

1 **Title:** The role of tactile interactions in flight responses in the Bronze Cory catfish (*Corydoras*
2 *aeneus*)

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11

12 **Abstract**

13

14 One of the primary functions of animal aggregations is defense against predators. Many
15 social animals enjoy reduced predation risk as a result of grouping, and individuals within groups
16 can benefit from information transferred by their group-mates about a potential predator. We
17 present evidence that a tactile interaction behavior we term ‘nudging’ substantially modified
18 group responses to a potential threat in a highly social catfish species, *Corydoras aeneus*. These
19 catfish deployed nudges during flight responses, and these nudges were associated with a greater
20 likelihood of group cohesion following a threat event. Increased nudging behavior resulted in
21 longer flight responses. In addition, individuals that perceived the threat first were more likely to
22 initiate nudges, implying that nudges could be used to alert group-mates to the presence of a
23 threat. Taken together, our results suggest that tactile communication plays an important role in
24 gaining anti-predator benefits from sociality in these fish.

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26 **Introduction:**

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1 Animal aggregations occur across the animal kingdom, with this ubiquitous sociality
2 likely arising through the profound advantages group living can offer. Among the most evident
3 of these benefits is reducing the risk of predation (Neill and Cullen, 1974, Major 1978).
4 Aggregative behaviors that reduce predation risk are observed in invertebrates such as aphids
5 (Turchin, 1989), in many fishes including minnows (Pitcher, 1986) and guppies (Magurran,
6 1994), in reptiles such as iguanas (Greene, 1978), in many birds including cliff swallows (Brown,
7 1988) and ostriches (Bertram, 1980), and in many mammals including prairie dogs (Hoogland,
8 1981). Predation risk also increases cohesion in many species, including walleye (Sogard, 1997)
9 and fiddler crabs in the context of a ‘selfish herd’ response (Viscido, 2002). By living in close
10 proximity to others, individuals gain the benefit of their conspecifics’ perception and attention,
11 and can dedicate less time to predator vigilance while still being more likely to escape an attack
12 (Bertram, 1980, Hoogland, 1981).

13 In addition to the benefit of seeing through their group-mates’ eyes, individuals also
14 avoid predators due to the active spread of information about potential threats through groups. In
15 some species, explicit signals such as alarm calls are delivered by one individual to alert its
16 conspecifics about a predator, as in primates such as vervet monkeys (Seyfarth, 1980) and birds
17 such as black-capped chickadees (Templeton, 2005); in the prior two examples, alarm calls
18 encode specific information about the predator that is utilized by the caller’s conspecifics. In
19 other systems, including fathead minnows and zebrafish, injured individuals release an alarm
20 pheromone that alerts conspecifics to danger, albeit without specific information about the
21 predator (Stensmyr, 2012, Brown, 2001). Predator inspection is another behavior that occurs in
22 many taxa, including birds (Hinde, 1954) and fishes (Pitcher, 1986), and is performed by
23 individuals or sub-groups but has consequences for the entire group. For example, in minnows a
24 small contingent of a much larger shoal will inspect a potential predator at great potential risk,
25 and if they perceive that the predator is a threat, they return to the shoal instead of hiding
26 immediately, after which their shoal-mates alter their behavior (Pitcher, 1986). This implies that
27 information about the predator was transferred, although it seems the individuals rely mostly on
28 personal information to ignite a flight response (Magurran, 1988).

29 The acquisition of information from conspecifics that is potentially costly to obtain
30 personally is certainly beneficial to individuals, and many species have evolved social behaviors
31 that allow individuals to convey information about predators to their group-mates or otherwise

