

Group structure in a restricted entry system is mediated by both resident and joiner preferences

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Abstract The benefits of grouping behaviour may not be equally distributed across all individuals within a group, leading to conflict over group membership among established group members, and between residents and outsiders attempting to join a group. Although the interaction between the preferences of joining individuals and existing group members may exert considerable pressure on group structure, empirical work on group living to date has focussed on free entry groups, in which all individuals are permitted entry. Using the humbug damselfish, *Dascyllus aruanus*, we examined a restricted entry grouping system, in which group residents control membership by aggressively rejecting potential new members. We found that the preferences shown by joining members were not always aligned with strategies that incurred the least harm from resident group members, suggesting a conflict between the preferences of residents and preferences of group joiners. Solitary fish preferred to join familiar groups and groups of

size-matched residents. Residents were less aggressive towards familiar group joiners. However, resident aggression towards unfamiliar individuals depended on the size of the joining individual, the size of the resident and the composition of the group. These results demonstrate that animal group structure is mediated by both the preferences of joining individuals and the preferences of residents.

Keywords Group living · Social organisation · *Dascyllus aruanus* · Membership preferences

Introduction

Grouping is a common strategy across animal taxa and involves a trade-off between the costs and benefits of joining a group or remaining solitary (Krause and Ruxton 2002). When studying the adaptive benefits of sociality, the fitness consequences of living in groups of different sizes, compositions, and locations must be considered (Wilson 1975). Alexander (1974) was the first to note that group living will only evolve when there are sufficient benefits to offset the costs of increased disease and parasite transmission and intensified competition (Booth 1995; Slotow and Paxinos 1997; Martinez and Marschall 1999; Coolen 2002; Krause and Ruxton 2002). The benefits of group living have been described for many taxa (Krause and Ruxton 2002) and generally include increased foraging success (Krebs et al. 1974; Morgan 1988) and reduced per capita predation risk, encompassing increased predator vigilance (Pitcher et al. 1982; Morgan 1988; Lima 1995; Lima et al. 1999), predator confusion (Pitcher et al. 1982; Grand and Dill 1999) and predation dilution (Pitcher et al. 1986; Krause and Ruxton 2002). Thus, a trade-off between survival benefits and growth

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costs may shape group membership decisions (Pulliam and Caraco 1984).

A key problem in the understanding of group living is the interaction between preferences of individuals attempting to join a group and the preferences of existing group members. To date, the bulk of research into group dynamics has focussed on ‘free entry’ groups, such as many bird flocks and fish shoals, where individuals are accepted into whichever group they choose (Krause and Ruxton 2002). These groups are often temporally unstable and may split and reform repeatedly over time. However, membership in many animal groups is relatively stable over time, for example, in mammals (meerkats; Clutton-Brock et al. 1999) and fish (cichlids; Taborsky 1984), and such groups are often characterised by well-established social hierarchies (Rubenstein 1981). In these cases, it may generally be beneficial to an outsider to join a group, but some or even all of the existing members of the group may be sufficiently disadvantaged by the addition of a new member that they attempt to exclude; we therefore describe these as ‘restricted entry’ groups (Stephens et al. 2005). This tension between joiners and residents may lead to potential conflicts over group membership. To date, research has focussed on the perspective of group joiners, while the potentially antagonistic interactions between the preferences of outsiders wishing to join a group and those of existing residents has been largely ignored.

We examined the decision-making process of individuals when joining a new group and the reaction of existing group members towards joining individuals, in laboratory and wild groups of the humbug damselfish, *Dascyllus aruanus*, a tropical marine pomacentrid species that forms stable size-based social hierarchies (Coates 1980) of unrelated individuals in close association with branching coral species (Forrester 1991). Like many other pomacentrid fishes, *D. aruanus* recruits prefer to settle on or near coral heads inhabited by conspecifics (Sweatman 1983; Ben-Tzvi et al. 2009). There have been a number of explanations posited for this preference: (1) the presence of conspecifics may indicate a continuous and adequate supply of food (Sweatman 1983, 1985; Booth 1992), (2) there may be increased vigilance and dilution effect advantages of being part of a larger school of phenotypically similar individuals (Sweatman 1985) and (3) future reproductive success may be increased by settling with potential future mates (Sweatman 1983, 1985). However, the presence of conspecifics may also have negative consequences for group members through intensified competition, and larger group sizes are associated with a reduction in average growth (Jones 1987a; Forrester 1990; Booth 1995), although per capita probability of survival increases in larger groups (Jones 1987b; Forrester 1990; Booth 1995). While social groups of *D. aruanus* are generally stable, migration does occur after settlement (Forrester 1990). However, *D.*

