

## RESEARCH PAPER

# Juvenile convict cichlids shoaling decisions in relation to shoal size and age

 Theresa Marlin<sup>1</sup> | Jennifer L. Snekser<sup>2</sup>  | Joseph M. Leese<sup>1</sup>
<sup>1</sup>DeSales University, Center Valley, Pennsylvania

<sup>2</sup>LIU Post, Brookville, New York
**Correspondence**
 Jennifer L. Snekser, LIU Post, Brookville, NY.  
 Email: jennifer.snekser@liu.edu

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**Abstract**

Many animals form groups and socialize in response to evolutionary pressures such as predation, food availability, and mate acquisition. Evidence of social choice based on various phenotypic characters (Group Phenotypic Composition [GPC]) has been observed in several animal species. In addition to the physical characteristics of the social group, it is also interesting to consider how decisions of who to socialize with might be expected to change for an individual over time. Younger individuals with limited life experience may discriminate differently between social groups than older conspecifics who have had the opportunity to learn and who may be faced with different ecological or environmental pressures. Here, we used a traditional two-choice design to explore the shoaling behavior of juvenile convict cichlids and determine whether the number of fish and/or the size/life stage of the individuals within a shoal influenced social choices. We found that juvenile convict cichlids spent more time shoaling with similarly sized juvenile individuals and also preferred to shoal with larger shoals, but not when shoals were comprised of adult fish. The size of the individuals in a shoal was a more influential factor than the size of the shoal itself. Size of individual juveniles was correlated with tendency to visit shoals, but was not correlated with overall time spent shoaling, regardless of shoal composition. As juveniles, convict cichlids can make discriminatory choices that are influenced by specific aspects of shoal composition.

**KEYWORDS**

cichlids, juvenile, oddity effect, shoaling discrimination, social behavior

## 1 | INTRODUCTION

Forming social groups is a behavior that is nearly ubiquitous across the animal kingdom (Krause & Ruxton, 2002). The evolutionary benefits that drive this behavior include increased efficiency in foraging (Lachlan, Crooks, & Laland, 1998; Potts, Baken, Ortmann, Watts, & Wrangham, 2015), higher vigilance (Godin, Classon, & Abrahams, 1988), and general advantages related to predator avoidance (reviewed in Krause & Ruxton, 2002). Despite these benefits, there are also costs associated with congregating in large groups, such as greater competition for limited resources, including mates and food

(Ford & Swearer, 2013), or an increased risk of disease (Seppälä, Karvonen, & Valtonen, 2008).

Based on these costs and benefits, predictions can be made regarding the optimal characteristics individuals should seek in their group mates. For example, based on the “dilution effect,” an animal should choose to be part of a larger, rather than a smaller, group because as numbers increase within the group, each individual is less and less likely to be the one that is targeted by a predator (Foster & Treherne, 1981). The “confusion effect” similarly predicts that individuals should select larger aggregations, as predators experience confusion when attacking larger groups and attack success rate is

inversely related to group size (Ioannou, Tosh, Neville, & Krause, 2008; Krause & Ruxton, 2002). Group size is not the only factor influencing the effectiveness of being part of a group. The “oddy effect” (Landeau & Terborgh, 1986; Ward, Axford, & Krause, 2002) suggests that individuals that are dissimilar to the rest of the crowd will be singled out and be more likely to be preyed upon; therefore, individuals should choose group mates that bear phenotypic resemblance. Taken together, these hypotheses and others lead to predictions as to the optimal Group Phenotypic Composition (GPC; Farine, Montiglio, & Spiegel, 2015). In considering many of the evolutionary pressures influencing GPC, animals generally benefit most from associating in large groups of phenotypically similar individuals. Individuals should discriminate based on group size, preferring larger groups (Bradner & McRobert, 2001; Dougherty, Ledesma, Bauer, & McRobert, 2010; Frommen, Hiermes, & Bakker, 2009; Hager & Helfman, 1991; Ruhl & McRobert, 2005), as well as morphologically similar features, such as color (Ledesma & McRobert, 2008a; McRobert & Bradner, 1998, but see Snekser, McRobert, Murphy, & Clotfelter, 2006; Snekser, Ruhl, Bauer, & McRobert, 2010), body pattern (Engeszer, Ryan, & Parichy, 2004), and/or body size (Hoare, Krause, Peuhkuri, & Godin, 2000; Krause, Godin, & Brown, 1996, 1998; Rodgers, Ward, Askwith, & Morrell, 2011).

