Original Article

Does the presence of an odd individual affect group choice?

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Group formation (shoaling) with conspecifics is common in fishes and provides several antipredator benefits, such as improved food and predator detection. However, coral reef fishes often form mixed-species shoals, which can generate costs for some group members. For example, individuals that stand out from a group are more likely to be targeted by predators according to the oddity effect. Consequently, the presence of an odd fish might reduce the risk of predation to other group members. Alternatively, an odd individual might attract predators and increase predation risk for the group as a whole. We examined three co-occurring species of coral reef fishes using 2-choice tests to investigate: 1) whether individuals chose to associate with conspecifics over heterospecifics (i.e. the oddity effect); and 2) whether individuals associate with or avoid shoals containing an odd individual under conditions of low- and high-predation pressure. One species actively avoided associating with heterospecifics, consistent with the oddity effect. In contrast, 2 species exhibited no preference for heterospecifics versus conspecifics, perhaps due to less pronounced phenotypic differences between species pairs resulting in a lower relative risk of being odd. None of the 3 species showed either active avoidance or preference for shoals containing an odd individual, irrespective of predation pressure. In instances where the oddity effect is apparent (one species in our study), lower individual predation risk from associating with an odd fish might be negated by greater predation risk to the group as a whole.

Key words: **Caesionidae, coral reef fish, Pomacentridae, predation, oddity effect, shoal**

INTRODUCTION

Group formation is a widespread behavior in terrestrial and aquatic animals (Krause and Ruxton 2002). In fishes, for example, individuals of the same species often aggregate to form unstructured groups (shoals) or groups that move in a coordinated fashion (schools) (Pitcher and Parrish 1993). Such aggregations provide advantages to individual members, such as improved food detection and protection from predators (Landeau and Terborgh 1986; Pitcher and Parrish 1993). Antipredator benefits arise from phenomena such as the selfish herd (individuals reduce their predation risk by putting other conspecifics between themselves and predators; Hamilton 1971), the "dilution effect" (the probability of being attacked is reduced to $1/n$ in a group of n individuals; Foster and Treherne 1981; Wrona and Dixon 1991), the "confusion effect" (predators have difficulties focusing on a single prey in a moving group; Welty 1934), and the "increased vigilance" or "many eyes" hypotheses (groups composed of many individuals are better at detecting approaching predators; Ward et al. 2011). However, being part of a group also has shortcomings. One notable disadvantage occurs when an individual conspicuously differs from other group members and thus becomes a preferred target of predators. This is known as the "oddity effect" (Mueller 1971; Milinski 1977; Landeau and Terborgh 1986).

Fish shoals are dynamic, with individuals constantly reassessing the costs and benefits of membership, resulting in decisions to join, stay, or leave the group (Pitcher and Parrish 1993). Given the common occurrence of the oddity effect (reviewed in Krause et al. 2000; Krause and Ruxton 2002; Rodgers et al. 2015), selection should favor individuals that carefully evaluate the risk of associating with a particular shoal. To avoid appearing odd, fishes tend to join homogeneous shoals by clustering with conspecifics that are similar in size (Theodorakis 1989; Ranta et al. 1992b; Rodgers et al. 2015) or coloration (Krause et al. 1996; McRobert and Bradner 1998; Bradner and McRobert 2001; Gómez-Laplaza 2005). Studies to date have focused largely on shoaling behavior among conspecifics whereas comparatively little work exists on assortment by species and species-related differential risks for members of mixed-species shoals (Ranta et al. 1994; Krause et al. 1996; Ward et al. 2002). This is surprising given that countless fish species live in sympatry and form mixed-species shoals, particularly in species-rich habitats such as coral reefs (e.g. Ehrlich and Ehrlich 1973; Wolf 1985; Overholtzer and Motta 2000). Evolutionary explanations for interspecific group formation include antipredatory vigilance benefits (Barnard et al. 1982), reduced competition for the

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rare species while maintaining the antipredator benefits of large group-size (Allan 1986), and reduced predator detection for cryptic species joining conspicuous ones (Tosh et al. 2007). However, as with single-species groups, the costs and benefits of group formation are likely to be asymmetric for members of mixed-species shoals (Hobson 1963; Tosh et al. 2007).