aruanus groups are ‘restricted entry’, as residents react aggressively and attack transient individuals that migrate between established groups (Sale 1971; Forrester 1991). Competition is greatest among similar-sized individuals (Booth and Wellington 1995), and so, residents may be most opposed to solitary fish of similar sizes attempting to join the group. However, a preference for phenotype matching may mean joining individuals prefer to join groups of similar-sized individuals (Ward and Krause 2001). Moreover, familiarity among individuals can play a key role in the social dynamics of many species (Ward and Hart 2003), including reducing aggression between individuals (Jaeger 1981) and stabilising group membership patterns (Croft et al. 2005). Migrating individuals must therefore balance the costs and benefits of joining familiar and unfamiliar groups of different sizes and social demographics, including expected aggression and likelihood of acceptance.

While there is a wealth of research examining group membership choices as a function of group size (Caraco and Wolf 1975; Giraldeau and Gillis 1988; Martinez and Marschall 1999; Ward and Hart 2005), group membership decisions may also be based on factors such as size demographics within the group (Ward and Krause 2001), dominance hierarchies within the groups (Rubenstein 1981) or familiarity of the group (Barber and Ruxton 2000). We tested the preferences of solitary individuals for familiar and unfamiliar groups, and for groups that differed in size demographics (and hence dominance structure; Forrester 1991) and predicted that joining fish would prefer to join familiar groups and groups of individuals of similar sizes. Alternatively, solitary fish may prefer groups that offer the greatest protection from predation and, therefore, join groups composed of fish larger than themselves (Heg et al. 2004). We also predicted that individuals rejoining their original colony would be attacked less than individuals joining a new colony in the field. However, we expected that residents would be most aggressive towards size-matched group joiners, as these individuals would pose the greatest competitive threat for available resources (Booth and Wellington 1995). Here, we examine how this conflict is manifested and resolved by studying both the preference of the individual and the reaction of the group members when humbug damselfish join new groups.

Methods

We conducted laboratory and field experiments at One Tree Island, Great Barrier Reef, Australia (23°30′29″S, 152°5′30″E), during September and October 2008 and April 2009. Field experiments were conducted in One Tree Island lagoon, while laboratory experiments were conducted in the aquarium facilities at One Tree Island research station.

Field observations

By swimming four 50-m transects across patch reefs in the lagoon, we sampled 57 *D. aruanus* groups, measuring at each size of coral head, distance to nearest neighbouring coral head, group size (number of individuals) and size distribution. The results of these observations were used to construct the groups used in the laboratory choice experiments and subsequent field release experiments.

Laboratory preference trials

For shoal preference trials, we collected seven to 12 fish from each of 15 groups of *D. aruanus* within One Tree Island lagoon and immediately transferred them to the laboratory facilities at One Tree Island Research Station. Fish from each group were held in individually labelled 20-L tanks with a continual flow-through of water from within the lagoon. After 48 h acclimation, fish were used in laboratory experiments. Fish were measured (SL) and assigned as either small (10–20 mm) or large (40–60 mm). Of approximately 150 fish used, a single fish died in captivity from unknown causes, all others were released within 5 days at site of capture. To measure preference behaviour, we used a standard binary shoal choice procedure. The test tank (100×50 cm and 60-cm high, filled to a depth of 25 cm) was divided into three compartments by the addition of two sheets of PennPlax© perforated plastic (perforation diameter ca. 1 mm, 5±1 perforations/cm²) 30 cm from either end of the tank along the longest axis. The use of clear perforated plastic allows chemical as well as visual stimuli to be detected by a focal fish. To facilitate the transmission of any chemical cues, water was added at a rate of 55 ml/min through tubes into each of the two outer compartments. We introduced two groups of six individuals into each end of the test tank, the composition of which depended on treatment. The stimulus fish were allowed to settle for 10 min prior to beginning experiments. We then selected a single focal fish to use in choice trials, again dependent on the treatment being tested. We added the focal fish to the centre of the test tank, allowed it to settle for 2 min, and measured the time it spent within two body lengths of each of the two stimulus shoals for 5 min. After 5 min, the focal and stimulus fish were removed and transferred to their respective holding aquaria. We filmed trials from above using a Canon G7 camera and later analysed the video data.

