates in the presence of neighbours is manifested through increased aggression (Hellmann & Hamilton, 2019). Thus, intrusions by large females in the presence of a neighbouring group may both increase the need for subordinate defensive contributions and reduce dominant tolerance of subordinates, exacerbating within-group aggressive interactions (prediction 4). Such an increase in within-group aggression would likely impact within-group submission and affiliation (prediction 5) because aggressed individuals often perform submissive displays

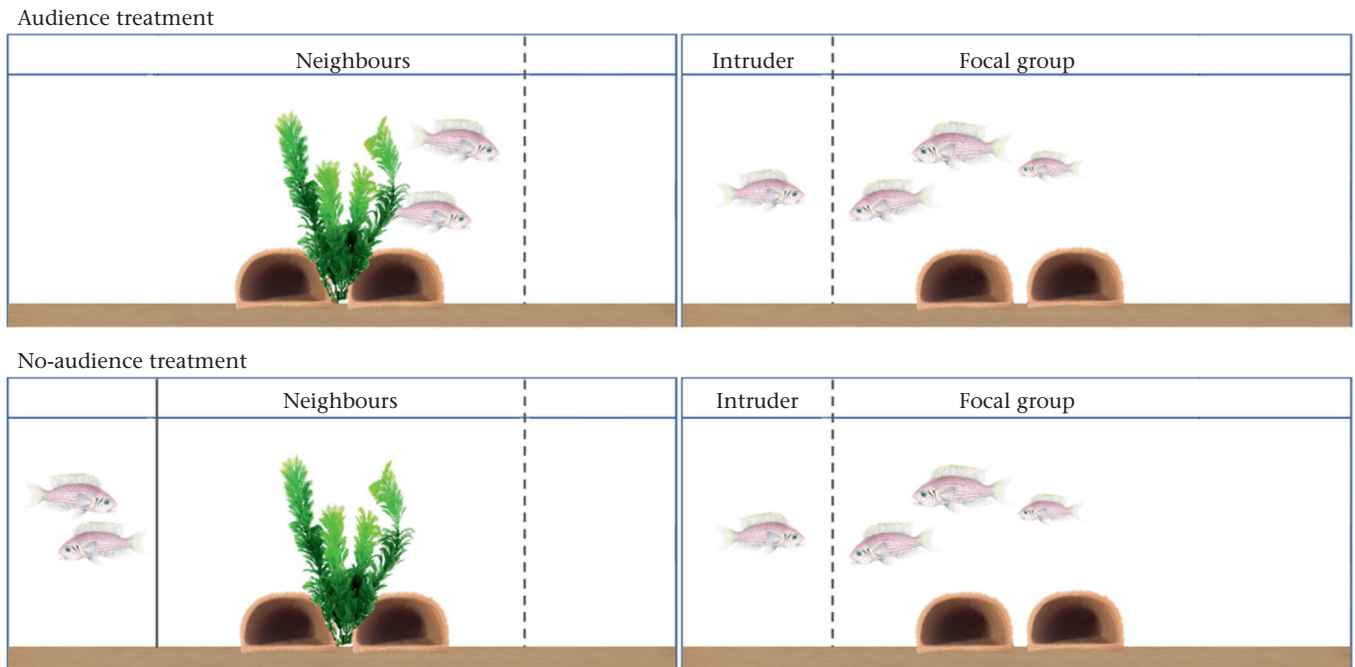


Figure 1. Schematic representation of the experimental treatments. Solid vertical line in neighbour tank represents an opaque partition; dashed vertical lines in both tanks represent transparent partitions.

and avoidance behaviours (Reddon et al., 2021), with the latter potentially reducing the opportunity for affiliative exchanges.

METHODS

Study Subjects and Husbandry

We conducted the study in August–September 2019 on a captive population of *N. pulcher* housed at the University of Bristol. We formed 15 focal groups consisting of three individuals: a dominant female (mean \pm SE standard length (SL) = 68.5 ± 1.4 mm), a dominant male (77.5 ± 1.6 mm SL) and a subordinate female (53.1 ± 1.1 mm SL). Subordinate females were visibly smaller than dominant females (mean \pm SE difference: 15.4 ± 1.7 mm). Groups of three, although small, are not uncommon in the wild (Balshine et al., 2001; Stiver et al., 2004) and are often used in laboratory studies (Bruintjes et al., 2016; Hamilton & Ligocki, 2012; Heg & Hamilton, 2008; Mileva et al., 2011; Zottl et al., 2013). We housed the groups in 70-litre tanks (width \times length \times height: $30 \times 61 \times 38$ cm) that formed their territories (Braga Goncalves & Radford, 2019). Each tank contained 2–3 cm of sand (Sansibar river sand), a 75 W heater (Eheim), a filter (Eheim Ecco pro 130), a thermometer (Eheim), two plant-pot halves (each 10 cm wide) for shelters and an artificial plant at the tank centre, and a tube shelter close to the water surface at the tank edge. We set water temperature to 27 °C and room lights on a 13:11 h light:dark cycle (daylight from 0700 to 2000 hours); water quality parameters were checked and kept within recommended ranges (pH: 7.5–8.2, ammonia: 0–0.25 ppm; nitrites: 0–0.25 ppm; nitrates: 20–80 ppm) through weekly partial water changes. We fed fish twice daily 6 days per week: a selection of frozen brine shrimp, water fleas, prawns, mosquito larvae, mysid shrimp, bloodworms, cichlid diet, spirulina, copepods, krill and sludge worms in the mornings on Monday to Friday, and dry fish flakes in the evenings and on Saturdays. Before the experimental set-up, focal tanks were visually isolated from neighbouring tanks by opaque ViPrint sheets (0.35 mm thickness).