Of course, while they can be experimentally separated, the factors driving group mate choice decisions must also be considered simultaneously. For example, different color morphs of mollies (*Poecilia latipinna*) discriminated joining groups based on both color and shoal size, but prioritized body coloration over shoal size (Bradner & McRobert, 2001). Frommen et al. (2009) found that three-spined sticklebacks (*Gasterosteus aculeatus*) prefer larger shoals over smaller shoals of conspecifics, but density also influences shoalmate choice. When the density of the different-sized shoals is equivalent, sticklebacks no longer exhibit a preference for the larger of two shoals. Thus, while predictions can be made as to which cues are important in choosing group mates and determining the GPC, when multiple aspects of group composition are in conflict with each other, individual animals must make difficult choices.

To further explore the factors that influence group mate choice, we explored the shoalmate choices of juvenile convict cichlids (*Amatitlania nigrofasciata*; Bagley et al., 2016; Schmitter-Soto, 2007). Shoaling, broadly defined as the practice of swimming together for social reasons (Pitcher, 1986), is observed in many diverse species of fishes. Adult convict cichlids form pair bonds and exhibit biparental care of their young. When they are not part of a breeding pair, adult convict cichlids form loose mixed-sex shoals. More cohesive shoals of convict cichlids are evident during very early development (the “fry” stage; from hatching for approximately 6 weeks) while parents are still tending to young and immediately after parental care is completed, during the juvenile stage (Wisenden, 1994). As juveniles grow into sexually mature adults, they are less likely to shoal in large groups, as they will be engaged in courtship and territorial behaviors with their mates.

In a controlled laboratory setting, we presented juvenile convict cichlids with shoals of either adult or juvenile convict cichlids