In a mixed-species shoal, according to the oddity effect, the less-abundant species should suffer from increased predation risk assuming that species are equally conspicuous. Indeed, several studies have documented that fish preferentially associate with conspecifics over heterospecifics when given a choice (sensu Krause et al. 2000). By extension, it is possible that individuals of the common species benefit from reduced predation risk via the presence of an odd individual. Thus, an individual of the common species might benefit from joining a shoal with an odd-group member present. In contrast, groups containing an odd individual might attract predators and experience greater overall predation risk at the expense of both species (Landeau and Terborgh 1986). In this case, individuals should always prefer uniform over heterogeneous shoals. These opposing predictions have never been experimentally tested. Here, we examined whether 3 species of coral reef fishes that often shoal together in nature prefer to 1) associate with con versus heterospecifics, and 2) associate or avoid shoals containing an odd individual.

MATERIALS AND METHODS

Fish collection and husbandry

Experiments were conducted in August-September 2015 at the Lizard Island Research Station (14°40'S; 145°28'E), Queensland, Australia. We studied 2 species of Pomacentridae (damselfishes): *Neopomacentrus azysron* and *Chromis viridis*; and 1 species of Caesionidae (fusilier): *Caesio teres* (Supplementary Figure S1). These species are abundant on the Great Barrier Reef and often form mixed-species shoals in the wild (Figure 1). Ninety fish per species were collected on reefs surrounding Lizard Island with a monofilament barrier net and hand-nets, and transported in 20-L buckets to the LIRS aquarium facility within 1 h of capture. Fishes were then housed by species in glass aquaria (38 × 94 × 38 cm, W × L × H; stocking density of 20 to 25 fish per aquarium or ~1.0 g L^{-1}) with air stones and flow-through water pumped directly from the reef. Cut PVC pipes were provided as shelter. The water temperature was 23 °C (±1 °C; actual variation), oxygen saturation was maintained above 95% (monitored with a FireStingO$_2$ Optical Oxygen Meter; PyroScience GmbH, Aachen, Germany), and the light cycle was *c.* 12:12 h light:dark. We fed fishes ad libitum with tropical fish flakes (ORCA, Taiwan) twice daily and syphoned uneaten food from the bottom of the tank daily. Eighty fish per species were used in the experiments: 60 as focal individuals and 20 to form shoals. A shoal contained 10 fishes, a size at which shoal members were found to be significantly less vulnerable to predation than either solitary individuals or individuals in smaller groups of 2 to 4 (Landeau and Terborgh 1986). Familiarity among individuals is known to influence assortative grouping (Warburton and Lees 1996; Killen et al. 2017); therefore, fish used to form stimulus shoals were housed separately from the focal fish (see the description of housing tanks above). Once tested, focal fish were used to form additional stimulus shoals, beyond the 2 previously mentioned, which were used in trials involving focal heterospecifics. Focal fish were similar in size to those comprising the shoals (1.0 cm range) to avoid any confounding effect of size (Krause et al. 1996). Fishes ranged between 3.0

Figure 1
The three study species swimming in mixed-species groups in the wild: (a) *Chromis viridis* with *Caesio teres*, (b) *Neopomacentrus azysron* with *C. viridis*, and (c) *N. azysron* with *C. teres*.

and 5.0 cm fork length (FL); based on size, *C. viridis* and *N. azysron* were juveniles and sub-adults, and *C. teres* were juveniles.

Fish collections were authorized by the Great Barrier Reef Marine Parks Authority (permit G14/36625.1 delivered to the LIRS).

Lateralization test

We used a detour test to assess behavioral lateralization (see Bisazza et al. 1997; Roche et al. 2013) and selected focal individuals with low lateralization scores (absolute lateralization index [L$_A$] below 40) to reduce biases due to individual directional preferences. Fish with a L$_A$ greater than 40 (considered significantly lateralized based on a binomial test) were used to form shoals.