Experimental Set-up

To investigate how the presence of a conspecific third-party outgroup audience affects defence behaviour against an intruding individual and within-group interactions during the intrusion, we performed an experiment where focal groups were subjected to two treatments that differed only in whether neighbours were visible or not during the intrusion. Focal groups were paired with a neighbouring breeding pair (male SL: 81.3 ± 3.1 mm; female SL: 69.4 ± 1.9 mm), in a separate tank, whose female was size-matched to the focal dominant female (1.3 ± 0.4 mm difference). One week prior to each group's first experimental trial, we removed the partition between the focal group and the neighbouring pair to allow them to familiarize visually. *Neolamprologus pulcher* are capable of individual recognition based only on visual information (Balshine-Earn & Lotem, 1998; Frostman & Sherman, 2004; Kohda et al., 2015; Sogawa et al., 2016) and establish familiar relationships with neighbours within 4–5 days (Sogawa et al., 2016). We gave each group two treatments in a repeated-measures design: during a simulated territorial intrusion by an unfamiliar large female, the neighbours were either visible in their territory (audience treatment) or out of sight from the focal group (no-audience treatment). The female intruder was also size-matched to the focal dominant female (1.0 ± 0.4 mm difference), and thus to the neighbour dominant female, to minimize size-related effects on behaviour (Milner et al., 2011). Large intruding females represent a credible outgroup threat for several reasons: breeder turnover is rapid in the wild, meaning that breeding positions regularly become available (Stiver et al., 2004); intruding females may threaten the position of breeding females (Stiver et al., 2006); and some males form polygynous territories that overlap multiple, smaller female territories (Desjardins, Fitzpatrick, et al., 2008), making it plausible that large females may attempt to carve out small breeding areas within a male's territory. Intrusions by breeding-size females have previously been shown to elicit group territorial defence (Braga Goncalves & Radford, 2019; Desjardins, Stiver, et al., 2008;

Ligocki et al., 2015). The same female intruder was used for both treatments to the same focal group, but different intruders were used for each focal group. Five female neighbours and three focal dominant females were used as intruders to other groups in weeks when they were not otherwise being used in the study; the remaining seven intruding females came from groups not used in the experiment. Neighbour pairs were sequentially used as neighbours to two focal groups. We performed trials to the same focal group on two consecutive days and counterbalanced treatment order between focal groups to control for intrusion experience and potential effects of intruder familiarity on day 2 (Dziewieczynski et al., 2012).

We conducted all intrusions in the morning to minimize natural daily variations in behaviour, hormone levels and hunger (Desjardins et al., 2011). We removed the filter inlet and outlet, the heater, plants and tube shelter from focal tanks in experimental trials approximately 10 min before the start of the trial, to facilitate observation during video analysis. The two plant-pot shelters were left in place to maintain the core breeding territory. Experimental trials followed a previously established intrusion protocol (Braga Goncalves & Radford, 2019). Prior to the start of a trial, we slid an opaque partition between the neighbour and focal tanks; we also slid two partitions (one opaque and one transparent) into the focal tank, through single-channel PVC tracks glued to the long walls, 8 cm from the tank edge closest to the neighbour tank (Fig. 1). The partitions in the focal tank created a compartment that provided enough space for the intruder to move. We then netted the intruder from her home tank, placed her in the compartment and left her to settle for 5 min; during this period, the intruder was hidden from sight from both the focal group and the neighbours by the opaque partitions.

While the intruder was settling, we prepared the neighbour tank according to treatment (Fig. 1). In the audience treatment, we slid a transparent partition through PVC tracks 8 cm from the tank edge closest to the focal tank, so that neighbours would be able to observe the intrusion from a short distance and be seen by the focal group. In the no-audience treatment, we first placed the transparent partition as in the audience treatment for visual consistency. Additionally, we gently used a large net to herd the pair to the end of the tank furthest from the focal tank, and then placed an opaque partition so that they were contained within a similar-sized compartment to the intruder; during intrusions, the focal group would therefore be able to see the majority of the neighbour territory but not the neighbours. A trial started immediately after we removed the partition between the two tanks, and the opaque partition between the intruder and the focal group, which allowed the focal group to interact visually with the intruder and to have a view of the neighbour territory. Trials lasted 10 min and were videorecorded (Sony Handycam HDR-XR520) for later extraction of behavioural data. At the end of the intrusion, we replaced the opaque partitions and netted the intruding female, out of sight of all other individuals, for immediate return to her home tank, then removed the remaining partitions.

Animal Welfare Note

This work was conducted with approval from the Ethical Review Group of the University of Bristol, U.K. (University Investigator Number: UB/19/059) and adhered to the ASAB/ABS Guidelines for the use of animals in research. 'Intruder' females twice experienced (on separate days) 5 min of social isolation and 10 min when they were subjected to the defensive actions of the focal group from behind a transparent divider. Careful monitoring of 'intruders' in the aftermath, when returned to their home tanks, indicated that all individuals were readily accepted back by their own groups, and displayed natural behaviour and recommenced feeding within minutes of being returned.

