Asymmetry in pay-off predicts how familiar individuals respond to one another

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Familiarity influences individual decision-making in many vertebrate species. Here, we propose that familiarity modulates behaviour to different extents depending on the social context of the interaction. Specifically, the more that one player stands to gain relative to the other, the less important familiarity will be in influencing their responses to one another. We test this prediction using pairs of male guppies (Poecilia reticulata) in three competitive scenarios of increasing asymmetry in outcome to the two players: schooling under potential threat (similar outcomes), competing for a defensible food source (some asymmetry) and competing for a receptive female (strongly asymmetrical outcomes). Males show a graded response as asymmetry increases, with familiarity producing marked behavioural differences under potential threat, minor changes when competing for food, but none at all in competition for mating opportunities. This suggests that mutualistic benefits can arise as a by-product of selfish behaviour, supporting the role of pseudo-reciprocity in the evolution of cooperation.

1. Introduction

It has been unequivocally demonstrated for many taxa that familiarity plays an important role in social interactions. In fish, for example, familiarity between schoolmates has been shown to lead to reduced aggression [1], improved vigilance [2] and modified mate choice [3], reducing the costs of competition [1,3] and risk of predation [2,4]. However, the benefits gained from associating with familiar individuals are likely to depend on the competitive context in which those interactions occur. In situations with a high level of competition, the gain from winning over a rival may be greater than any benefits of being less aggressive or more cooperative with familiar individuals.

This can be quantified in terms of the asymmetry in the outcome of the competition. For instance, because familiarity improves predator avoidance [4], an individual has a high pay-off from associating with familiar individuals when predation risk is elevated, as do its companions. On the other hand, if two males are competing for a single female, the outcome cannot be the same for each competitor and familiarity may be irrelevant in how they respond to one another. The asymmetry in the potential gain (or loss) to each player should predict how much an individual’s behaviour changes in an encounter with a familiar conspecific compared with an unfamiliar one. Specifically, we predict that familiarity-dependent behavioural modification will be more pronounced when the pay-off asymmetry is low and less when it is high.

We test these ideas using guppies (Poecilia reticulata), a species of fish in which individuals have the cognitive capacity to recognize familiar conspecifics [5,6]. Our experiments track the influence of familiarity on interactions between two males across a gradient of increasing asymmetry in outcomes of
competition: where asymmetry is expected to be low (schooling under potential threat), intermediate (foraging) and high (competition for mating opportunities).

We simulate threat using a novel, unknown environment, perceived by fish as potentially dangerous [7,8]. Fish perform more effective anti-predator behaviours if they associate with familiar individuals [4], and gains are similar for all interactors. Here, we predict increased schooling behaviour between familiar individuals. Male–male aggression is rare when fish are under threat [9], so we expect little modulation of agonistic behaviour in this context. Competition for food, however, can change the school’s dynamics [10,11]. Minnows (Phoxinus phoxinus), for example, associate preferentially with poorer competitors [12], and in guppies, agonistic behaviour becomes more common when males compete for food [9]. Food eaten by one fish is unavailable to the other, so two competitors do not gain equally when foraging together on limited resources. However, foraging with familiar individuals can bring benefits, such as prior knowledge of an associate’s ability to find food [9]. In competition for limited food, therefore, we expect these costs and benefits of associating with familiar individuals to balance each other; feeding itself may not be affected, but benefits may be expressed as reduced aggression between familiar competitors. Competition amongst male guppies is most evident over reproduction because male reproductive success is highly skewed [13]. Guppy males compete vigorously for mating opportunities, including using direct aggression [9], and may sacrifice safety and feeding for access to females [14–16]. We therefore predict that a male’s mating behaviour will not be influenced by the status—familiar or unfamiliar—of his rival in a reproductive context. As an overarching test of our hypothesis, we expect aggression levels to show an interaction between competitive context and familiarity across foraging and reproduction, the two contexts where agonistic behaviour is common.