Laboratory trial I—familiarity preference

We tested the preference of 14 small and 13 large focal individuals for familiar versus unfamiliar groups using stimulus fish that were matched in size.

Laboratory trial II—size preference

We tested the preference of 12 small and 12 large focal individuals for a stimulus group composed of large, unfamiliar fish versus a stimulus group composed of small, unfamiliar fish taken randomly from two collected groups.

Field introduction of fish to established groups

We marked 50 groups of *D. aruanus* of between four and 12 individuals ($X=6.3\pm 3.7$) with flagging tape attached to nearby dead coral pieces. All colonies were spatially separated from nearest neighbours, and no natural movement of individuals between colonies was observed. We recorded the number of individuals in each group, the size of the coral head, the distance to the nearest neighbouring group and the size distribution of individuals within the group. Fish were collected using hand nets while snorkelling and placed into holding vessels made from 40-cm lengths of 15-cm diameter PVC tubing with mesh screens on each side to permit water flow. These vessels were used to carry the fish while snorkelling and were uncapped in order to remove a single fish at a time for introductions. From collection to release, fish were kept in holding vessels for between 160 and 200 min. Individual fish were identified on the basis of their size and markings.

Field introduction I—familiarity

To each of 20 groups marked with flagging tape attached to a nearby rock, we introduced one small and one large fish to either its original group or an unfamiliar group. Introduction order of small and large fish was randomised, and the first introduced fish was removed from the colony, and the colony left to settle for 20 min before the second fish was introduced. For 2 min, we recorded whether the fish was accepted (was allowed to enter the coral head) or rejected (was driven further than 2 m from the coral head), and the number of aggressive acts (biting and chasing; Katzir 1981) towards introduced individuals, as well as the size of the participating resident fish. Recordings were taken using dive slates while snorkelling, with observers at least 2 m from the group.

Field introduction II—group demographics

Using the same method as the previous experiment (introduction I), we introduced one small and one large fish into six unfamiliar groups each of the following treatments: (1) groups naturally containing only small fish, (2) groups manipulated to contain only small fish (i.e. all large fish removed), (3) groups naturally containing only large fish and (4) groups manipulated to contain only large

fish (i.e. all small fish removed). Removed fish were later returned to their original colonies.

Data analysis

Statistical analyses were conducted using SPSS 17.0. Data for familiarity, and size preference trials were non-normally distributed and were therefore analysed using a nonparametric Wilcoxon rank test. Binary shoal choice data were analysed by comparing time spent with group *a* against time spent with group *b*. Field data were analysed using a general linear model. For both field experiments, there was no effect of introduction order, coral size or group size, and these variables were dropped from the model. Frequency of within size class aggression was analysed using Chi-squared tests on pooled introduction II data.

Results

Laboratory trial I—familiarity preference

When stimulus group size distribution was uniform, small focal fish significantly preferred a familiar stimulus group to an unfamiliar group (Wilcoxon rank test, $Z=2.36$, $N=12$, $p=0.019$, Fig. 1); however, large fish did not show a significant preference for either stimulus group (Wilcoxon rank test, $Z=0.45$, $N=12$, $p=0.65$, Fig. 1).

Laboratory trial II—size preference

Small focal fish significantly preferred a stimulus group composed of small fish over a stimulus group composed of large fish (Wilcoxon rank test, $Z=2.75$, $N=12$, $p=0.006$, Fig. 2), whereas large focal fish significantly preferred a stimulus group composed of large fish (Wilcoxon rank test, $Z=2.2$, $N=12$, $p=0.028$, Fig. 2).

Field observations

The average size of coral heads was 110 cm (± 103 SD), and the average distance to the nearest neighbouring coral head was 186 cm (± 240 SD). The average group size was 3.3 (± 3.7 SD) individuals, and groups on average contained 0.29 (± 0.8 SD) individuals smaller than 20 mm, 1.2 (± 2.1 SD) individuals between 20 and 40 mm and 1.8 (± 1.5 SD) individuals larger than 40 mm.