Data Collection and Analysis

We gave the videos coded names so that the observer (I.B.G.) who collected data from all of them was blind to the treatment when scoring the behaviours. There was no evidence of any systematic change in scoring as video analysis progressed – no significant relationship between the point in the scoring sequence and group level performance scores (Spearman rank correlation, number of defensive acts: $r_s = -0.04$, $N = 30$, $P = 0.849$; time spent in defensive action: $r_s = -0.23$, $N = 30$, $P = 0.219$) – as would be expected with an experienced scorer of *N. pulcher* behaviour. We analysed the videos using JWatcher (v.1.0, <http://www.jwatcher.ucla.edu/>) to score relevant behaviours. We scored intruding female responsiveness to the focal group as the proportion of time the intruder spent actively swimming and facing the group (as in Braga Goncalves & Radford, 2019); it did not differ significantly between treatments (paired t test: $t_{14} = 1.14$, $P = 0.273$). We scored all other behaviours, used to test our predictions, according to previously published ethograms for *N. pulcher* (Reddon et al., 2015; Sopinka et al., 2009), which provide an objective categorization. Specifically, from each 10 min intrusion and for each category of focal individual (dominant male, dominant female, subordinate female), we scored all defence behaviour displayed towards the intruder as counts of all attacks (rams and bites) and aggressive displays (aggressive postures, frontal displays and aggressive approaches), and the time invested in defensive displays; because attacks are always very short, attack durations were not recorded. We also scored all counts of affiliation (follows, parallel swimming, bumps and joins), aggression (attacks and aggressive displays as for defence, plus chases) and submission (submissive postures, quivers and hooks) displayed by each category of focal individual towards groupmates in the 10 min intrusion period. Aggressive behaviour directed towards the intruder was clearly distinguished from equivalent behaviour directed at groupmates because attacks require physical contact (either with the partition or with the groupmate) and displays almost always involve approaching the target individual and elicit a behavioural response, be it avoidance, submission or aggression.

Statistical Analysis

All analyses were conducted in RStudio (v.1.4.1717, RStudio, 2020). For some analyses, we used matched-sample tests (paired t tests, Wilcoxon signed-rank tests, repeated-measures ANOVAs). In these cases, we either plotted treatment differences and used Shapiro–Wilk normality tests or plotted the residuals to assess whether they conformed with parametric assumptions, and conducted parametric or nonparametric tests accordingly. For other analyses, we used linear mixed-effects models (LMMs) (package 'lme4'; Bates et al., 2015, v.1.1–21) or generalized linear mixed-effects models (GLMMs) with either a Poisson distribution and a log-link function (package 'glmmTMB'; Brooks et al., 2017, v.1.1.2.3) or a gamma distribution and an identity-link function (package 'lme4'; Bates et al., 2015, v.1.1–21), where appropriate. We used the package 'performance' (Lüdtke et al., 2021, v.0.8.0) to assess whether residual distributions conformed with linearity assumptions, and used the package 'effects' (Fox & Weisberg, 2018, v.4.1–1) to inspect the effects of the fixed factors visually. We assessed term significance using χ^2 tests (Bolker et al., 2009), to test the change in deviance between a model with a term and one without the term. We removed nonsignificant interaction terms from the models; significant interactions and all main effects were retained in the 'full' model. The significance level (α) was set at 0.05 for all tests. Full GLMMs and LMMs and deviance tests are reported in the Appendix (Tables A1–A3).

To determine whether predictions 1–3 were met, we assessed how the presence of an audience affected group level and individual category defensive behaviour towards the intruder. We first analysed treatment differences in group defensive actions (number of defensive behaviours and total time invested in defence) with paired *t* tests. We then analysed the relative contributions of the three categories of individual to the treatment differences in defensive behaviour, using repeated-measures ANOVAs to compare standardized between-treatment differences ((audience minus no audience)/no audience \times 100) in the number of defensive behaviours and total time invested in defence. We standardized values because we were interested in the relative increase in contributions and because different categories of individual contribute different absolute levels of defence. Finally, we analysed specifically how different categories of individual changed their defensive behaviour, in terms of number of attacks, number of aggressive displays and mean duration of aggressive displays, in response to an audience, using GLMMs. All models included treatment, individual category and the treatment-by-individual interaction as fixed effects, as well as trial order (days 1 and 2) as a fixed categorical factor, intruder responsiveness as a covariate, and group and individual (nested within group) identities as random factors. Where the interaction between treatment and individual category was found to be significant, we assessed treatment effects on the behaviour of each individual category using pairwise tests. Subordinate females had a reduced sample size ($N = 13$) in the analysis of mean duration of aggressive displays, because two females did not perform any aggressive displays in at least one of their trials.

To determine whether predictions 4 and 5 were met, we assessed how the presence of an audience affected within-group interactions during intrusions. First, we analysed the number of affiliative, aggressive and submissive displays performed between focal group members in the whole 10 min trial period, using separate LMMs. We also reran the models using individual rates of within-group behaviours that corrected for time unavailable for such actions when group members were engaged in defence (i.e. number of behavioural events divided by the time available for within-group interactions). All models included treatment, individual category and the treatment-by-individual interaction as fixed effects, as well as trial order (days 1 and 2) as a fixed categorical factor, intruder responsiveness as a covariate, and group and individual (nested within group) identities as random factors. We included only the dominant categories (dominant female and dominant male) in the analyses of within-group aggression because subordinates were rarely aggressive towards dominant individuals. Similarly, we included only the females (dominant female and subordinate female) in the analyses of submissive displays because dominant males were rarely submissive towards the dominant females and never towards the subordinate females.

RESULTS

Defence Against an Intruder

In the presence of an audience, focal groups performed more defensive acts (paired *t* test: $t_{14} = 2.55$, $P = 0.023$; Fig. 2a) and spent more time defending against the intruder ($t_{14} = 4.74$, $P < 0.001$; Fig. 2b) compared to when their neighbours were out of sight. The three categories of individual (dominant female, dominant male and subordinate female) contributed similarly to this greater overall defensive effort when an audience was present, as they did not differ significantly in standardized between-treatment differences in the number of defensive acts (repeated-measures ANOVA: $F_{2,28} = 1.24$, $P = 0.306$; Fig. 2c) or in time spent in defence ($F_{2,28} = 2.27$, $P = 0.122$; Fig. 2d).