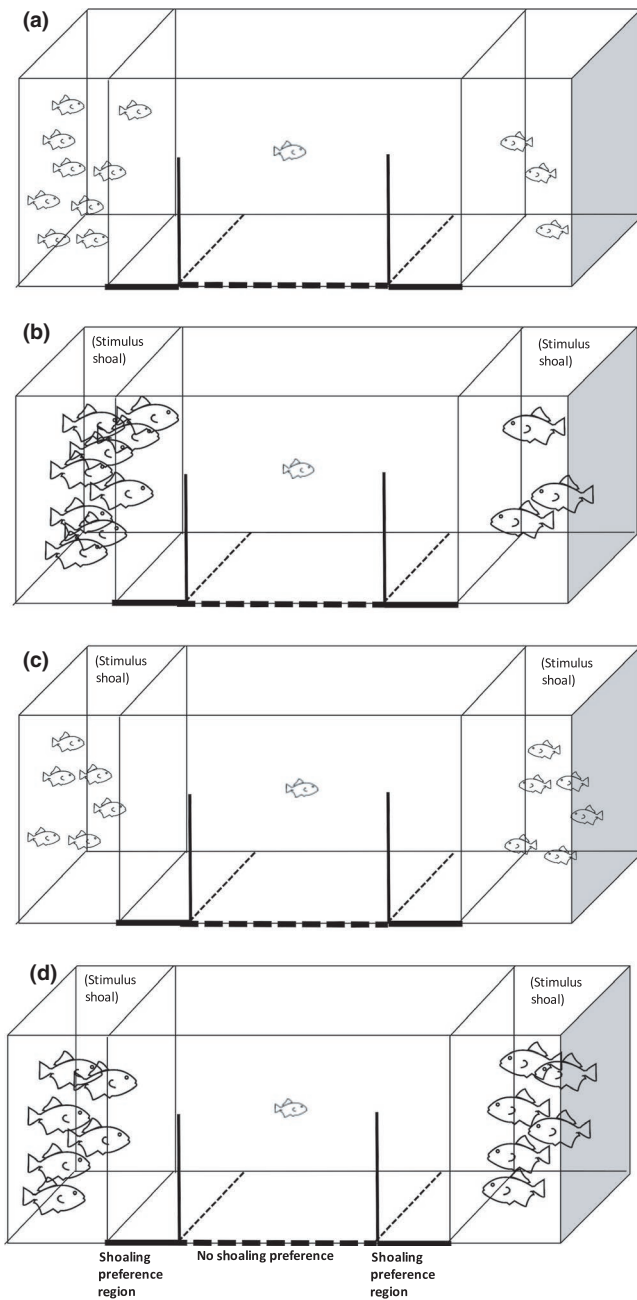
to examine how group size influenced shoal mate decisions in two different situations: when faced with same-sized juveniles or larger adults. We predicted that, regardless of the age of the fish within the shoals, individual juvenile fish would prefer to shoal with the larger group. We also predicted that more time would be spent with juvenile shoals (compared to adult shoals), as juveniles are more phenotypically similar and larger adults (that are phenotypically different) should not be as attractive as shoalmates. In addition to the time spent associating with shoals, we also examined the number of visits made to each of the two groups, to try and understand whether the shoal compositions would affect exploration and shoal discrimination. We predicted that the number of visits to shoals would also differ when encountering adults compared to juveniles. To further explore the shoaling propensity in the presence of adults versus juvenile fish, we also presented shoals of equivalent group size. This allowed for comparisons of shoaling behaviors in regard to the age of the fish in the shoals independent of group size. Together, these contrived shoaling conditions should reveal more about the prioritization of factors that ultimately lead to Group Phenotypic Composition.

## 2 | MATERIALS AND METHODS

The protocol for this experiment was reviewed and approved by the IACUC committee at Muhlenberg College. We studied convict cichlids, *Amatitlania nigrofasciata* (Günther, 1867), from laboratory-bred stocks originally purchased from commercial suppliers. Under a recent taxonomic arrangement, convict cichlids from various populations in Central America have been ascribed to various species, such as *A. siquia*, *A. nigrofasciata*, and *A. kanna* (Schmitter-Soto, 2007); however, subsequent genetic results suggest that this species is polytypic due to imperfect taxonomy, and it is likely that domestic stock populations, such as those used within this experiment, belong to *A. nigrofasciata* (Bagley et al., 2016).

Prior to the experimentation, fish were housed in 76-l holding tanks and fed commercial pellet food daily. All tanks were maintained at  $22^{\circ}\text{C} \pm 2^{\circ}\text{C}$  throughout the study. Tanks contained river rock gravel as a substrate and were illuminated by overhead fluorescent lighting on a 14:10 light:dark cycle. Water was constantly filtered with standard external sponge filtration system, and partial water changes were completed weekly.

The focal fish used were immature juveniles, between 3 and 6 months old. The standard length (SL) of each focal fish was measured prior to the testing. Size did not differ among the four experimental groups (described below) for SL (Overall  $\bar{x} \pm SE = 29.22 \pm 0.94$  mm, range of  $\bar{x} = 26.7\text{--}32.9$  mm;  $F_{3,35} = 2.457$ ,  $p = 0.079$ ). Convict cichlid fish are considered to be adult when they become reproductively active, typically after they reach 50 mm SL (Wisenden, 1995). Juvenile fish used as focal fish were obtained from ten lab-reared broods, and thus, occasionally siblings may have been used throughout the study, though focal fish were chosen haphazardly, and therefore, siblings should be evenly distributed across all four experimental



