Millersville University

Influence of Social Context on Individual Behavior of a Common Estuarian Killifish

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By

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Abstract

In shoaling and schooling fish, being a part of a group means directly competing with group members for valuable resources. However, groups provide benefits that individuals would normally lack, such as safety in numbers and ease of mating access. When alone, the apparent benefits of a group are lost, and the behaviors of individuals may change based on social context. I investigated differences in the behavior of individual and grouped striped killifish, *Fundulus majalis*. Fish were observed alone and in groups using video recordings to score two traits: activity level, measured by the number of squares entered, and risk aversiveness, measured by position in the arena. Using these two tests both in isolation and with conspecifics, I determined that the presence of conspecifics resulted in individuals exhibiting significantly lower activity levels. Risk aversiveness was not significantly impacted.

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Introduction

While animals navigate the challenges and opportunities present in their environment, living within a group potentially lowers the associated risks. Foraging competition and predation risk are two costs that may motivate group formation as grouping may allow more efficient exploitation of foraging resources and effective avoidance of predation. The long-term fitness benefits from these factors require group maintenance as temporary associations between individuals may not impart the same fitness advantage (Alexander 1974, Rubenstein 1978). Social living may also impose costs if individuals face greater competition for resources or reduced mating opportunities in hierarchical social systems (Alexander 1974, Rubenstein 1978). For species that do form social groups, the collective benefits are expected to outweigh the costs in terms of lifetime fitness. For example, an individual benefitting from reduced predation risk in a group may live longer than it would alone, allowing for more reproductive opportunities over its lifetime (Alexander 1974, Rubenstein 1978). Social interactions within groups, and the behavioral variation between individuals in those groups also influence these fitness tradeoffs; these interactions may result in changes in individual behavior, including whether or not they remain in the group.

Predation Risk

Joining a social group may reduce individual predation risk in several ways. Grouping for the added safety in numbers positively impacts an individual's survival, while those who are alone experienced a much higher risk of predation (Hass 2002, Alexander 1974). For many species, there are multiple proposed mechanisms for how predation avoidance may be

accomplished, including the increased likelihood of seeing a potential predator before an attack

occurs, commonly known as the "many eyes hypothesis" (Elgar 1989). Under this hypothesis,

groups can maintain continuous predator surveillance without having all individuals constantly

focused on predator detection, as more members being able to watch more directions (Elgar

1989). In fish schools, individuals may utilize this collective information to determine

movements and avoid predators without being separated from the group (Handegard et. al.

2012). The collective view of a school results in formations that move around the predator or

move away at given angles relative to the predator's position. (Elgar 1989, Handegard et. al.

2012).

The dilution effect is another mechanism for predation avoidance; when an individual is a

member of a group, that individual may have a lower probability of being predated upon

(Morgan & Godin 1985). Similarly, the selfish herd hypothesis states that individuals in groups

can protect themselves by schooling with potentially easier targets for predators or strategically

positioning themselves in safer parts of the school (Hamilton 1971). These two hypotheses are

distinct in that the dilution effect assumes a reduction in the likelihood of being predated upon

due to other conspecifics in the area, regardless of positioning or other factors (Landeau &

Terborgh 1986; Morgan & Godin 1985; Hamilton 1971). The selfish herd hypothesis states that

an individual can position itself within a herd to avoid predation, giving the potential threat

another target than themselves (Landeau & Terborgh 1986; Morgan & Godin 1985; Hamilton

1971). These effects may be further influenced by predator confusion; in a large enough group of

similar individuals, predators may face too many similar targets, preventing a predator from

focusing on and capturing any one individual (Landeau & Terborgh 1986, Hamilton 1971). A

study by Landeau and Terborgh (1986) investigated this hypothesis combined with the addition

of marked individuals meant to stand out within the group (Landeau & Terborgh 1986). Largemouth bass, *Micropterus salmoides,* were more successful foraging for silvery minnows, *Hybognathus nuchalis*, when the minnow schools included visually marked individuals (Landeau and Terborgh 1986). Once the group reached a large enough size, however, this trend no longer held (Landeau & Terborgh 1986). In banded killifish, *Fundulus diaphanus*, individuals in larger groups show a lower likelihood of being predated upon than those in smaller groups or those lagging outside of the group, suggesting that both the dilution effect and the selfish herd hypotheses may be relevant (Morgan & Godin 1985), however they did not find any evidence that the confusion effect influenced predation patterns.

Within fish schools, there is often a positive relationship between group size and the efficacy of the response to predators. In Atlantic herring, *Clupea herengus*, larger schools of fish can utilize stronger diving responses, an anti-predator evasive reaction (Rieucau et. al. 2014). Another tactic involves swimming directly away from the predator only to turn around once the predator has passed to face it, termed the "fountain effect" (Handegard et. al. 2012). A group provides individuals with increased vigilance, which then allows for avoidance of predators and the effective execution of anti-predator behavioral tactics (Magurran 1990). Flash expansion is a behavioral tactic in which a school of fish will respond to a quick attack by darting from the middle of the group and scattering into the surroundings until the threat has passed, at which time they will reform and continue (Partridge 1982). For species that live in complex environments (e.g. coral reefs), this behavior may result in individuals being separated when their environment can provide other forms of evasion such as hiding among stones or coral (Magurran & Pitcher 1987).