Field introductions

Introduction I—familiarity

There was significantly more aggression towards fish introduced into unfamiliar groups than fish introduced into

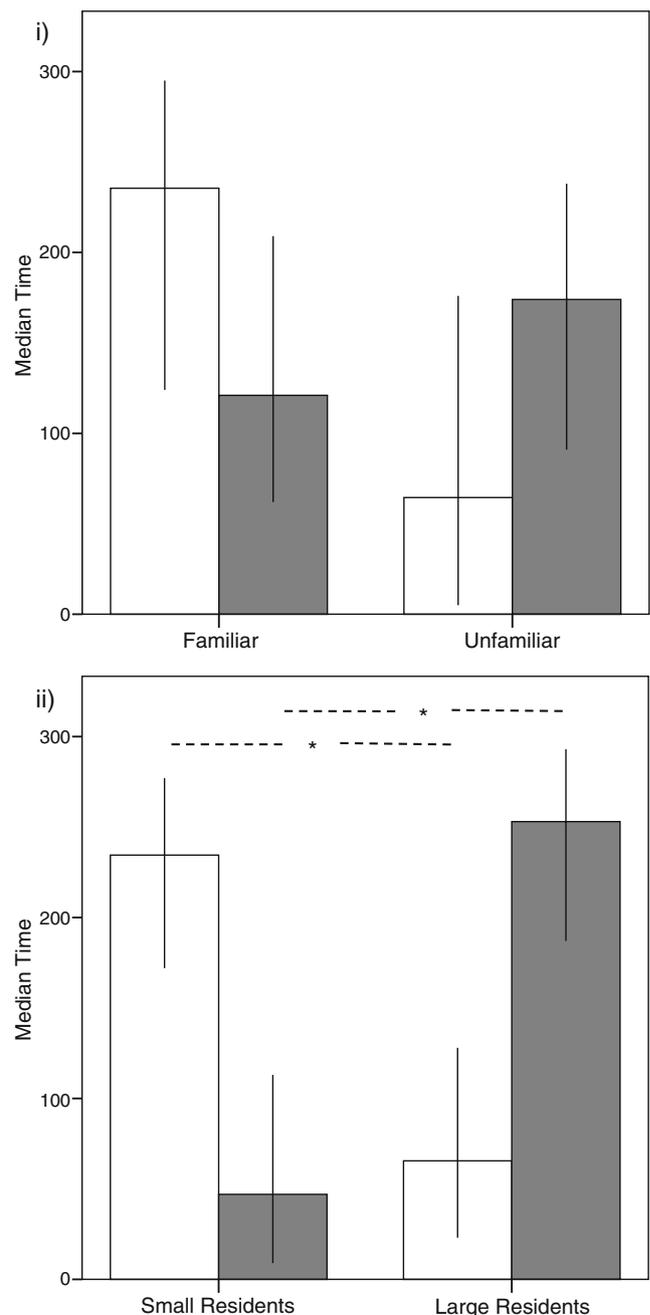


Fig. 1 Median time (seconds \pm 95% confidence interval) spent associating with stimulus groups by either small (10–20 mm SL; open bars) or large (40–60 mm SL; shaded bars) focal individuals where (1) stimulus groups were composed of either familiar or unfamiliar conspecifics and (2) stimulus groups were composed of either small or large conspecifics. Asterisk: significant difference at $p < 0.05$

familiar groups (bites $F_{1,36}=15.49$, $p < 0.001$; chases $F_{1,36}=4.15$, $p=0.049$). Body length of focal fish did not have a significant effect on aggression (bites $F_{1,36}=0.34$, $p=0.57$; chases $F_{1,36}=3.52$, $p=0.069$).

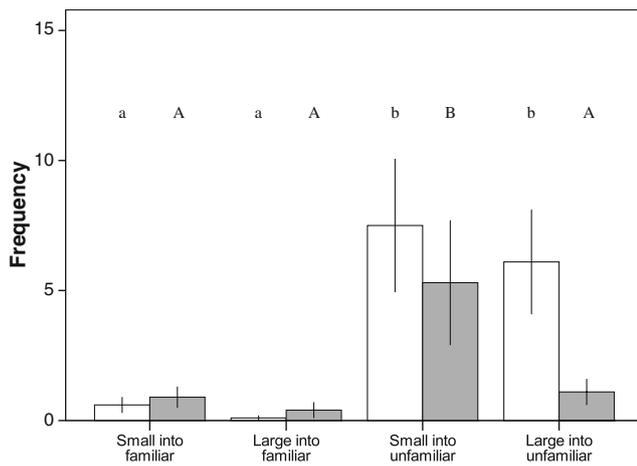


Fig. 2 Mean (\pm SE) frequency of bites (open bars, with significant differences signified by lowercase letters) or chases (shaded bars, with significant differences signified by uppercase letters) for each of four introduction types: (1) small fish into familiar groups, (2) large fish into familiar groups, (3) small fish into unfamiliar groups and (4) large fish into unfamiliar groups