**FIGURE 1** The experimental tank was divided into three sections by the insertion of two clear, plexi-glass barriers. The center compartment housed the juvenile focal fish, and the side compartments hosted the stimulus shoals. Preference zones were marked eight centimeters from each of the plexi-glass barriers. Four experimental groups were examined, giving the focal juvenile fish the choice between: (a) small fish in different-sized shoals; (b) large fish in different-sized shoals; (c) small fish in same-sized shoals; and (d) large fish in same-sized shoals

groups. Adult and juvenile fish used within stimulus shoals were obtained from separate stock tanks (containing approximately two dozen fish each) and did not interact with each other, nor with focal juveniles prior to the testing. Forty different fish were used as stimuli throughout the trials. Because juvenile convict cichlids do not display distinguishable secondary sexual characteristics, the sex of the

focal individuals and the juvenile stimulus shoal individuals was not determined. Adult stimulus fish were male.

A 76-l test aquarium (76 × 30 × 30 cm) was used for all trials. Transparent plastic barriers were inserted on the left and right sides of the tank, 12 cm from the sides of the tank, creating three sections. These plastic barriers were not sealed with silicone, and thus, we cannot exclude water exchange between areas. The left and right areas ("shoal compartments") housed stimulus shoals, and the middle area ("focal compartment") housed the focal fish. Within the focal compartment, two 8 cm regions in front of each barrier were designated as shoaling preference regions (indicated with a ruler on the outside bottom of the tank, visible to the experimenter, but not to the fish; Figure 1). The test aquarium contained river rock gravel identical to stock tanks and was also lighted from above. Testing occurred within a secluded area, away from where stock tanks were located.

At the start of each trial, stimulus shoals were placed in each of the two shoaling compartments. A focal fish was then placed in the center compartment within a 250 ml flask for a 5-min acclimation period. During this time, the focal fish became familiar with its environment and was able to visually assess the two shoals. After the acclimation period, the flask was removed by hand and the trial began immediately. The movements of the focal fish were recorded for 900 s using a digital video recorder for later behavioral analysis. The digital recorder was started prior to the removal of the flask and was positioned directly in front of the test aquarium. Disturbance was minimized during recording as researchers left the room. Behaviors were recorded using Solomon Coder beta 15.11.19.

Overall, four experimental groups were designed to explore the variables of shoalmate size and the size of the shoal (number of fish in the shoal). Shoalmate size varied in that stimulus shoals either contained small (juvenile) fish that were the same size as the focal fish (<40 mm) or larger (adult) fish (>60 mm). Shoal size varied in that focal fish were either presented with shoals of fish that contained different numbers of individuals (9 fish vs. 3 fish) or equal number of individuals (6 fish each). To control for side bias, the sides housing the 9-fish and 3-fish shoals were alternated after every trial. Fish used within stimulus shoals were rearranged with each trial, over multiple days, with individual fish occasionally being re-used throughout the experiment, but never within exactly the same shoals for the same trials. Fish size (small juveniles and large adults) and shoal size (9 vs. 3 fish or 6 vs. 6 fish) were explored concurrently resulting in four experimental groups: small fish in different-sized shoals (Figure 1a;  $N = 10$ ); large fish in different-sized shoals (Figure 1b;  $N = 10$ ); small fish in same-sized shoals (Figure 1c;  $N = 10$ ); and large fish in same-sized shoals (Figure 1d;  $N = 9$ ). Different focal individuals were tested across experimental groups; none of the focal individuals were tested more than once.

Videos were reviewed to measure the amount of time the focal fish spent with each shoal and the number of visits it paid to each shoal. A visit was defined as the act of the entire fish crossing into a shoaling preference region.  $2 \times 2$  Factorial ANOVAs for time spent with each shoal and number of visits to each shoal were performed

for the two trials with different shoal sizes to further explore effects of shoal size. The total time spent shoaling and the number of visits were compared among all four experimental groups using one-way ANOVAs with Tukey's HSD post hoc analysis. Pearson's  $r$  correlations were performed to compare the size of juvenile focal fish with their total time spent shoaling and the number of visits they paid to shoals across all experimental groups. All statistical analyses were performed using SPSS Statistics v23.