1 influence their group-mates' behavior in mutually beneficial ways. Understanding how an
2 individual's behavior can impact the coordination of its group is of particular importance to
3 understanding how groups function, and how group living provides the myriad of advantages we
4 see across taxa. One factor that strongly affects group coordination is familiarity, defined as
5 previous experience with a given other individual. Familiarity leads to improved coordination in
6 a variety of taxa, including birds (Senar, 1990) and schooling fishes (Ward, 2003). In particular,
7 familiarity improves a group's anti-predator defenses, such as in great tits, in which previous
8 experience with nest-site neighbors results in a higher probability of a familiar neighbor
9 contributing to the defense of a conspecific's nest (Grabowska-Zhang, 2012). In fathead
10 minnows, cohesion is greater and anti-predator behaviors (i.e. predator inspection) more
11 effective in familiar groups when compared to unfamiliar groups (Chivers, 1995), and the same
12 effect has been observed in juvenile trout (Griffiths, 2004). Given the advantages of familiarity,
13 it makes sense that individuals often prefer familiar individuals over unfamiliar ones in a number
14 of species, including cowbirds (Kohn, 2015) and guppies (Griffiths, 1997).

15 This study investigated how individual *Corydoras aeneus*, the Bronze Cory catfish, can
16 initiate or mediate a coordinated group response to a potential predator attack, how familiarity
17 affects interactions during a group response to a predator attack, and how individuals can
18 maximize group coordination under stressful circumstances. The Bronze Cory catfish is a highly
19 social neotropical species (Lambourne, 1995) that uses an unusual tactile interaction behavior in
20 which individuals physically nudge one another during coordinated movements (Riley, 2018).
21 To investigate how individuals use nudges in response to a potential threat, and how nudges
22 affect group coordination, we scrutinized this behavior in a controlled laboratory setting. We
23 predict that familiarity will impact nudging tendencies, and individuals will be more likely to
24 both deliver nudges and successfully recruit their familiar partner over their unfamiliar partner.
25 We also predict that nudging may serve an important function for both the spread of information
26 about a potential predator, as well as maintaining proximity between group members following a
27 flight response.

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29 **Methods:**

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31 *Study species*

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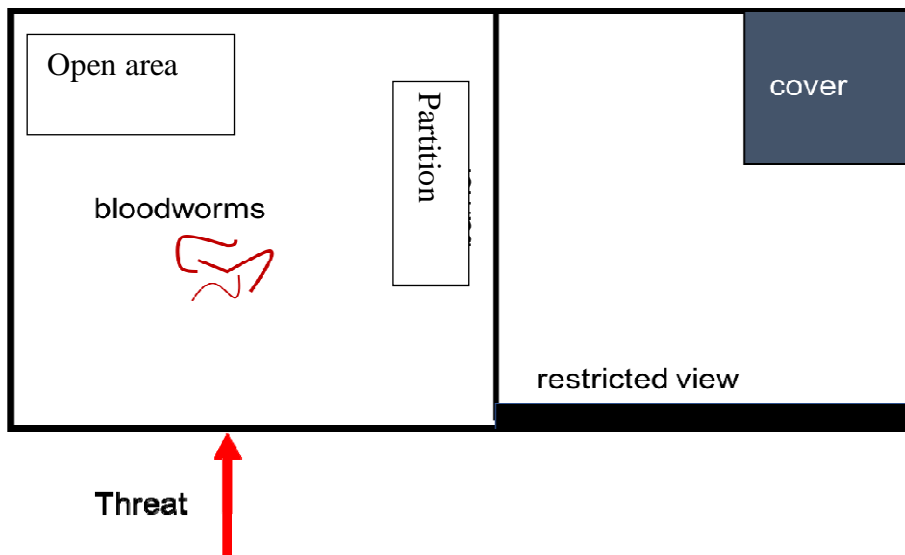
In the wild, *Corydoras aeneus* are social foragers that live in groups of variable size consisting of males, females, and juveniles (Lambourne, 1995). Because they are bottom-dwelling they shoal in 2 dimensions and their social behaviour can be accurately and reliably recorded from above. We have observed that both wild-caught and captive-bred individuals exhibit an unusual tactile interaction behaviour during coordinated activities and following a startle response in aquarium settings (as in Riley, 2018). Wild fish were observed utilizing this behavior in several small streams in the Madre de Dios locality of the Peruvian Amazon in 2011 and 2013, particularly when fleeing the observer (RJR, pers. obs.).