Experimental setup

The experimental setup resembled the apparatus used in previous tests of the oddity effect in fishes (e.g. Krause and Godin 1994; Ward and Krause 2001). Trials were conducted in a glass aquarium (38 × 88 × 38 cm, W × L × H) with 3 opaque sides. A smaller

aquarium (26 × 38 × 20 cm, W × L × H) was placed adjacent to the transparent side: this tank was either empty or contained a common predator of our study species, the peacock grouper (*Cephalopolis cyanostigma*). The predatory stimulus was visual in nature; there was no exchange of water between the tanks containing the predator and the focal fish. Four *C. cyanostigma* (range = 25.5–30.0 cm total length) were used in the study; they were kept in individual, flow-through tanks (45 × 68 × 39 cm, W × L × H), fed frozen pilchard twice daily, and randomly assigned to sequences of 5 consecutive trials (there were never more than 5 trials per day involving a predator). Opposite the tank for the predator, inside the main aquarium, 2 stimulus shoals were placed in small aquaria (17.7 × 17.7 × 20.2 cm, W × L × H) built of transparent acrylic (Figure 2). These aquaria contained holes to allow water exchanges since chemical cues are known to influence group choice (Ward et al. 2002; Wisenden et al. 2003; Ward and Currie 2013).

Fish comprising the shoals were introduced in the test arena 10 min before each trial. The acrylic tanks containing the stimulus shoals were designed such that they could easily be moved to and from the test arena to minimize stress to the fish from netting and air exposure. Five minutes prior to the trial, a focal fish was introduced in the center of the test zone inside a bottomless acrylic rectangular container with holes so water could circulate through the walls (Figure 2). Focal fish were gently netted in an adjacent tank and transferred to the test arena with minimal air exposure (<5 s). An opaque partition between the test arena and the adjacent aquarium prevented fish from seeing the aquarium when it was empty or contained a predator (Figure 2). This barrier was removed 3 min before the start of a trial. The trial began when the acrylic container was removed by the experimenter, allowing the focal fish to move freely in the arena.

Experimental treatments

Different focal fish were tested under 4 conditions (60 fish were used per species, resulting in a sample size of 15 independent fish per combination of condition and species). Focal fish were never used more than once. The control consisted of a choice between

2 shoals of conspecifics. Treatment 1 was a choice between a shoal of conspecifics and a shoal of heterospecifics. Treatment 2 was a choice between a shoal of conspecifics and a shoal of conspecifics containing an odd individual (i.e. a heterospecific). Treatment 3 was the same as treatment 2, but with a predator placed in the adjacent tank. The experiments were designed so each species was used once as focal individuals and once as the odd species. Species pairs were determined randomly: *N. azysron* was tested with *C. viridis* (odd species), *C. viridis* with *Caesio teres* (odd species), and *Caesio teres* with *N. azysron* (odd species).

The experiment was conducted inside a closed room of the Sir John Proud Aquarium Facility at the LIRS. Each trial lasted 10 min during which the behavior of the focal fish was recorded with a GoPro Hero 3+ (GoPro, San Mateo USA) positioned above the aquarium. The stock lens of the camera was replaced with a commercially available non-distortive lens (4.14 mm f/3.0 86° HFOV 5MP GP41430; Peau Productions Inc., San Diego, USA). The experimenter remotely controlled the camera with an Ipad® (Apple Inc., California, USA) from behind a wet lab bench, at a distance greater than 3 m to avoid disturbing the fish during the experiments.

We tested 10 focal fish per day. Trials for one species in the 4 conditions were completed in 6 days. The identity of the shoals and their position in the test arena were randomly assigned for each trial using a random number generator in Microsoft Excel. Every evening, 5 fish were randomly chosen and transferred between stimulus shoals such that different shoals were used every day. Different odd individuals were used every day.

Behavioral experiments were approved by the Queensland Government's Department of Agriculture and Fisheries Animal Ethics Committee (permit CA 2015-06-868). Mortality was less than 2% and fishes were released on the reef, near their site of capture, at the end of the study.