Introduction II—group demographics

Group demographics had a significant effect on aggressive behaviour towards small introduced fish (bites $F_{3,20}=19.65$, $p<0.001$; chases $F_{3,20}=6.65$, $p=0.003$) and large introduced fish (bites $F_{3,20}=9.35$, $p<0.001$; chases $F_{3,20}=3.56$,

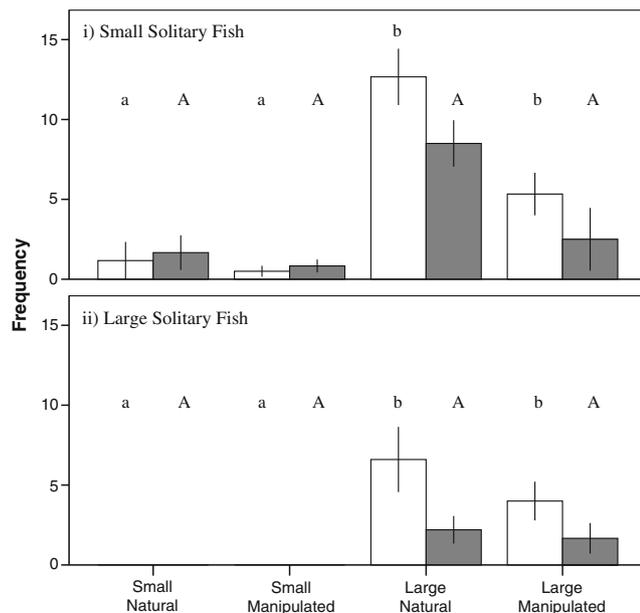


Fig. 3 Mean (\pm SE) frequency of bites (open bars, with significant differences signified by lowercase letters), chases (shaded bars, with significant differences signified by uppercase letters) for small or large solitary fish into each of four group types: (1) groups naturally containing only small fish ('natural'), (2) groups with all but small fish removed ('manipulated'), (3) groups naturally containing only large fish ('natural') and (4) groups with all but large fish removed ('manipulated')

$p=0.033$). Large residents were significantly more aggressive than small residents towards solitary fish ($\chi_{(1)}^2=22.5$, $p<0.001$). Small resident fish were significantly more aggressive towards small solitary fish than large solitary fish (within size class bite frequency: $\chi_{(1)}^2=13$, $p<0.001$), whereas large resident fish were not significantly more aggressive to either size of solitary fish (within size class bite frequency: $\chi_{(1)}^2=1.59$, $p=0.207$; Fig. 3).

Discussion

Our results show that individual humbug damselfish are able to recognise and show preferences for groups on the basis of familiarity, as well as being able to assess the composition of groups and actively choose among groups based on these assessments. Consistent with our predictions, small solitary humbug damselfish showed a preference for joining familiar groups in laboratory trials, and in field studies, solitary fish of all sizes received significantly less aggression when joining groups of familiar individuals. However, large solitary fish did not show a preference for familiar groups in laboratory tests, even though unfamiliar groups were significantly more aggressive than familiar colonies to large introduced fish in the field. This result may be due to state-dependence of costs of aggression for joining individuals; the costs may be prohibitive for small group joiners, while large individuals may suffer relatively less from resident aggression. A preference for returning to a familiar group may minimise the possibility of entering a new and potentially unfavourable social hierarchy, especially for smaller individuals. Larger individuals did not show a preference for their own group, potentially because large individuals entering new groups will most likely encounter smaller and therefore socially subordinate individuals (Forrester 1991), decreasing the chance of displacement. There may also be different costs for large and small individuals in searching or moving among groups, such that the costs of moving between groups are prohibitive for smaller individuals. Further, because sexually mature *D. aruanus* move into new groups of large individuals when ready to breed (Sale 1971; Asoh 2003), the reproductive benefits of moving into unfamiliar groups may be greater for larger individuals than for smaller, reproductively immature individuals, and therefore sufficient to offset the costs of increased aggression in these groups. For the group, reacceptance of a familiar group member acts to stabilise group membership and the social hierarchy within the group, leading to a reduction in aggression (Jaeger 1981). Association with familiar individuals benefits all group members by reducing intra-group aggression and allowing members to devote a greater proportion of their time to activities such as foraging (Griffiths et al. 2004).