Husbandry

We obtained Bronze Cory catfish from three local pet shops in Cambridgeshire: Maidenhead Aquatics Cambridge, Pet Paks LTD, and Ely Aquatics and Reptiles. All fish used in both experiments were at least 24 weeks of age, and had been housed in the lab for at least six weeks prior to the start of experiments. We maintained the fish on reverse osmosis (RO) water purified to 15ppm or less total dissolved solids (TDS) and re-mineralized to 105-110ppm TDS using a commercially prepared RO re-mineralizing mix (Tropic Marin Re-mineral Tropic). The fish lived on a 12:12 light:dark cycle at a temperature of 23 +/- 1 degree Celsius. Prior to the start of the experiment, we housed the fish in mixed-sex social housing tanks (60cmx30cmx34cm) of 6-10 fish. The tanks were equipped with 4 Interpet Mini internal filters and an air stone. We fed the fish daily on a varied diet of alternating Hikari wafers (Hikari brand, USA), Tetra Prima granules (Tetra brand, Germany), and thawed frozen bloodworms (SuperFish, UK). The group composition of social housing tanks was stable for at least six weeks prior to experiment, and unfamiliar fish (see below) had not been exposed to each other for at least six months prior to the experiment, if at all. At the conclusion of each experiment, all fish were returned to their respective social housing tanks.

Triplet study experiment procedure:

1 We investigated the behavior of triplets over three weeks in May-June 2017, as in (Riley,
2 2018). We analyzed 18 triplets for a total of 54 individuals. Each triplet consisted of two familiar
3 individuals taken from the same social housing tank and an unfamiliar individual taken from a
4 different tank. Triplets were composed of same-sex individuals to avoid courtship interactions,
5 and fish were not fed prior to the trial to encourage exploratory movement in search of food.
6 Each triplet was placed in a testing arena situated on a very low shelf 3cm off of the floor (Figure
7 1; two identical setups were utilized in parallel). The arena had water 29 cm deep and a thin layer
8 of aquarium sand as substrate (mimicking the Bronze Cory catfish's natural habitat) and an
9 opaque barrier so that each open (initially partitioned) arena was (47cm x 30 cm). We placed a
10 piece of opaque acrylic outside the half of the tank where a sheltered 'cover' area was provided
11 so that fish could not see any potentially threatening stimuli from outside the tank while in cover.
12 Fish were left in the open part of the arena for an hour to acclimate to their group-mates, and
13 were filmed during this time so that nudging patterns at 'baseline' (in the absence of threat
14 stimuli) could be analyzed. The partition was then removed, and fish were allowed to explore the
15 entire tank (91cm x 30cm) for 30 minutes prior to the threat event period in order to explore the
16 testing arena and become familiar with the location of cover. We used a GOPRO HERO 3
17 camera to film each triplet for the entire duration of the acclimation periods and threat events.
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20 Figure 1: Schematic of test tank. Fish were initially allowed to acclimate in the open (initially
21 partitioned) area without food. After acclimation, the barrier was removed, and fish were allowed

1 to explore the entire test tank. Bloodworms were then added to the open area to encourage fish to
2 leave cover. The threat stimulus was only applied when fish were in the open area.

3
4 *Providing the threat stimulus*

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6 After fish were allowed to explore the entire test tank, i.e. 1.5 hours after introduction, the
7 threat event period commenced. Threat events were delivered by RJR or ERG and were given
8 through rapid approach of the test tank from a distance of 1.5 meters. Threat events were
9 delivered in similar clothing every day (blue jeans and the same shoes during each event) and
10 happened with an approach speed of roughly 2-2.5 m/s. Triplets responded to the vast majority
11 of these threat events with a clear anti-predator response, and most responses to threat events fell
12 into two categories: (i) fish responded to the threat by swimming rapidly to cover, often at speeds
13 that required frame-by-frame video analysis for data extraction. (ii) fish responded to the threat
14 with rapid movement, then froze in place outside of cover. We considered both reaching cover
15 and freezing (following an initial burst of movement) as complete threat responses, thus
16 considering a given threat event as ‘complete’ once all fish of a triplet had fled to cover or frozen.
17 Following each threat event, we used an aquarium net to chase into cover any individuals in the
18 exposed area. If the aquarium net appeared before all individuals had frozen or reached cover,
19 the threat was considered incomplete.