Video analysis

We recorded the movements of focal fishes using the behavior logging software ODLog (Macropod Software, Yarraville, VIC,
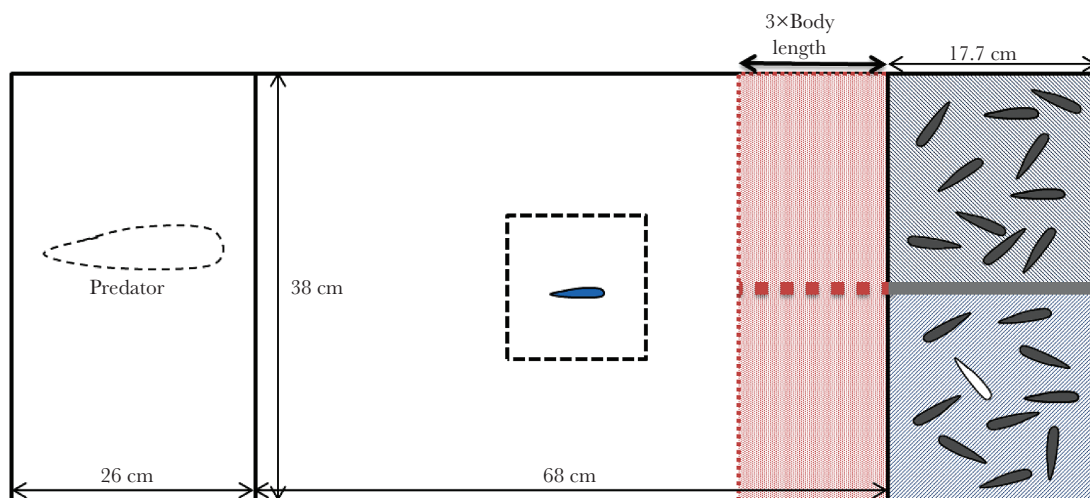

Figure 2
The experimental arena. A focal fish (in blue) was introduced in a removable prism at a distance of 30 cm from 2 smaller aquaria (in gray), each containing one shoal of ten fish separated by an opaque partition. The association zone (in red) corresponds to 3 times the body length of the focal fish. The focal fish could smell and see the 2 shoals. A smaller aquarium at the opposite end was either empty (control, treatments 1 and 2) or contained a predator (peacock grouper; treatment 3). There was no exchange of water between the tank containing the predator and the focal fish; hence, the focal fish could see but not smell the predator in treatment 3.

Australia), which logs keystrokes representing events or states. Cropped videos were coded (by DGR), enabling blind analysis by a single observer (FQ) (Clark et al. 2016). A focal fish was considered to associate with a shoal when it was within 3 body-lengths in front of a shoal compartment (*c.* 14 cm for *C. viridis* and *Caesio teres*; *c.* 11 cm for *N. azysron*) (Ward et al. 2002; Gómez-Laplaza 2005; Gomez-Laplaza 2009). A fish was not considered in association with a shoal if any part of its body was on the line drawn between the zones in front of the 2 shoals (Figure 2). We recorded the total time that the focal fish spent associating with each shoal and the number of times it moved between shoals (Gomez-Laplaza 2009).

Statistical analysis

One *C. teres* and one *C. viridis* were excluded from treatment 3 because of video recording issues. We compared the absolute time spent by focal fish associating with either shoal in the different conditions using paired t-tests. We used a Wilcoxon signed-rank test when the difference between association times in each zone was non-normally distributed. We compared the percentage of time that fish spent outside the 3 BL association zone and the number of times they switched shoals in the different conditions using Kruskal–Wallis tests. We did not correct for multiple hypothesis testing but interpret our results conservatively (Moran 2003; Nakagawa 2004). Statistical analyses were done in R v3.2.2 (R Core Team 2016).

RESULTS

Individuals from all three species spent most of their time in the association zone and readily moved between shoals (Table 1, Supplementary Figure S2). Control fishes did not display any preference for a particular shoal of conspecifics, indicating no inherent bias in our experimental setup (all *P*s > 0.35, Table 2). *N. azysron* preferred to shoal with conspecifics over heterospecifics (*s* = 0, *P* < 0.001; Figure 3a) but *C. viridis* and *C. teres* exhibited no preference for either group (Table 2, Figure 3b and c). None of the 3 species displayed active avoidance or preference for shoals containing an odd individual, regardless of whether a predator was present or not (Table 2, Figure 3).