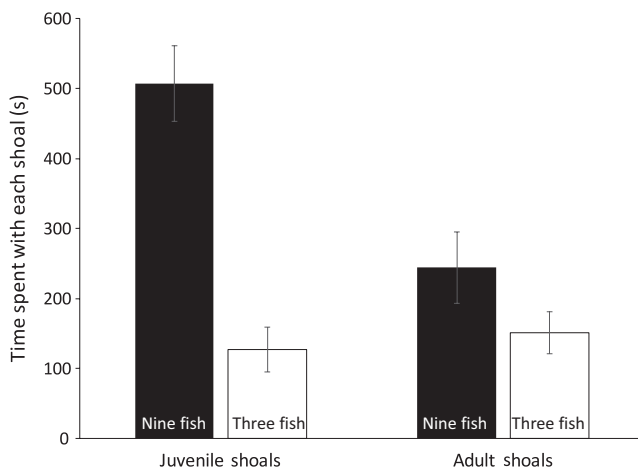
### 3 | RESULTS

#### 3.1 | Different-sized shoal choice

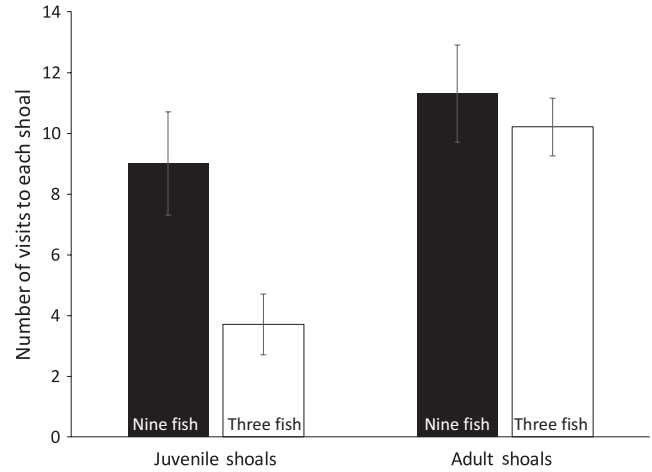
Examination of the trials in which the juvenile focal fish were given the choice between two different-sized shoals (9 fish vs. 3 fish; Figure 1a,b) revealed significant differences for both time spent shoaling (Figure 2) and number of visits (Figure 3). For the amount of time spent near a shoal, there was a significant interaction of the stimulus shoalmate size and the number of fish within the shoal ( $F_{1,17} = 8.525, p = 0.010$ ). Due to this significant interaction, simple main effects were explored. A significantly stronger preference for the larger shoal was seen when shoals were comprised of juvenile fish ( $F_{1,34} = 36.151, p < 0.0001$ ) compared to shoals comprised of adult fish ( $F_{1,34} = 2.409, p = 0.130$ ). In regard to the switching activity of the focal fish as they visited one shoal or the other, there was not a significant interaction of shoalmate size and the number of fish in the shoal ( $F_{1,17} = 2.271, p = 0.15$ ). A significant main effect of shoal size was found ( $F_{1,17} = 5.343, p = 0.034$ ), as well as a significant main effect of stimulus shoalmate size ( $F_{1,17} = 9.512, p = 0.007$ ).

#### 3.2 | Same-sized shoal choice

To explore the shoaling proclivity of juvenile cichlids further, in addition to the different-sized shoals, juveniles also considered shoals of