20 Threats were only delivered when all fish were out of cover in the open area. Thawed
21 frozen bloodworms were delivered to the open area to provide an incentive for fish to leave
22 cover. Additional bloodworms were provided after threat events. Triplets were allowed to
23 recover in between threat events, which occurred at least 4 minutes apart. Groups varied in how
24 long they spent in the open area, as well as how long they needed to recover from the threat
25 event and resume normal activities following a threat event, and the threat event period lasted a
26 maximum of 4.5 hours. After the threat event period, all individuals were returned to social
27 housing tanks. Consequently, the total number of threats each triplet received differed.

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30 *Analysis*

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1 *Recorded behaviors*

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3 For each triplet, we recorded (1) how many threat events took place, (2) the order that the
4 group responded in (i.e. which individual responded first, second, or third), (3) how many times
5 each group member nudged each of its groupmates, (4) whether any given nudge resulted in a
6 previously stationary fish initiating a flight response, a case we defined as ‘recruitment’, and (5)
7 the ‘flight time’ of each individual, defined as the time taken by each individual to either reach
8 cover or freeze; ‘flight time’ refers to the duration of each individual’s flight response, starting at
9 the onset of the threat event and ending when the individual reached cover or froze in place. For
10 our analysis of mean flight times, we only used threat events that were considered complete.
11 Finally, we assessed general measures of cohesion. These include whether or not all three group
12 members were in proximity (within 7cm, or roughly two body lengths) to one another 30 seconds
13 before the threat, three seconds before the threat, and three seconds after the threat event.

14

15 *Analysis*

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17 All statistical analyses were carried out in R version 3.2.2 (R core developer team), and
18 generalized linear mixed effects models (GLMMs) were fitted using the lme4 package (Bates et
19 al 2013). All GLMMs were used to investigate count data and were thus fitted assuming a
20 Poisson error distribution.

21 To test whether a triplet’s baseline nudging tendency was correlated with their nudging
22 tendency during flight responses, we used a Spearman’s rank correlation test. We tested the
23 correlation between a triplet’s total number of nudges during the acclimation phase and that
24 triplet’s average number of nudges per threat event.

25 We used a GLMM to analyse whether familiarity influenced individual nudging
26 preferences during threat events. The model included the number of nudges an individual
27 initiated as response variable, the familiarity between initiator and receiver as explanatory
28 variable (binary: receiver familiar or unfamiliar to the initiator), and two random effects (initiator
29 ID and group ID).

30 Similarly, to analyse whether familiarity influenced recruitment rates during threat events,
31 we used a GLMM with the number of successful recruitments by an individual as response

1 variable. As above, the model included the familiarity between initiator and recruit as
2 explanatory variables (binary: recruit familiar or unfamiliar to initiator), and two random effects
3 (initiator ID and group ID).

4 To test whether nudging frequency during threat events was correlated with the
5 probability of group cohesion following a threat event, we used a Spearman's rank correlation
6 test. We tested the correlation between the average number of nudges a triplet performed during
7 threat events and the proportion of all threat responses that ended with that triplet showing group
8 cohesion (as defined above).

9 We analysed whether nudging rate during threat events influenced flight times and/or
10 whether nudging rates changed throughout consecutive exposures to threat events using a further
11 GLMM. The model included median flight time during a threat event (i.e. the median time it
12 took a triplet's individuals to complete their threat response to a given threat event) as an
13 explanatory variable, the sequence of the treat event as an explanatory variable, the total number
14 of nudges performed by the triplet during the threat event as the response variable, and group ID
15 as random effect.

16 Finally, to analyse whether the order in which individuals of a triplet reacted to the threat
17 influenced the number of nudges a given individual initiated and/or whether this changed
18 throughout consecutive exposures to threat events, we used a GLMM. The model included the
19 total number of nudges an individual initiated during a given threat event as response variable,
20 two explanatory variables (that individual's rank in the order of response: 1st, 2nd, 3rd responder;
21 count of threat events the triplet had experienced), and group ID as random effect.