What did differ between individual categories was the type of defensive action that increased when there was an audience. The number of attacks displayed towards the intruder was affected by the interaction between treatment and individual category (GLMM: $\chi^2_2 = 30.54$, $P < 0.001$; Appendix, Table A1): in the presence of an audience, dominant females attacked intruders more than when no audience was visible (Wilcoxon signed-rank test: $V = 79$, $N = 15$, $P = 0.021$; Fig. 3a), but there was no significant treatment difference for dominant males (paired *t* test: $t_{14} = 0.36$, $P = 0.721$) or subordinate females (Wilcoxon signed-rank test: $V = 46.5$, $N = 15$, $P = 0.247$). The number of aggressive displays performed towards intruders increased when the audience was present (GLMM: $\chi^2_1 = 14.31$, $P < 0.001$), but this effect was not dependent on individual category (no significant interaction: $\chi^2_2 = 1.26$, $P = 0.533$; Appendix, Table A1). However, the mean duration of aggressive displays was affected by the interaction between treatment and individual category ($\chi^2_2 = 16.20$, $P < 0.001$; Appendix, Table A1). Specifically, subordinate females (paired *t* test: $t_{12} = 3.23$, $P = 0.007$), but not dominant females ($t_{14} = 0.08$, $P = 0.937$), increased the mean duration of their aggressive displays when the neighbours were present compared to absent (Fig. 3b); dominant males showed a nonsignificant tendency to display aggressively for longer when there was an audience compared to when there was not (Wilcoxon signed-rank test: $V = 94$, $N = 15$, $P = 0.055$).

Within-group Interactions

Within-group interactions during the territorial intrusions were not significantly affected by the presence of an audience (LMMs: aggression: $\chi^2_1 = 0.03$, $P = 0.866$; affiliation: $\chi^2_1 = 0.13$, $P = 0.717$; submission: $\chi^2_1 = 2.42$, $P = 0.120$), when controlling for individual category, trial order and intruder responsiveness (Appendix, Table A2). Analyses of rates of within-group aggression, affiliation and submission, using time available for within-group interactions (see Methods), resulted in qualitatively similar results; i.e. no significant effect of either treatment or its interaction with individual category (Appendix, Table A3).

DISCUSSION

We found clear evidence of a positive audience effect on defence when *N. pulcher* groups were intruded by an unfamiliar female rival in the presence of neighbours (as per prediction 1). Although subordinates did not appear to display a greater increase in defensive efforts relative to dominants when in the presence of neighbours (contrary to prediction 2), group members differed in the type of defensive behaviours directed at intruders when their neighbours were visible (as per prediction 3). Also contrary to our expectations, dominant individuals did not display increased aggression towards subordinates (prediction 4) and, more broadly, within-group interactions were not impacted (prediction 5) by the presence of the audience during territorial intrusions. Our experimental study demonstrating how neighbour presence can influence collective defence expands the small current literature on audience effects and social monitoring in group-living species (Barve et al., 2020; Hellmann & Hamilton, 2014), and thus contributes to our understanding of within- and between-group social dynamics.

Focal groups performed more defensive acts and invested more time in defence when neighbours were visible than when they were out of sight; effects that were not mediated indirectly by any noticeable treatment effects on intruder behaviour. These findings are broadly in line with studies investigating how single audiences affect dyadic competitive interactions, where opponents become more aggressive in the presence of an individual observer

(zebrafish, *Danio rerio*: Cruz & Oliveira, 2015; fiddler crabs: dos Santos et al., 2017; crickets: Fitzsimmons & Bertram, 2013; Montroy et al., 2016; Siamese fighting fish: Matos & McGregor, 2002). Elevated group level aggression in the presence of neighbours may serve to advertise control over their own territory or to reinforce between-group dominance relationships and deter

potentially costly conflicts (Johnstone, 2001). The intergroup dominance hypothesis postulates that conflict between rival groups leads to the formation of population wide social hierarchies (Crofoot & Wrangham, 2010), with groups that are dominant over neighbours accruing fitness benefits over time. For instance, larger groups of African lions, *Panthera leo*, have better-quality territories