DISCUSSION

The oddity effect in mixed-species shoals

We found evidence for the oddity effect in one of the 3 pairs of coral reef fishes tested: *N. azysron* was the only species that preferred shoaling with conspecifics over heterospecifics (Figure 3a). Two reasons might explain the occurrence of the oddity effect in this species. First, darkish blue-gray *N. azysron* appear highly conspicuous in a group of pale blue-green *C. viridis*. Second, in the wild, *N. azysron* typically escape in the water column when threatened (Hoggett 2016), whereas *C. viridis* dart for refuge among coral

branches (Myers and Lieske 2004), potentially leaving the former isolated and vulnerable. Similar differences in escape strategies among members of mixed-species shoals have previously been documented in field and semi-natural experiments (e.g. Wolf 1985; Allan and Pitcher 1986).

The other 2 species tested (*C. viridis* and *C. teres*) showed no obvious preference for associating with hetero or conspecifics (Figure 3b and c). Although the oddity effect is predicted to operate strongly in small groups such as those tested in our study (Landeau and Terborgh 1986), its influence on assortative behavior also depends on the type and degree of asymmetry between group members (Krause and Ruxton 2002; Rodgers et al. 2015). For example, though large individuals preferentially associate with similar-sized fish, small-bodied fish sometimes exhibit no preference for groups of different-size individuals (Svensson et al. 2000; Rodgers et al. 2011) or even prefer larger bodied conspecifics (Jones et al. 2010). Such non-assortment might result because: 1) small individuals benefit from joining larger ones if the latter are more profitable to predators (assuming similar handling costs) and hence at greater risk of predation (Peuhkuri 1997; Rodgers et al. 2015); or 2) factors such as aggression and competition override the influence of predation on group choice (Krause and Godin 1994; Jones et al. 2010). Thus, the lack of an oddity effect in 2 of the species pairs tested might occur because these fishes often shoal together in nature and blend relatively well, such that the perceived risk of joining a group of heterospecifics is low.

Importantly, we did not test all possible combinations of species pairs in our study and note that different species combinations could have led to different outcomes. Which species comprises the alternative shoal in a 2-choice test appears to have a strong influence on whether fish exhibit a preference for conspecifics or not. For example, threespine sticklebacks (*Gasterosteus aculeatus*) prefer conspecifics when presented with an alternative shoal of bitterlings (*Rhodeus sericeus*) but not with an alternative shoal of roach (*Rutilus rutilus*) (Keenleyside 1955). Similarly, Krause et al. (2000) noted evidence for the oddity effect when *G. aculeatus* are given the choice between conspecifics and sympatric blackspotted sticklebacks (*Gasterosteus wheatlandi*) (FitzGerald and Morrissette 1992) but not when given a choice between conspecifics and the European

Table 1

Mean (± one standard deviation) association time with a shoal (any of the 2 shoals) and number of times focal fishes switched shoal for the 3 species examined

Species	Association time (%)	No. of switches
Neopomacentrus azysron	87.38 ± 11.26	27.93 ± 19.61
Caesio teres	87.88 ± 8.74	13.24 ± 8.00
Chromis viridis	93.81 ± 7.55	14.66 ± 13.76

Table 2

Results of the paired *t*-tests (paired) and Wilcoxon signed-rank tests (wilcox) to compare the association time between 2 shoals

Species	Treatment	test	df	t/v value	P value
Neopomacentrus azysron	control	paired	14	0.648	0.505
	treatment 1	wilcox	14	0	<0.001
	treatment 2	paired	14	1.653	0.121
	treatment 3	paired	14	0.894	0.387
Caesio teres	control	paired	14	0.939	0.364
	treatment 1	paired	14	0.552	0.590
	treatment 2	paired	14	−0.462	0.651
	treatment 3	paired	13	2.099	0.056
Chromis viridis	control	wilcox	14	68	0.670
	treatment 1	paired	14	−0.941	0.362
	treatment 2	paired	13	0.597	0.561
	treatment 3	paired	14	−0.349	0.732