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26 **Results:**

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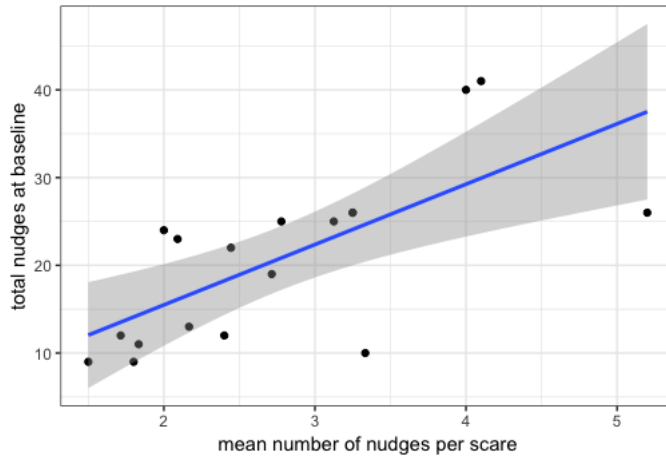
28 *Comparison to baseline*

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30 Group nudging behavior at baseline was significantly correlated with the average number
31 of nudges per threat event (Spearman's rank correlation, $S = 427.44$, $p\text{-value} = 0.016$, figure 2).

1 Groups that nudged more during a set duration while exploring in the absence of simulated
2 threats tended to nudge more during threat events.

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6 Figure 2: the mean number of nudges per threat event vs the total nudges at baseline. The blue
7 line represents the line of best fit for this relationship. The shaded area represents the 95%
8 confidence interval

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11 *General*

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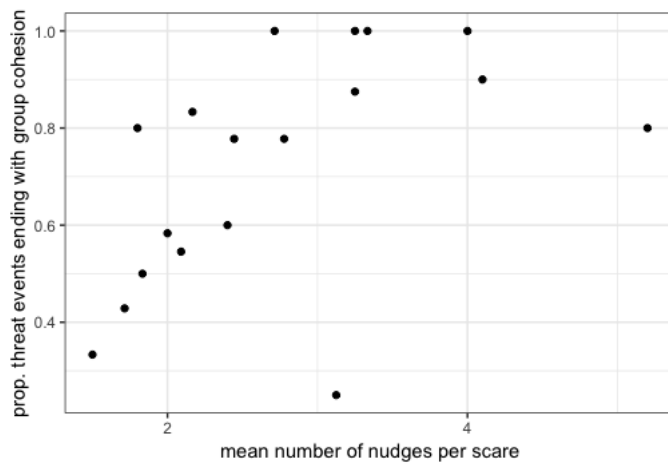
13 Overall, out of 135 threat events, 121 threat events were complete (all fish of a triplet fled to
14 cover or froze in place). The 14 incomplete events involve fish either not responding to the
15 stimulus at all, or still being in motion by the time the aquarium net chased them to cover. Out of
16 the 121 complete threat events, 105 threat events involved one or more nudges. Individuals
17 displayed no preference for delivering nudges with familiar partners as opposed to unfamiliar
18 partners (Poisson generalized mixed effects model with individual and group ID as random
19 effects, $\chi^2_1=2.8$, $p=0.093$). There was also no effect of familiarity on nudge frequencies during
20 baseline (Riley, 2018). The proportion of nudges that resulted in recruitment was 0.26.

21 Individuals did not respond with higher recruitment rates to nudges received from familiar vs
22 unfamiliar group-mates. (GLMM with individual and group ID as random effects, $\chi^2_1= 1.11$,
23 $p=0.292$)