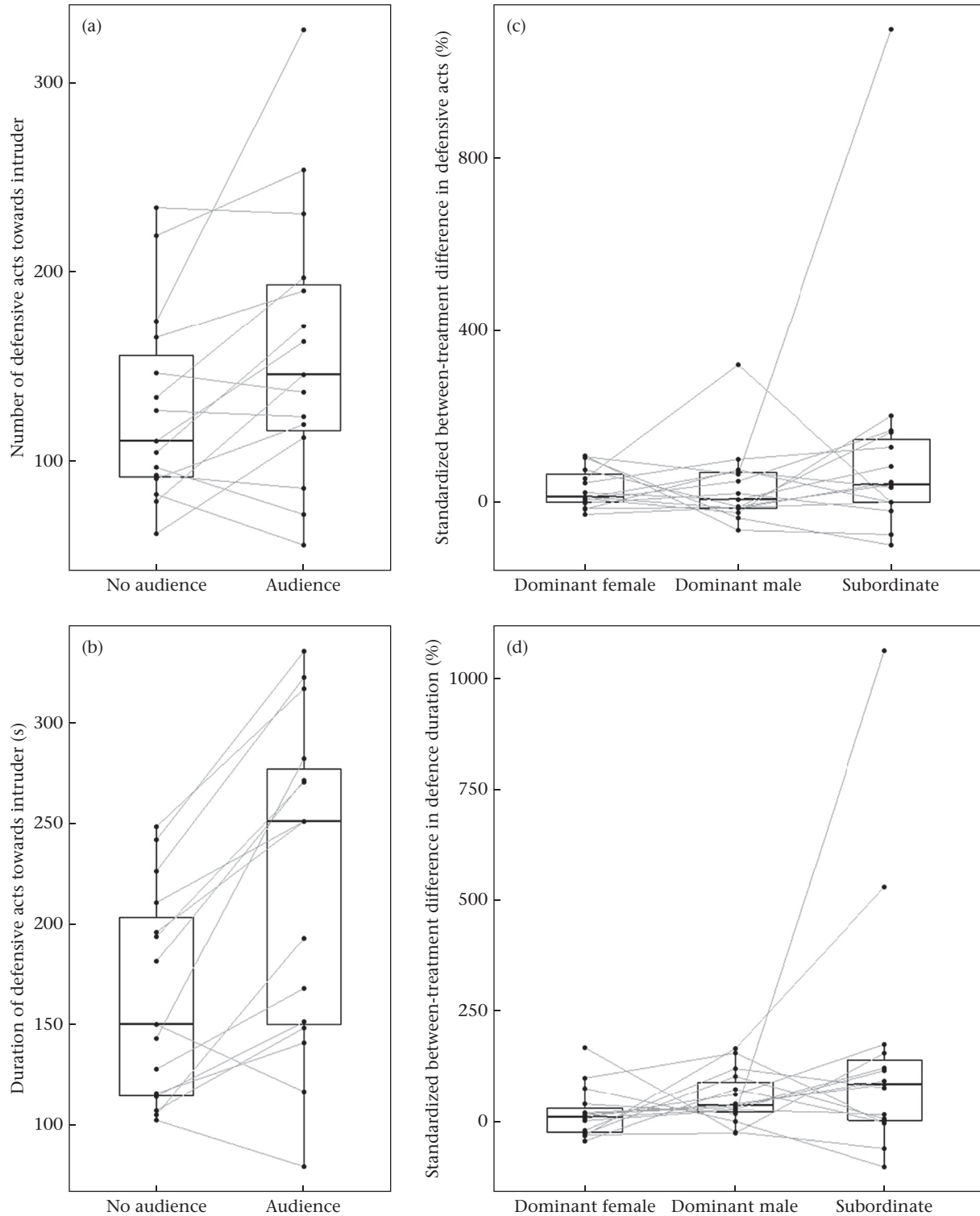


Figure 2. The effect of a conspecific audience on defence against an unfamiliar intruding individual. Group level (a) number of defensive acts performed and (b) total time invested in defence, and relative differences in individual level (c) number of defensive acts performed and (d) defence duration. Box plots show median and 25% and 75% quartiles; dots are raw data, with lines connecting groups (a,b) and individuals (c,d) across treatments. $N_{\text{groups}} = 15$, $N_{\text{individuals}} = 45$.