Three species were tested in 4 conditions: the control was a choice between 2 shoals of conspecifics; treatment 1 was a choice between a shoal of conspecifics and a shoal of heterospecifics; treatment 2 was a choice between a shoal of conspecifics and a shoal of conspecifics containing an odd individual (i.e. a heterospecific); treatment 3 was the same as treatment 2 but with a predator placed in an adjacent tank.
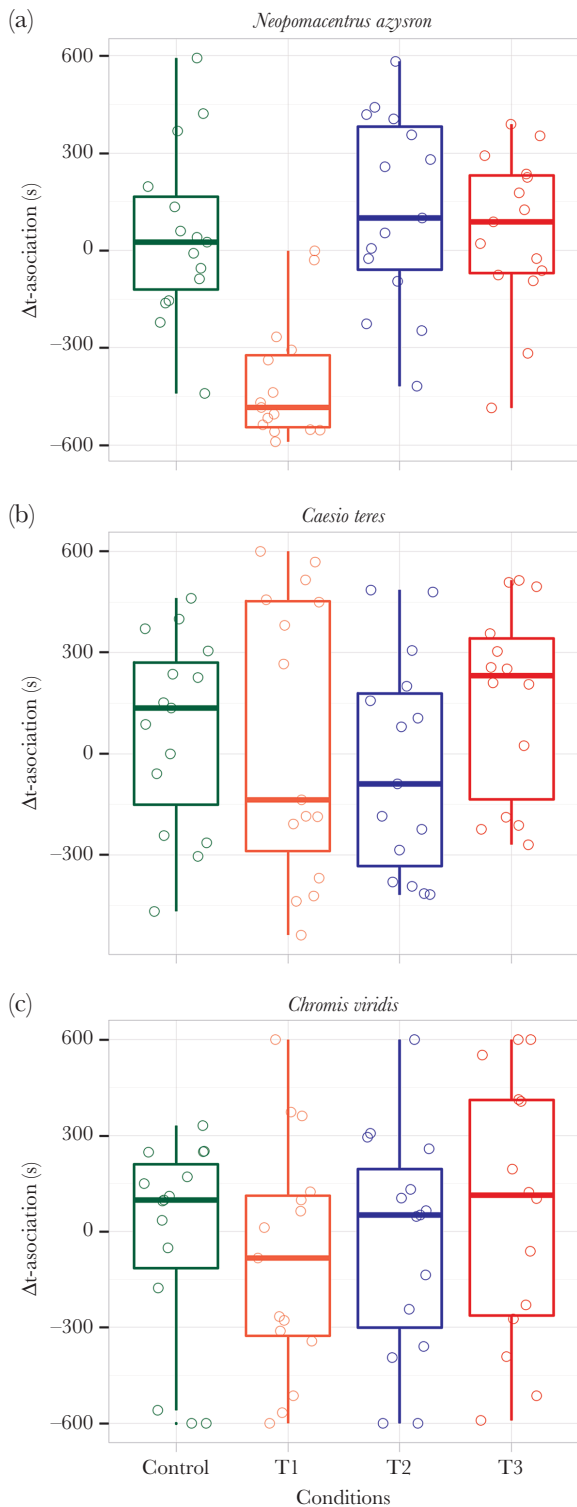
(a)

(b)

(c)

Figure 3
Box-plots showing the difference in the association time ($\Delta t_{\text{association}}$; in seconds) of focal fishes with shoals in four conditions: two shoals of conspecifics (control); a shoal of conspecifics and a shoal of heterospecifics (treatment 1; T1); a shoal of conspecifics and a shoal of conspecifics containing a heterospecific (treatment 2; T2); a shoal of conspecifics and a shoal of conspecifics containing a heterospecific in the presence of a predator (treatment 3; T3). Differences are calculated as: $\Delta t_{\text{association}} = t_{\text{(left shoal)}} - t_{\text{(right shoal)}}$ (control) or $\Delta t_{\text{association}} = t_{\text{(shoal containing heterospecific individual(s))}} - t_{\text{(shoal of conspecifics)}}$ (treatments 1, 2, and 3). A $\Delta t_{\text{association}}$ of zero indicates that fish associated equally with both shoals. Empty circles represent individual data points (i.e. focal individuals).