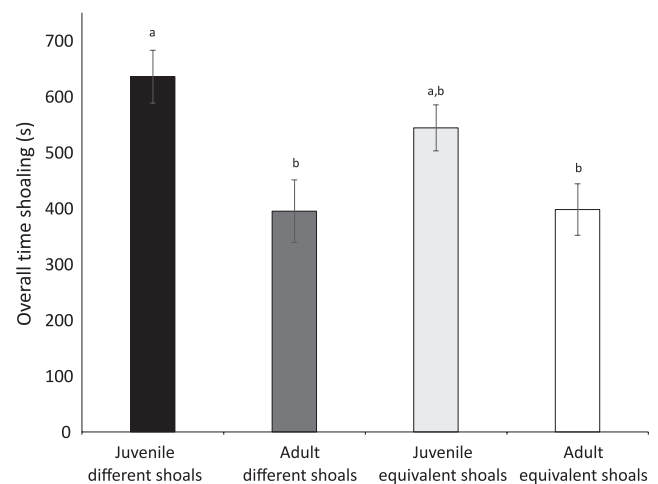


**FIGURE 2** Mean  $\pm$  SE time (s) spent with shoals of 9 fish or 3 fish. Shoals were comprised of either juvenile fish or adult fish. A significant interaction revealed that juvenile focal fish associated far more with the larger shoal of fish when the shoals were comprised of juveniles and not adult fish



**FIGURE 3** Mean  $\pm$  SE number of visits with each of the shoals of 9 fish or 3 fish. Juvenile focal fish paid significantly more visits to the larger shoal, and significantly more visits were paid to the shoals of adult fish than the juvenile shoals, regardless of the number of fish in the shoal

adults and juveniles that were equivalent in shoal size (6 fish each; Figure 1c,d). Significant differences in the total time spent shoaling were observed across the four experimental groups ( $F_{3,35} = 5.853, p = 0.002$ ; Figure 4). The focal fish presented with two different-sized shoals comprised of small juvenile fish spent the most time shoaling overall which was similar to focal fish presented with juveniles in same-sized shoals ( $p = 0.551$ ) but significantly different than focal fish that were presented with larger adult fish, either in different-sized shoals ( $p = 0.007$ ) or same-sized shoals ( $p = 0.008$ ). Focal fish presented with small juvenile shoals of equal size also did not significantly differ in their total time spent shoaling from focal fish that were presented with larger adult fish, either in different-sized shoals ( $p = 0.137$ ) or same-sized shoals ( $p = 0.149$ ). Focal fish presented with large adult fish did not differ ( $p = 1.000$ ) in the amount of time they spent shoaling,



**FIGURE 4** Mean  $\pm$  SE overall time spent shoaling by focal fish when presented with different-sized shoals (9 fish vs. 3 fish) and equivalent shoals (6 fish each) comprised of either juveniles or adults. Letters represent significantly different experimental groups

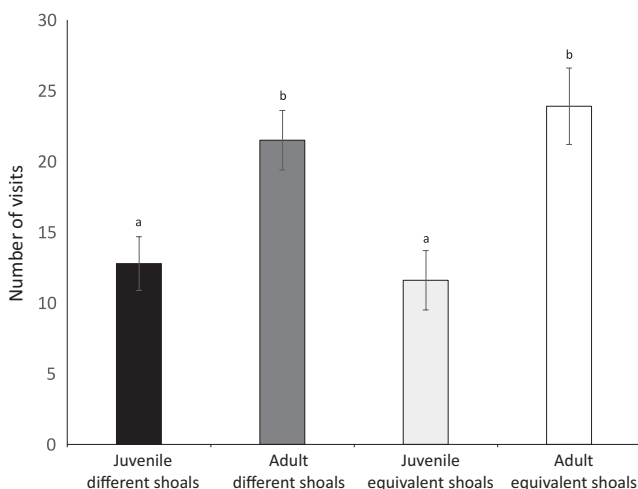
regardless of shoal sizes. The number of visits that focal fish paid to each shoal was also significantly different across the four experimental groups ( $F_{3,35} = 7.659$ ,  $p < 0.001$ ; Figure 5). When focal fish were presented with small juvenile fish, they performed relatively few visits whether they were presented with different-sized shoals or same-sized shoals, as compared to when focal fish were presented with adult stimulus shoals ( $p = 0.983$ ). Focal fish presented with adult fish of different-sized shoals moved between shoals significantly more often than focal fish presented with juvenile fish of different-sized shoals ( $p = 0.047$ ) and juvenile shoals of the same size ( $p = 0.016$ ). Focal fish presented with adult fish of same-sized shoals also switched between shoals significantly more often than focal fish presented with juvenile fish of different-sized shoals ( $p = 0.007$ ) and juvenile shoals of the same size ( $p = 0.002$ ). Juvenile focal fish presented with shoals of adult fish switched between the shoals a similar number of times, regardless of whether the shoals were the same size or different size ( $p = 0.868$ ).