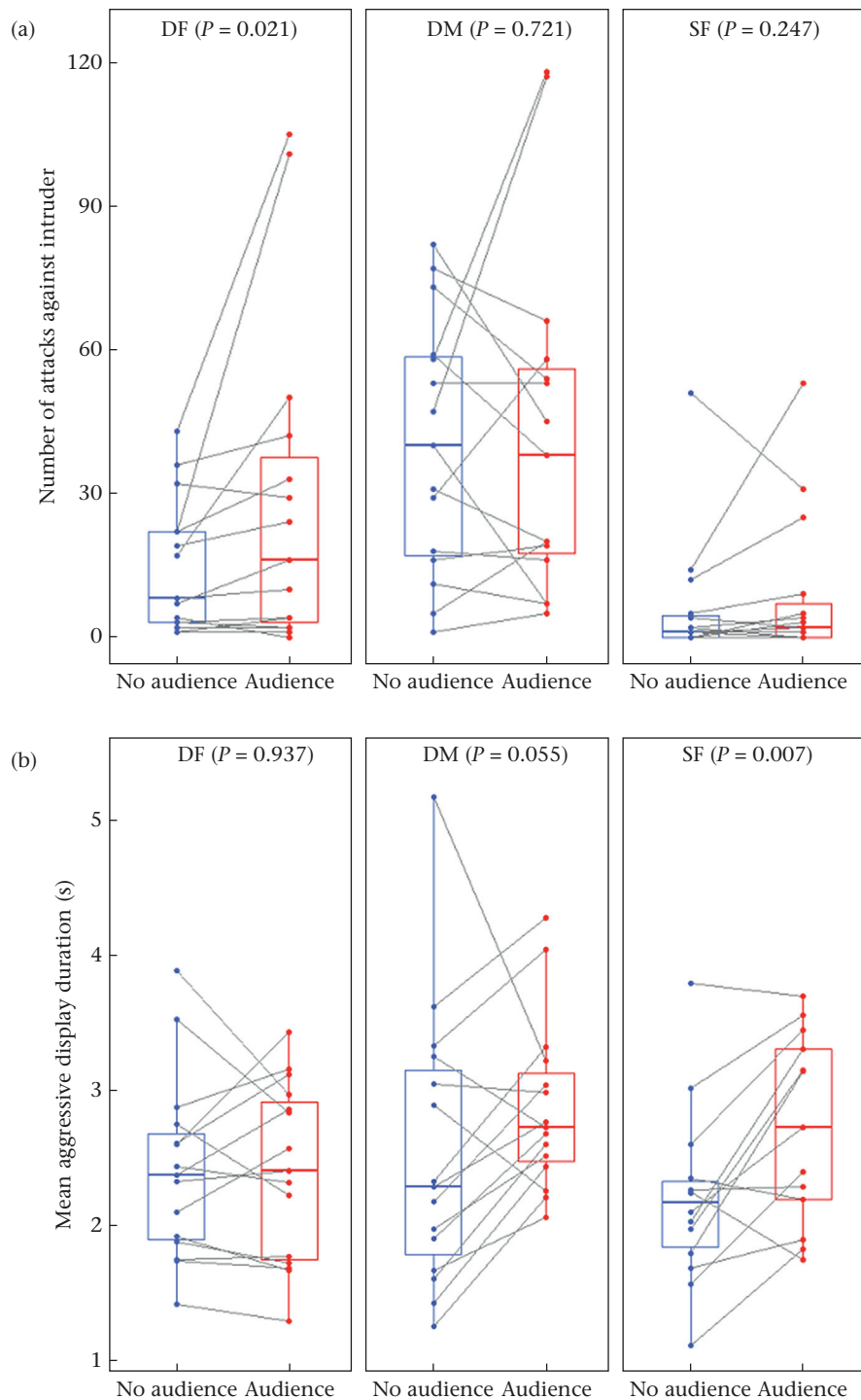


Figure 3. The effect of a conspecific audience on specific types of defence exhibited against an unfamiliar intruding individual. Shown are the (a) number of attacks and (b) mean aggressive display duration performed by focal group dominant females (DF), dominant males (DM) and subordinate females (SF). Box plots show median and 25% and 75% quartiles; dots are raw data, with lines connecting individuals across treatments. $N_{\text{groups}} = 15$ (a, b), $N_{\text{individuals}} = 45$ (a), $N_{\text{individuals}} = 43$ (b).

and experience lower intergroup conflict with neighbours, resulting in lower mortality (Mosser & Packer, 2009). Similarly, larger chimpanzee, *Pan troglodytes verus*, groups defend larger territories and experience lower threat of neighbour territorial intrusions (Lemoine, Boesch, et al., 2020); lower levels of neighbour pressure are associated with higher reproductive success (Lemoine, Preis, et al., 2020). Increased aggression towards intruders when neighbours are visible could signal the group's strength to other potential

rivals; such reinforcement of group social hierarchies through audience effects may have the benefit of lowering levels of overt intergroup conflict and associated risks of injury and death.

Contrary to our expectation of greater subordinate responsiveness to an audience, all three categories of group member increased relative defensive contributions against a conspecific intruder similarly when the neighbours were visible. Previous work on the daffodil cichlid identified audience effects on subordinates, but not

on dominants, during intrusions by a heterospecific fry predator (Hellmann & Hamilton, 2014). The suggestion was that the presence of neighbours altered the perceived risks and/or benefits of engaging the intruder for subordinates, but not for dominants; helping opportunities may enable subordinates to advertise their value to neighbours, facilitating a future dispersal attempt (Hellmann & Hamilton, 2014, 2019). The different findings from our experiment and this past work in the same species lend support to the idea that audience effects are context dependent (Dziewieczynski et al., 2005).

The greater intraspecific variation in the type of defensive responses when neighbours were present highlights an important degree of complexity that arises in the audience effects of social species: rivals and neighbours do not match the sex, size and status of all group members, and thus provide distinct levels of threat and opportunity to each. In our experiment, dominant females increased their number of attacks, which are risky, metabolically costly behaviours that require physical contact, signalling escalation in aggressive intent (Ros et al., 2006). Game theory models predict an escalation in aggression in the presence of an audience due to the reputational benefits that can be accrued from the interaction (Johnstone, 2001). For the dominant females, the presence of the audience likely amplified the perceived costs of the conflict (against a sex- and size-matched intruder) as a potential competitor (the size-matched female neighbour) could gain current information regarding its fighting ability (Danchin et al., 2004; Fitzsimmons & Bertram, 2013; Peake & McGregor, 2004). In contrast to dominant females, subordinate females and, to a lesser extent, dominant males performed longer aggressive displays in the presence of an audience. Displays are low-cost forms of aggression, commonly used for individual evaluation, that may both be performed from a safe distance (Ros et al., 2006) and, likely, also be perceived at greater distances. It is possible that subordinate females and dominant males directed aggressive displays at both the intruder and the neighbours (Danchin et al., 2004), but future work would be needed to tease these apart because the intruder and neighbours were on the same side of the focal group's territory in our experiment. In principle, focal groups may also have perceived the treatments as threats from different-sized neighbouring groups. However, previous work has demonstrated that *N. pulcher* are capable of individual recognition based on visual information alone (Balshine-Earn & Lotem, 1998; Kohda et al., 2015) and that they establish familiar relationships with neighbours within days (Frostman & Sherman, 2004; Sogawa et al., 2016). Thus, we believe it unlikely that focal groups perceived the intruder as a member of the neighbouring group; it is likely that the neighbours also perceived the unfamiliar individual as an intruder, as in other cichlid species (Weitekamp & Hofmann, 2017).

Our predictions about how the presence of an audience during outgroup conflict would affect associated within-group behaviour – specifically, induce increased dominant aggression towards subordinates, which in turn would impact within-group submissive and affiliative interactions – were not upheld. There are several nonmutually exclusive hypotheses that may explain this lack of an audience effect. First, although the presence of neighbours is associated with general increases in within-group aggression and submission (Hellmann & Hamilton, 2019), our no-audience 10 min intrusion treatment may not have been long enough to induce changes in social dynamics relative to our baseline of neighbour presence, particularly as groups concurrently dealt with an intruder. Second, the enhanced subordinate defence may have appeased the dominants, precluding aggression (Bergmüller & Taborsky, 2005) and its impacts on other behaviours. Lastly, changes in within-group interactions may be more salient in the aftermath of a conflict once the immediate threat subsides (Bruintjes et al., 2016); assessment of post-conflict social

interactions in the presence and absence of neighbours would enlighten this matter further. Future work could also consider the possibility of increased coordination or synchronization of defensive behaviour by groupmates in the presence of an audience.