minnow (*Phoxinus phoxinus*) (Barber et al. 1998). In our study, *C. viridis* exhibited no preference when given a choice to join a group of conspecifics over a group of *C. teres*, which are relatively similar in colouration. Had we tested the opposite scenario and presented *C. teres* with a shoal of *C. teres* and a shoal of *C. viridis*, focal individuals might have exhibited choices consistent with the oddity effect. This is because, similar to *N. azysron*, *C. teres* occupies upper levels of the water column on the reef and would be left isolated when *C. viridis* retreats to shelter in response to a threat. Our experiments were not designed to test this hypothesis explicitly, but future studies should explore the interesting possibility that behavioral differences in predator evasion might mediate assortative grouping in addition to heterogeneity in size, coloration, and species identity (see Eshel 1978; Wolf 1985; Allan and Pitcher 1986).

Group choice in the presence of an odd individual

Early experiments on predator preference and hunting success indicate that predatory fishes selectively target odd-group members (Milinski 1977; Landeau and Terborgh 1986; Theodorakis 1989). Given the vulnerability of odd individuals to predation and the ability of many fishes to identify odd-group members (including themselves), fish might benefit from associating with vulnerable individuals to lower their own predation risk. For example, under high-predation risk, armored brook sticklebacks (*Culaea inconstans*) prefer to associate with more vulnerable, non-armored fathead minnows (*Pimephales promelas*) despite this choice resulting in higher competition for food (Mathis and Chivers 2003). Here, we predicted that fish would either 1) join a shoal with an odd individual to reduce their own predation risk, or 2) avoid a shoal with an odd individual because all group members might suffer from increased predation risk. There is evidence that the presence of odd individuals in a shoal increases not only their own vulnerability to predation, but also that of the common phenotype: Landeau and Terborgh (1986) observed that the presence of 1 or 2 odd individuals in a shoal increases predatory attacks on the group by almost 3-fold and the incidence of capture by almost 5-fold.

Interestingly, none of the 3 species we tested was attracted or repelled by a shoal containing an odd individual, including the species that exhibited a significant preference for conspecifics, consistent with the oddity effect. This behavior was unaffected by an increase in predation pressure (Figure 3). We note that experimentally simulating increased predation risk sometimes alters fish behavior and group choice (e.g. Krause 1994; Krause and Godin 1994; Mathis and Chivers 2003) but not always (e.g. Pitcher et al. 1986; Theodorakis 1989; Ranta et al. 1992a; Peuhkuri 1997). As such, even when the oddity effect is apparent, our results suggest that any benefit of lower predation risk from associating with an odd fish might be negated by elevated predation risk on the group as a whole.

CONCLUSION

We tested the oddity effect in three co-occurring species of coral reef fishes, exposing focal individuals to con and heterospecific visual and olfactory stimuli simultaneously (see Ward et al. 2002). Our results are consistent with previous studies suggesting that the oddity effect is not a universal phenomenon in mixed-species shoals (sensu Krause et al. 2000), and that the choice of species pairs appears to be important in eliciting a preference for conspecifics. We hypothesize that behavioral differences in predator evasion might be an important but overlooked trait affecting assortative

grouping, in addition to factors such as size, coloration, harassment, and competition. Finally, our results extend the findings of early predation experiments on the oddity effect (Landeau and Terborgh 1986) by suggesting that the potential for reduced individual predation risk from joining a group with an odd member might be offset by an elevated predation risk to the entire group. Since size differences appear to be more consistently associated with the oddity effect than species differences (Krause et al. 2000), future studies should test the generality of this hypothesis with intraspecific group-choice experiments based on size differences—for example, by using a stimulus shoal comprising a large odd individual in a group of small conspecifics.

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