### 3.3 | Shoaling behavior correlations with size of individual

Pearson's  $r$  correlations revealed a significant positive correlation between the size of juvenile focal fish (SL mm) and the total number of visits paid to shoals ( $N = 39$ ;  $r = 0.438$ ;  $p = 0.005$ ; Figure 6). There was not a significant correlation between the size of juvenile focal fish (SL mm) and the overall time spent shoaling ( $N = 39$ ;  $r = 0.177$ ;  $p = 0.282$ ).

## 4 | DISCUSSION

Understanding how the average Group Phenotypic Composition (GPC) influences individual choice can have implications for the evolution of ecological and social processes (Farine et al., 2015). Examining group mate choices also allows us to better understand the relative influence of the different ecological pressures that



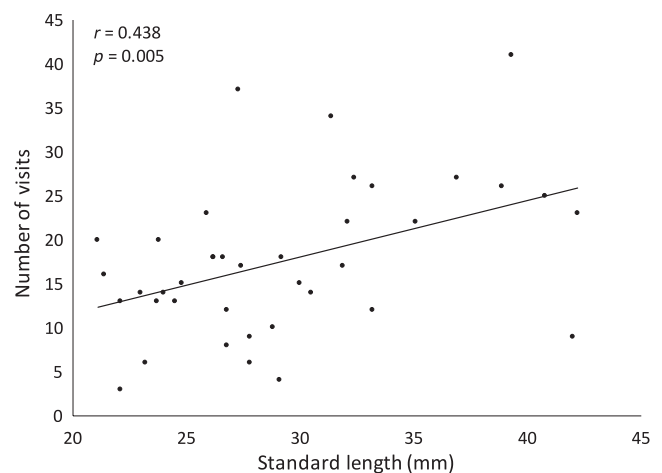
**FIGURE 5** Mean  $\pm$  SE overall number of visits to shoals by focal fish when presented with different-sized shoals (9 fish vs. 3 fish) and equivalent shoals (6 fish each) comprised of either juveniles or adults. Letters represent significantly different experimental groups

dictate grouping decisions, especially when the group options represent factors that conflict (Krause & Ruxton, 2002).

Here, juvenile convict cichlids favored larger shoals over smaller shoals, in agreement with previous studies (Bradner & McRobert, 2001; Dougherty et al., 2010; Frommen et al., 2009; Hager & Helfman, 1991; Ruhl & McRobert, 2005) and predictions of group behavior theory (Foster & Treherne, 1981; Krause & Ruxton, 2002). However, a statistical interaction revealed that this preference was more prominent when the presented shoals were comprised of other juvenile individuals, as opposed to shoals of larger adult fish.

Interestingly, despite less overall association time with adults, focal juveniles paid a significantly greater number of visits to adult shoals (regardless of the shoal size), seemingly switching back and forth between the two adult shoals. In contrast, the juvenile focal fish visited both juvenile shoals, but rarely visited the smaller shoal of juvenile fish. The significant difference in exploratory visits to the different-sized shoals based on shoalmate size (juvenile vs. adult) seems to indicate that shoalmate choices are situational (Barley & Coleman, 2010) and are not just a binary decision. That is, convict cichlid juveniles are not simply following a "shoal with largest group" rule; they are following that tenet in one circumstance, but not in another.