In group-living species, behavioural interactions often involve multiple participants and take place where they could be detected by multiple third parties (McGregor & Peake, 2000). Yet, studies of audience effects have traditionally focused on dyadic interactions observed by single audiences (Fitzsimmons & Bertram, 2013; Matos & McGregor, 2002; but see Hellmann & Hamilton, 2014). Our work provides evidence of significant intraspecific variation in audience effects, suggesting that the presence of neighbours modifies the risks and opportunities presented by outgroup conflict to individuals depending on their sex and rank as well as the intruder's attributes. In our experiment, we standardized the time focal groups could familiarize with neighbours, but previous work on the daffodil cichlid has indicated that neighbour familiarity is important in mediating interactions among groupmates (Hellmann & Hamilton, 2019) and with predators (Hellmann & Hamilton, 2014), and could thus also be important during interactions with conspecific outsiders. Although species that defend relatively small, contiguous territories and that interact with neighbours frequently are good candidates for the study of eavesdropping and audience effects during outgroup conflict, audiences need not always be composed of immediate neighbours (Barve et al., 2020). As eavesdropping provides a relatively low-cost but effective means of monitoring the wider social environment (McGregor & Peake, 2000), audience effects in outgroup contexts may be more widespread than so far considered.

Author Contributions

Ines Braga Goncalves: conceptualization, methodology, formal analysis, investigations, writing – original draft preparation, writing-review & editing, visualization, project administration. **Andrew N. Radford:** conceptualization, writing – review & editing, supervision, funding acquisition.

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Declaration of Competing Interest

We declare that we have no competing interests.

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APPENDIX

Table A1

Statistical summary of generalized linear mixed models testing the effects of a conspecific audience on the number of defensive acts (Poisson distribution, log-link function), number of aggressive displays (Poisson distribution, log-link function) and mean aggressive display duration (gamma distribution, identity-link function) against an unfamiliar female intruder

	Estimate ± SE	Z	P	CI	χ^2
Number of attacks (N = 45 individuals)					
Random terms: Group/Individual: 1.72; Group: 0.00					
Full model					
Intercept	1.14 ± 0.45	2.51	0.012	0.25, 2.02	
Treatment (Audience)	0.55 ± 0.09			0.38, 0.71	
Individual category (DM)	1.30 ± 0.49			0.34, 2.27	
Individual category (SF)	−1.51 ± 0.52			−2.53, −0.49	
Trial order (Day 2)	0.27 ± 0.05	5.71	<0.001	0.18, 0.37	
Intruder responsiveness	1.03 ± 0.38	2.75	0.006	0.30, 1.77	
Treatment: Individual category			<0.001		30.54
Audience: Dominant male	−0.46 ± 0.10	−4.49	<0.001	−0.67, −0.26	
Audience: Subordinate	0.13 ± 0.17	0.74	0.460	−0.21, 0.46	
	Estimate ± SE	Z	P	CI	χ^2
Number of aggressive displays (N = 45 individuals)					
Random terms: Group/Individual: 0.30; Group: 0.05					
Full model					
Intercept	3.12 ± 0.30	10.32	<0.001	2.53, 3.71	
Treatment			<0.001		14.31
Audience	0.17 ± 0.04	3.79	<0.001	0.08, 0.25	
Individual category (DM)	0.05 ± 0.02	0.23	0.822	−0.36, 0.45	
Individual category (SF)	−1.29 ± 0.22	−6.02	<0.001	−1.72, −0.87	
Trial order (Day 2)	−0.16 ± 0.04	−3.66	<0.001	−0.24, −0.07	
Intruder responsiveness	0.25 ± 0.33	0.74	0.460	−0.41, 0.90	
Removed nonsignificant interaction			P	df	χ^2
Treatment: Individual category			0.533	2	1.26
	Estimate ± SE	T	P	CI	χ^2
Mean aggressive display duration (N = 43 individuals)					
Random terms: Group/Individual: 0.19; Group: 0.06; Residual: 0.03					
Full model					
Intercept	2.56 ± 0.45	5.64	<0.001	1.67, 3.44	
Treatment (Audience)	−0.02 ± 0.13			−0.28, 0.25	
Individual category (DM)	0.00 ± 0.21			−0.41, 0.42	
Individual category (SF)	−0.25 ± 0.21			−0.66, 0.17	
Trial order (Day 2)	0.11 ± 0.09	1.31	0.192	−0.06, 0.28	
Intruder responsiveness	−0.31 ± 0.54	−0.58	0.560	−1.37, 0.74	
Treatment: Individual category			<0.001		16.20
Audience: Dominant male	0.53 ± 0.20	2.63	0.009	0.14, 0.93	
Audience: Subordinate	0.57 ± 0.20	2.85	0.004	0.18, 0.97	

DM: dominant male; SF: subordinate female. Individual identity nested within group identity and group identity were fitted as random intercepts (with variances shown). The reference level was no-audience for treatment, dominant female (DF) for individual category and day 1 for trial order.