There is also the possibility that association with familiar individuals facilitates kin-selected reciprocal behaviours with related individuals, for although the dispersive phase of most marine larvae diminishes the likelihood of associating with kin as adults, recent work has demonstrated that within groups of *D. aruanus* pairs of related individuals are often present (Buston et al. 2009), and recognition of familiar individuals may therefore act as a proxy for kin-recognition.

Both small and large individuals preferred to associate with fish similar in size to themselves. By avoiding groups containing larger, dominant members, juveniles may reduce their exposure to aggression and may increase their access to food items that would otherwise be consumed by higher ranking individuals (Forrester 1991), as well as avoiding increased predation risk due to oddity effect. Moreover, a lower social position in groups of large individuals may lead directly to increased predation risk; in the closely related species *Dascyllus flavicaudus* and *Dascyllus trimaculatus*, group members are most at risk of predation when located near or just outside the perimeter of a coral shelter, and the likelihood that an individual would need to shelter near to the edge of the coral head is related to the density and hierarchy in the group. Aggressive or socially dominant individuals displace subordinate fish to the perimeter, where they were much more likely to be predated upon (Holbrook and Schmitt 2002). However, in another species of group living fish, *Neolamprologus pulcher*, association with groups of larger individuals leads to lower predation risk (Heg et al. 2004). That the small individuals did not prefer groups composed of large members suggests that they were not reacting on the basis of predator fight status nor were they moving toward the group that presented the largest search image.

For a large individual, joining a colony of small individuals has some apparent benefits—groups composed of small members showed no aggression towards large joiners, and small individuals are not likely to compete with large individuals for food resources (e.g. wasps *Cerceris arenaria*; Willmer 1985). However, the preference of large fish for groups composed of size-matched individuals suggests factors other than feeding rate are important in their group membership decisions. Groups containing large members may be indicators of suitable territory and food supply and may also be better at detecting predators (Karpilus et al. 2006). Further, by preferentially moving into groups containing large members, a large individual may maximise its chances of encountering reproductive adults and potential mates (Asoh 2003). The potential for reproduction in groups likely plays an important role in group membership decisions (Jordan et al. 2010), for example, male *Gambusia holbrooki* prefer to join groups composed of females to mixed sex groups (Agrillo et al. 2008), potentially due to the greater potential for reproduc-

tion in groups containing members of the opposite sex. However, there are no external sex differences in *D. aruanus*, and individuals may change sex throughout their lives (Asoh 2003), precluding our assessment of this factor in group membership decisions for this study.

The demographics of groups were a strong predictor of the behaviour of residents towards solitary individuals. Groups comprised only of small members, whether naturally or by experimental removal of other size classes, showed little aggression to either small or large solitary fish. The limited aggression by small residents towards group joiners may indicate either that small residents cannot effectively exclude competing phenotypes (suggesting that preferences are shared equally among size classes but are only able to be expressed by larger members) or that small residents are willing to accept all group joiners due to advantages associated with group augmentation. In contrast, groups naturally composed of large residents were highly aggressive to all joining members. Interestingly, groups that were naturally composed of large individuals were significantly more aggressive to small solitary individuals than manipulated groups of large residents that previously contained small members. Although small residents were less aggressive overall, the aggression they did show was restricted to small group joiners. By contrast, large residents were equally aggressive towards small and large group joiners, indicating that small residents either did not risk conflict with larger group joiners or that different size residents had opposing group membership preferences.

The opposing preferences shown by residents and non-residents over group membership in this study reveal an interesting mechanism in animal group formation. Although partner and group preferences based on the phenotype of the chosen individual(s) have been observed across numerous vertebrate and invertebrate taxa (see Dugatkin and Sih 1998), the reaction of the group itself to these preferences has received less interest. In many animal groups, the strongest mediator of group formation may be the preferences of individuals within the group rather than those of external individuals choosing among groups. It is important that future work on animal group formation takes into account phenotype specific group membership preferences of both joining and resident individuals.

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Conflict of interest The authors declare that they have no conflict of interest.

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