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Nudging and group cohesion

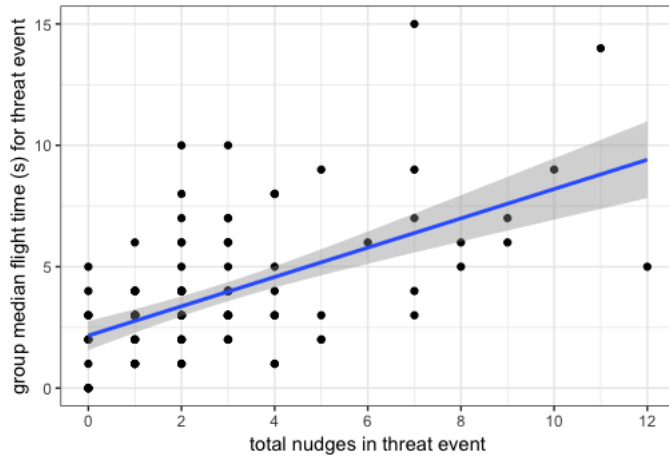
We found a significant correlation between a group's mean number of nudges per threat event and the proportion of threat events where all group-members were together three seconds following the event (Spearman's rank correlation, $S = 335.24$, $p\text{-value} = 0.003$, Figure 3). Groups that had a higher mean number of nudges per threat event exhibited higher cohesion following the threat event.



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Figure 3: proportion of threats that ended with all group members together vs mean nudges per threat event

Threat events in which group members exhibited more nudges had longer flight times (generalized mixed-effects model with Poisson error structure; Group ID as a random effect, $\chi^2_1 = 43.6$, $p < 0.001$, Figure 4.) The threat event number did not have a significant effect on group median flight time ($\chi^2_1 = 2.4$, $p = 0.120$)



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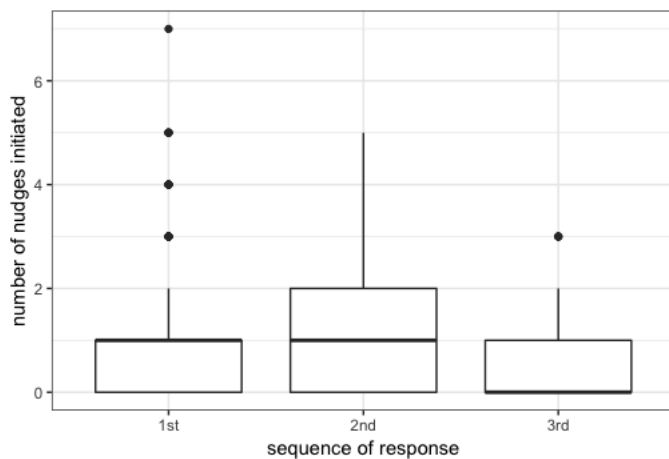
2 Figure 4: group median flight time total nudges in threat event. The blue line represents the line
3 of best fit. The shaded region represents the 95% confidence interval

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5 The sequence in which individuals responded to the threat event had an effect on the number of
6 nudge initiations: earlier responders initiated more nudges (generalized mixed-effects model with
7 Poisson-distributed error structure; Group ID as a random effect $\chi^2_1=4.6$, $p=0.032$, figure 5. The
8 scare event number did not have a significant effect on the number of nudges an individual
9 initiated (LRT=2.86, $df=1$, $p=0.09$).

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13 Figure 5: nudges initiated by the first, second, and third fish to respond to a threat.

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15 Discussion

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1 Our results show that, for triplets, nudging patterns are consistent across context, and
2 groups that nudge more frequently during environmental exploration nudge more frequently
3 during a flight response. Familiarity of group-mates did not impact nudging behavior, and
4 unfamiliar and familiar individuals were equally likely to initiate or receive nudges following a
5 potential threat. This is somewhat surprising, as familiarity has clear effects on individual
6 preference in other taxa, and individuals are more likely to assist the defense of familiar
7 conspecifics (Grabowska-Zhang, 2012). However, given the high costs associated with a
8 potential predator attack, and the fact that the Bronze Cory catfish have been shown to use
9 nudging to compensate for lack of familiarity when foraging in the absence of a threat (Riley,
10 2018) it seems likely that the use of nudges by Bronze Cory catfish make familiarity irrelevant in
11 such high-stakes circumstances.