Table A2

Statistical summary of linear mixed models testing the effects of a conspecific audience on rates of within-group aggressive, affiliative and submissive behaviours displayed during the 10 min intrusions by an unfamiliar female

	Estimate ± SE	T	P	CI	χ^2
Within-group aggression displayed (N = 30 individuals)					
Random terms: Group/Individual: 32.22; Group: 0.00; Residual: 9.37					
Full model					
Intercept	10.46 ± 4.58	2.29	0.026	1.34, 19.53	
Treatment			0.866		0.03
Audience	−0.13 ± 0.81	−0.16	0.874	−1.69, 1.47	
Individual category (DM)	4.77 ± 2.22	2.15	0.041	0.45, 9.08	
Trial order (Day 2)	0.93 ± 0.79	1.17	0.253	−0.61, 2.46	
Intruder responsiveness	−8.54 ± 5.46	−1.56	0.130	−19.36, 2.47	
Removed nonsignificant interaction			P	df	χ^2
Treatment: Individual category			0.350	1	0.873

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Table A2 (continued)

	Estimate ± SE	T	P	CI	χ ²
	Estimate ± SE	T	P	CI	χ ²
Within-group affiliation displayed (N = 45 individuals)					
Random terms: Group/Individual: 25.88; Group: 33.05; Residual: 19.92					
Full model					
Intercept	19.66 ± 5.94	3.31	0.002	8.13, 31.19	
Treatment	-0.43 ± 0.98	-0.44	0.662	-2.31, 1.48	
Audience			0.448		2.66
Individual category (DM)	-6.80 ± 2.19	-3.11	0.004	-11.08, -2.53	
Individual category (SF)	-8.17 ± 2.19	-3.74	<0.001	-12.44, -3.89	
Trial order (Day 2)	-0.66 ± 0.94	-0.70	0.489	-2.49, 1.17	
Intruder responsiveness	-2.68 ± 7.04	-0.38	0.704	-16.34, 11.09	
<i>Removed nonsignificant interaction</i>					
Treatment: Individual category			P	df	χ ²
			0.293	2	2.45
	Estimate ± SE	T	P	CI	χ ²
Within-group submission displayed (N = 30 individuals)					
Random terms: Group/Individual: 16.58; Group: 0.00; Residual: 7.92					
Full model					
Intercept	8.75 ± 3.79	2.31	0.025	1.18, 16.60	
Treatment			0.158		2.00
Audience	1.02 ± 0.74	1.37	0.183	-0.41, 2.48	
Individual category (SF)	0.4 ± 1.65	0.24	0.811	-2.81, 3.61	
Trial order (Day 2)	-0.05 ± 0.73	-0.07	0.943	-1.47, 1.36	
Intruder responsiveness	-3.27 ± 4.57	-0.72	0.477	-12.80, 5.94	
<i>Removed nonsignificant interaction</i>					
Treatment: Individual category			P	df	χ ²
			0.206	1	1.60

DM: dominant male; SF: subordinate female. Individual identity nested within group identity and group identity were fitted as random intercepts (with variances shown). The reference level was no-audience for treatment, dominant female (DF) for individual category and day 1 for trial order.

Table A3

Statistical summary of linear mixed models testing the effects of a conspecific audience on rates of within-group aggressive, affiliative and submissive behaviours displayed during the 10 min intrusions by an unfamiliar female, corrected for time spent in defensive actions

	Estimate ± SE	T	P	CI	χ ²
	Estimate ± SE	T	P	CI	χ ²
Within-group aggression displayed (N = 30 individuals)					
Random terms: Group/Individual: 0.47; Group: 0.00; Residual: 0.13					
Full model					
Intercept	1.18 ± 0.54	2.20	0.033	0.10, 2.26	
Treatment			0.828		0.05
Audience	0.02 ± 0.09	0.21	0.835	-0.16, 0.21	
Individual category (DM)	0.59 ± 0.27	2.23	0.034	0.08, 1.02	
Trial order (Day 2)	0.10 ± 0.09	1.12	0.274	-0.08, 0.28	
Intruder responsiveness	-0.99 ± 0.64	-1.55	0.129	-2.27, 0.31	
<i>Removed nonsignificant interaction</i>					
Treatment: Individual category			P	df	χ ²
			0.597	1	0.28
	Estimate ± SE	T	P	CI	χ ²
Within-group affiliation displayed (N = 45 individuals)					
Random terms: Group/Individual: 0.28; Group: 0.41; Residual: 0.27					
Full model					
Intercept	2.23 ± 0.68	0.68	0.002	0.92, 3.56	
Treatment			0.765		0.09
Audience	-0.03 ± 0.11	0.11	0.771	-0.25, 0.19	
Individual category (DM)	-0.74 ± 0.24	0.24	0.004	-1.21, -0.28	
Individual category (SF)	-0.99 ± 0.24	0.24	<0.001	-1.45, -0.53	
Trial order (Day 2)	-0.09 ± 0.11	0.11	0.421	0.30, 0.12	
Intruder responsiveness	-0.31 ± 0.81	0.81	0.704	-1.88, 1.27	
<i>Removed nonsignificant interaction</i>					
Treatment: Individual category			P	df	χ ²
			0.294	2	2.45
	Estimate ± SE	T	P	CI	χ ²
Within-group submission displayed (N = 30 individuals)					
Random terms: Group/Individual: 0.24; Group: 0.00; Residual: 0.09					
Full model					
Intercept	0.93 ± 0.43	2.19	0.033	0.09, 1.78	
Treatment			0.087		2.93
Audience	0.13 ± 0.08	1.67	0.107	-0.02, 0.29	
Individual category (SF)	-0.04 ± 0.19	-0.20	0.847	-0.41, 0.34	
Trial order (Day 2)	-0.001 ± 0.08	-0.01	0.990	-0.15, 0.15	
Intruder responsiveness	-0.28 ± 0.51	-0.54	0.589	-1.30, 0.75	
<i>Removed nonsignificant interaction</i>					
Treatment: Individual category			P	df	χ ²
			0.293	1	1.10

DM: dominant male; SF: subordinate female. Individual identity nested within individual identity nested within group identity and group identity were fitted as random intercepts (with variances shown). The reference level was no-audience for treatment, dominant female (DF) for individual category and day 1 for trial order.