2. Material and methods

Male guppies were kept in groups of four in seven visually isolated ‘home’ tanks. These were left undisturbed for two weeks to ensure the establishment of familiarity between tank-mates [5,6]. Males were individually distinguishable by their unique colour patterns. Trials were conducted in three separate ‘observation’ tanks. ‘Familiar’ males were from the same home tank, and ‘unfamiliar’ males had had no previous contact, visual or olfactory, with each other. Focal males were selected haphazardly from each home tank in turn; the accompanying male was randomly selected but constrained so that no unfamiliar pairing was repeated. All males were tested twice (familiar or unfamiliar companion) in each experiment, with treatment order randomized. Further details on fish husbandry and experimental set-ups are given in the electronic supplementary material.

In experiment 1 (potential threat), a refuge was placed in an observation tank. This was a novel environment, associated with raised threat. The male pair was released into the refuge and the following were recorded: time taken for each male to exit the refuge (as in [17]), the subsequent time the pair spent schooling (within two body lengths) for 10 min and the number of aggression events.

In experiment 2 (foraging), hunger levels were standardized and the male pair placed in an observation tank with a known defensible food source (a pebble coated in flake food). For 5 min, the sequence and number of bites each fish took were recorded, along with all aggression events.

In experiment 3 (reproduction), the male pair was placed in a tank with one virgin and one non-virgin female. After settling (following [14]), the focal male’s behaviour was observed for 15 min. The number of stereotyped behaviours (sigmoid displays, thrusts and fin displays) and aggressive male–male interactions were recorded, as well as the time spent following each female.

The work was consistent with guidelines from the Association for the Study of Animal Behaviour (ASAB) for the use of animals in behavioural research [18] and in line with the University of St Andrews’ animal welfare requirements at the time of the work. Analysis was done in R 2.15.0 [19]. Unless stated, models are (generalized) linear mixed models (GLMMs; R package nlme [20]), including focal male identity as a random factor. Data were transformed to fulfil the assumption of normality or analysed non-parametrically if they could not be normalized (see table 1). All data have been made available online [21].

3. Results

In a novel environment—experiment 1—familiar fish tended to follow each other more closely out from the refuge than unfamiliar fish did (linear regression of focal male’s exit time on companion’s in familiar pairs \( r^2 = 0.119, \text{d.f.} = 19, \text{slope} = 0.61, p = 0.069; \) in unfamiliar pairs \( r^2 = -0.047, \text{d.f.} = 21, \text{slope} = 0.01, p = 0.951; \) interaction in a mixed model, table 1). Outside the refuge, familiar pairs spent more time schooling than unfamiliar pairs did (table 1 and figure 1).

In competition for food—experiment 2—familiarity did not affect how much food was eaten (table 1). However, in unfamiliar pairs there was significantly more aggression (table 1 and figure 1).

In reproductive competition—experiment 3—aggression was not affected by familiarity (table 1 and figure 1), nor did familiarity affect how much time males spent with the virgin and non-virgin females (table 1).

Aggression was the only behaviour that occurred throughout the study, but aggression levels differed significantly between contexts (Kruskal–Wallis test: \( \chi^2 = 50.845, \text{d.f.} = 2, \ p < 0.001, \) medians of 0, 0 and 2 instances for experiments 1, 2 and 3, respectively; post-hoc pairwise Wilcoxon test with Bonferroni corrections, all differences between groups \( p < 0.01 \)). Because aggression occurred infrequently and was particularly rare in the schooling trials, we were unable to formally test for an interaction between familiarity and aggression across all contexts (see discussion in the electronic supplementary material). Nonetheless, such an interaction was apparent when considering those contexts in which aggression is an important part of the behavioural repertoire (foraging and reproduction; familiarity \( \times \) context using a poisson GLMM, \( \ell = -3.36, p < 0.001 \)).

4. Discussion

Familiarity is known to play an important role in shaping individual decision-making. Prior experience of conspecifics has been found to improve anti-predator responses [2,4] and affect mate choice [3]. However, as we have shown here, this experience is used conditionally. Male guppies behaved differently towards familiar individuals under potential predation, less so in competition for food and not at all in competition for a female. This indicates that the role which familiarity plays in encounters between
individuals depends on the relative gain for each of the two interactants. The more one gains at the expense of the other, i.e. the greater the asymmetry in pay-off, the less relevant familiarity is in how they respond to one another.