12 In Cories, nudging was beneficial to all group members, and had a potentially selfish
13 advantage for the initiator of the nudge. During a flight response, nudges were positively
14 associated with a higher likelihood of maintaining cohesion following threat events and longer
15 flight times. Meanwhile, an individual's early detection of a threat relative to its group-mates is
16 associated with initiating more nudges during the group's threat response. These results suggest
17 that individuals deploy nudging in response to potential threats, and that it fundamentally alters a
18 group's behavior by increasing the probability of group cohesion. For this reason, familiarity
19 may not affect an individual's decision of who to nudge, as the incentive to maintain cohesion is
20 paramount. Furthermore, Bronze Cory catfish nudge group-mates extensively regardless of
21 familiarity, and can also use increased nudging to coordinate effectively with unfamiliar partners
22 (Riley, 2018). Given the serious consequences of a potential predator attack and the ubiquity of
23 nudging directed to both familiar and unfamiliar individuals, it is perhaps practical that
24 familiarity does not affect the flight response. This mirrors findings in other systems, such as rats,
25 in which reciprocity of cooperative behaviors is related solely to prior experience of cooperation,
26 and not familiarity with the current beneficiary of cooperation (Rutte, 2007).

27 Furthermore, social animals with an incentive to maintain proximity with conspecifics
28 have often been shown to use behaviors to coordinate with others. In green woodhoopoes,
29 vocalizations are used to maintain group cohesion while moving to new territory (Radford, 2004),
30 and white-tailed deer exhibit a low-cost flagging alarm signal to recruit other individuals to join
31 it in a flight response to a potential predator (LaGory, 1987). The Bronze Cory catfish also

1 appears to utilize an interactive behavior in order to influence the dynamics of its group
2 following a flight response to a potential threat. The nature of this behavior, a tactile nudge,
3 perhaps lends itself to maintaining cohesion, as the initiator must be in such close physical
4 proximity as to touch the receiver of its nudge.

5 Bronze Cory catfish may have evolved this behavior for a variety of reasons. They tend
6 to live in small, murky streams (Nijssen in Lambourne, 1995), which we observed at our field
7 site (RJR, personal observation), and were observed in other experiments to have poor vision
8 (Kohda 2002), a characteristic we have also noted in wild and laboratory populations. Under
9 these conditions, living in shallow water with poor visibility, a tactile mode of interacting with
10 one another might be the most effective way for individuals to transfer information and maintain
11 contact. This may also allow groups to maintain higher levels of cohesion: if an individual loses
12 contact with its group-mates, it might be difficult to find them again, and individuals will be
13 vulnerable while they search for one another. Tactile communication is present in another
14 interspecific association, the well-documented shrimp-goby association, under similar
15 circumstances, as the shrimp in that association has relatively poor vision (Kramer, 2009). In this
16 system, shrimps convey their location outside the burrow by touching the goby with their
17 antennae, and gobies, who have superior vision and serve as lookouts for predators, convey
18 information about predators to their shrimp via a flick of the tail, a tactile signal that the shrimp
19 can perceive, and after which both the shrimp and goby take shelter inside the burrow dug by the
20 shrimp (Preston, 1978).

21 In this way, the Cories' poor eyesight may have led to the evolution of an intraspecific
22 tactile interaction method that can be deployed to spread information about predators and
23 maintain cohesion following an attack. Individuals that reacted to a threat earlier initiated more
24 nudges, which implies that this behavior may be used more frequently by individuals who have
25 already perceived the threat and are altering their behavior in a way that transfers information to
26 a group-mate. The fact that some of these nudges resulted in 'recruitment' in the sense that the
27 receiver had been stationary prior to the nudge and then initiated a flight response following the
28 nudge implies that nudges can alter the behavior of receivers and potentially alert them to the
29 presence of a threat. It seems very likely that nudges modify the behavior of groups following a
30 potential threat, and provide the benefit of increasing the likelihood of maintaining group
31 cohesion while also encouraging a group to flee from a potentially dangerous area.

1 Our study suggests that the Bronze Cory catfish’s nudging behavior can provide benefits
2 when groups are responding to a potential attack. Nudges were also associated with coordinated
3 movements in pairs of fish (Riley, 2018), and the consistency in nudging in triplets during
4 exploration/foraging and while responding to potential threats suggests that nudging is a
5 behavior that is useful for coordination under different conditions, and that nudging more
6 frequently during exploration/foraging may contribute to a group’s coordination during
7 responses to a potential threat. In this way, nudging appears to be a versatile behavior that plays
8 a pivotal role in many aspects of the Bronze Cory catfish’s social life.

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