To further explore this interesting finding, we considered the choices of juvenile convict cichlids when presented with two shoals of the same group size. In comparing general shoaling behavior in the presence of adult shoals with behavior in the presence of juvenile shoals, we found that overall time spent shoaling was the greatest when stimulus shoals were comprised of juvenile fish. Less overall time was spent associating with shoals of adult conspecifics. As expected from the initial experiment, the number of visits to each of the shoals, however, was significantly higher when stimulus shoals were made up of adults. Juvenile convict cichlids spent less overall time shoaling with adult shoals but visited those shoals much more often, again suggesting that they are more exploratory when faced with groups of larger adult fish. This higher level of exploration is



**FIGURE 6** Standard length (SL; mm) of juvenile focal fish was significantly, positively correlated with the number of visits they paid to shoals across all experimental groups



evident regardless of the size of the shoal; that is, the number of visits to the adult shoals was high when there were 9 versus 3 fish and also when each of the shoals contained 6 fish, indicating that the shoalmates themselves (adults vs. juveniles), and not the size of the group, induced the behavior.

This difference in behavior when comparing presented shoals of adults or juveniles seems likely to be due to the difference in body size. Theoretical and empirical studies have long supported the idea of homogeneity in body size within shoals (Hoare et al., 2000; Krause, Godin, & Brown, 1996, 1998; Ledesma & McRobert, 2008b; Rodgers et al., 2011). The well-documented oddity effect serves as a possible explanation for this: if one fish is substantially and conspicuously different from the other fish in a shoal, it is at a higher risk of predation (Landeau & Terborgh, 1986; Ward et al., 2002). However, the reason for our observed shoaling differences may actually be more complex than the simple difference in body size of the juvenile and adult shoals and the phenotypic difference that represents. It is likely that juvenile convict cichlids would not benefit from shoaling with adults. If intra-shoal resource competition occurred, a juvenile within a shoal of adults would likely fare poorly. In some species of fish, including the model system used in this study, mature individuals will eat younger, developing individuals of the same species (Wisenden & Keenleyside, 1992), another possible risk factor. In natural populations, adult convict cichlids are much less likely to shoal than juveniles, though occasionally loose groups of small adult fish are seen (J. Sneksner & J. Leese, personal observation). The lack of preference for the larger shoal of adults, despite an overall significant preference to shoal with the larger group, may be, in part, due to fear or stress associated with such a large number of adult fish. A study examining the oddity effect in various species of the aquatic invertebrate *Daphnia* revealed that a predator preferred larger individuals, regardless if those large individuals were in the minority ("odd") or in the majority (Raveh, Langen, Bakker, Josephs, & Frommen, 2019). It is possible that predators may be drawn to shoals of larger convict cichlid fish and so juveniles may benefit by avoiding them in general.

Moss et al. (2015) found individual variation in behavior among juvenile convict cichlids in terms of aggression and their shoaling tendencies, suggesting there may be individual differences in other behaviors, such as boldness or exploration. Though not reported by Moss et al. (2015), we suspected that the size/stage of the juveniles may have influenced their behavior and performed simple correlations to determine relationships between size (SL) and shoaling and visits. We did not find a significant correlation between overall shoaling time and size of the fish. There was, however, a significant positive relationship between SL of the focal juvenile and the number of visits they paid to each of the shoals. This suggests that the effect of juvenile size on number of visits was independent of the types of shoals presented. Thus, it seems that as convict cichlids approach adult size, when they may be less likely to join shoals (Wisenden, 1994), they become more exploratory, switching among potential shoal groups more often.

Taken together, the interaction between the individual fish size/developmental stage and shoal size, in terms of overall time spent

associating with shoals and the number of exploratory visits to those different shoals, supports a general conclusion that juvenile convict cichlids have a sophisticated mechanism of shoaling discrimination. They are able to incorporate both shoal-related and individual-related factors to maximize the benefits and minimize the costs of shoaling. In considering the many evolutionary pressures that can influence GPC, our results again provide support that animals generally benefit most from associating with larger groups of phenotypically similar individuals. These findings have interesting implications for further understanding the evolutionary influences on group-forming behaviors.

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## ORCID

Jennifer L. Sneksner  <https://orcid.org/0000-0002-2472-4412>

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