In guppies, this increase in asymmetry corresponds to an increase in competition intensity. Interpreting the results from a perspective of asymmetry rather than competition intensity, however, has theoretical and pragmatic advantages. Theoretically, pay-off asymmetry may apply to a broader range of animal interactions, not only overtly competitive scenarios. Pragmatically, the outcomes of competition are more easily quantified than the strength of competition itself, allowing our framework to be applied to a broader range of systems.

**Table 1.** Results of linear mixed effects models analysing how familiarity changes behaviour in the three competitive contexts. The interaction model in experiment 1 is described fully in the text. All other models were fitted only to familiarity as a fixed factor and focal male ID as a random factor. Where necessary, data were transformed to conform to the assumption of normality. Significances are denoted as: 0, **0.01, *0.05, –0.1.

<table>
<thead>
<tr>
<th>response</th>
<th>transformation or non-parametric test</th>
<th>means</th>
<th>test statistic</th>
<th>d.f.</th>
<th>p-value</th>
<th>significance</th>
</tr>
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<tbody>
<tr>
<td>familiar pairs</td>
<td>unfamiliar pairs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>schooling time (s)</td>
<td>cube root</td>
<td>384</td>
<td>318</td>
<td>t = 4.11</td>
<td>1, 20</td>
<td>0.001**</td>
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<tr>
<td>interaction: correlation of exit times × familiarity</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>none</td>
<td>slope: 0.61</td>
<td>slope: 0.01</td>
<td>t = 1.81</td>
<td>1, 18</td>
<td>0.088 –</td>
<td></td>
</tr>
<tr>
<td>experiment 2: competition for food</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>total food eaten by both fish (bites taken)</td>
<td>none</td>
<td>52.3</td>
<td>55.2</td>
<td>t = 0.342</td>
<td>1, 25</td>
<td>0.736 n.s.</td>
</tr>
<tr>
<td>total direct aggression</td>
<td>square root</td>
<td>1.0</td>
<td>4.0</td>
<td>t = 2.52</td>
<td>1, 25</td>
<td>0.019*</td>
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<tr>
<td>experiment 3: reproductive competition</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>total direct aggression</td>
<td>log (x + 1)</td>
<td>3.5</td>
<td>5.2</td>
<td>t = 1.44</td>
<td>1, 26</td>
<td>0.161 n.s.</td>
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<tr>
<td>proportion of time spent with receptive female</td>
<td>paired Wilcoxon rank</td>
<td>43%</td>
<td>37%</td>
<td>V = 97</td>
<td>n = 26</td>
<td>0.531 n.s.</td>
</tr>
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</table>

**Figure 1.** Outcome of the three experiments: (a) potential threat, (b) competition for food and (c) competition for mating. The results are presented as box-plots of the raw data as the data are non-normal before transformation. Familiarity modulated behaviour substantially in (a), less so in (b) and not at all in (c). See table 1 for statistics. The box shows the interquartile range and the thick line denotes the median. The whiskers show the most extreme data point within one interquartile range of the end of the box, and circles show points beyond this.
There has been considerable debate in the literature about the evolution of cooperation. Interactions between individual fish during predator inspection have provided evidence for cooperation [22,23], although other more parsimonious explanations for this apparently altruistic behaviour have been suggested [24,25]. Our data show that responses to familiar individuals are graded depending on the context. Accordingly, memory of past interactions—a key requirement for the evolution of reciprocity [26]—needs to take account of the different circumstances in which these interactions occurred. The cognitive capabilities that this necessitates [27] may limit the scope for reciprocal altruism in fish such as guppies that face many mating, foraging and predator avoidance challenges on a daily basis. It would be interesting in future work to ask how the type and frequency of interactions between familiar individuals influence their responses in different contexts. Indeed, the association patterns linked to the pay-off gradient quantified in this paper are consistent with by-product mutualism [28,29]. In a situation where both parties gain equally from apparent cooperation with familiar individuals, selfish behaviour will benefit the other player. However, when the gains are asymmetric, as in competition for a limited resource, selfish behaviour only benefits the actor. Our results suggest that fish are able to assess the pay-offs associated with different activities and use information about the familiarity of a particular individual in a subtle and adaptive way.

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References