Foraging Efficiency

The added protection of a group allows individuals to dedicate time to other necessary aspects of life, such as foraging or reproduction (Elgar 1989). In predatory animals, hunting and feeding as a group is regarded as one of the most successful traits in the animal kingdom and exists as a multitude of mechanisms that allow the success of social foraging (Lang & Farine 2017). Social predation allows groups to capture and process prey that is too costly to hunt for an individual (Lang & Farine 2017; Oftadeh et. al. 2010). When hunting as a group, individuals often encircle the prey before eventually constricting the circle and capturing it, each participating individual adjusting position based on those around them (Oftadeh et. al. 2010). In the ocean environment, this behavior is observed in aquatic mammals such as orcas and dolphins; the latter of which will form groups where each individual has a specialized role (Gazda et. al. 2005) further increasing hunting success (Creel & Creel 1995).

The interactions within foraging social groups function differently depending on their food source. While many predatory species depend on the social group to successfully capture food, other species that are capable of effectively foraging alone may still form groups because they benefit from increased vigilance. The increased ability to spread information allows for resources, especially in areas where they are sparse, to be defended from competitors and exploited more effectively (Clark & Mangel 1986). Groups can profit from the discoveries of a few members when resources are scarce and, as a result, have better fitness than solitary individuals of these species.

Individual flocking birds can benefit from public information provided by a group, such as food locations and quality (Fernández-Juricic et. al. 2004). Social foraging allows fish to forage more effectively with similar benefits, which may vary with group size (Morgan 1988). Larger groups may experience greater predator defense but also face increased foraging

competition within the group (Morgan 1988). These larger shoals, however, can defend against the territory aggression of other species. For example, large schools of blue tangs, *Acanthurus coeruleus*, can overwhelm territorial groups of dusky damselfish, *Stegastes dorsopunicans*, and feed on the algal mats defended by the damselfish (Foster 1985).

The striped killifish, *F. majalis*, is a near-shore, shallow water, estuarian killifish with a native range along the Atlantic coast of North America, preferring sandy subtidal or front beach areas (Yetsko & Sancho 2015). They are relatively hardy social fish, able to adapt to fluctuating salinities and temperatures (Yetsko & Sancho 2015). *F. majalis* are omnivorous, often feeding on small clams and crustaceans in sandy substrates, which may have an impact on species distribution in benthic intertidal communities (Brousseau et. al. 2008). These fish generally prefer to school with conspecifics rather than remain solitary. A similar species, *F. diaphanus*, preferentially schools with conspecifics of comparable size profiles but, when size profiles are not a factor, individuals will prefer a larger group when given an option (Krause & Godin 1994). These fish have also been observed joining multispecies shoals (Krause & Godin 1994). Grouping in these species is likely influenced by predation risk and foraging success in the natural environment.

I investigated differences in exploratory and risk-aversive behavior of solitary and grouped striped killifish, *F. majalis*. Specifically, I predicted that if the presence of conspecifics reduces perceived predation risk in *F. majalis*, individuals within a group will display greater exploratory behavior and reduced risk aversive behavior. It is also possible that differences in behavior across treatments could result from increased foraging effort in a social group. In both cases, I predict focal fish will move more, and display fewer risk-averse behaviors when in a group.

Methods

Striped killifish, *F. majalis*, were collected using seine nets in Tom's Cove in the Assateague Island National Seashore (Virginia, USA). These fish were transferred to Millersville University where they were marked with fluorescent elastomer tags to track individuals. Fish were kept in 75 and 150 L aquaria, connected to a flow-through system, maintained at a salinity of approximately 30ppt and an average temperature of 20°C. Each tank contained crushed shell substrate and terracotta hides. Focal fish underwent a behavioral trial twice, once alone and again in a group of conspecifics. Observations took place in behavioral arenas that measured 61cm x 61cm, with a 5 cm grid printed on the arena's base (see Figure 1). These arenas contained 5cm of seawater (see conditions above) to limit vertical movement, and better reflect their natural shallow water environment these fish experience in the wild (personal observation of Dr. Isaac Ligocki). A 5 cm diameter white cup was placed in the center of the arena to act as an interior "wall"; however, this area was not approached and was not included in subsequent analysis.

All behavioral trials were recorded for 30 minutes, starting before the fish was added to the tank and ending 25 minutes after the blind around the arena was closed. Once fish were introduced into the arena, a 5 minutes habituation period started afterwards a 15-minute observation was recorded using Sony™ Cyber-Shot DSC-W800 camera that was mounted above each arena. Video observations were scored to quantify the number of lines crossed (a measure of activity level), and which square they occupied at each 10-second interval (to determine whether the fish was in a "center" or "edge" region of the arena, a measure of risk aversion). If a fish crossed a line and immediately crossed back, this was counted as two lines crossed so long as the body of the fish fully crossed the line before returning. Trials in the "grouping" treatment

followed the same protocol, but fish were introduced into the arena in cohorts of 3 or 4

unfamiliar individuals. Following behavioral trials, fish were returned to their home tanks in the

flow through system.

I used a paired t-test to compare the number of lines a fish crossed, and the relative time

spent in edge vs. center squares by fish depending on whether they were alone or with

conspecifics. All data analysis was performed in Microsoft Excel.

Ethical note:

The protocols carried out in this study were approved by the Millersville University
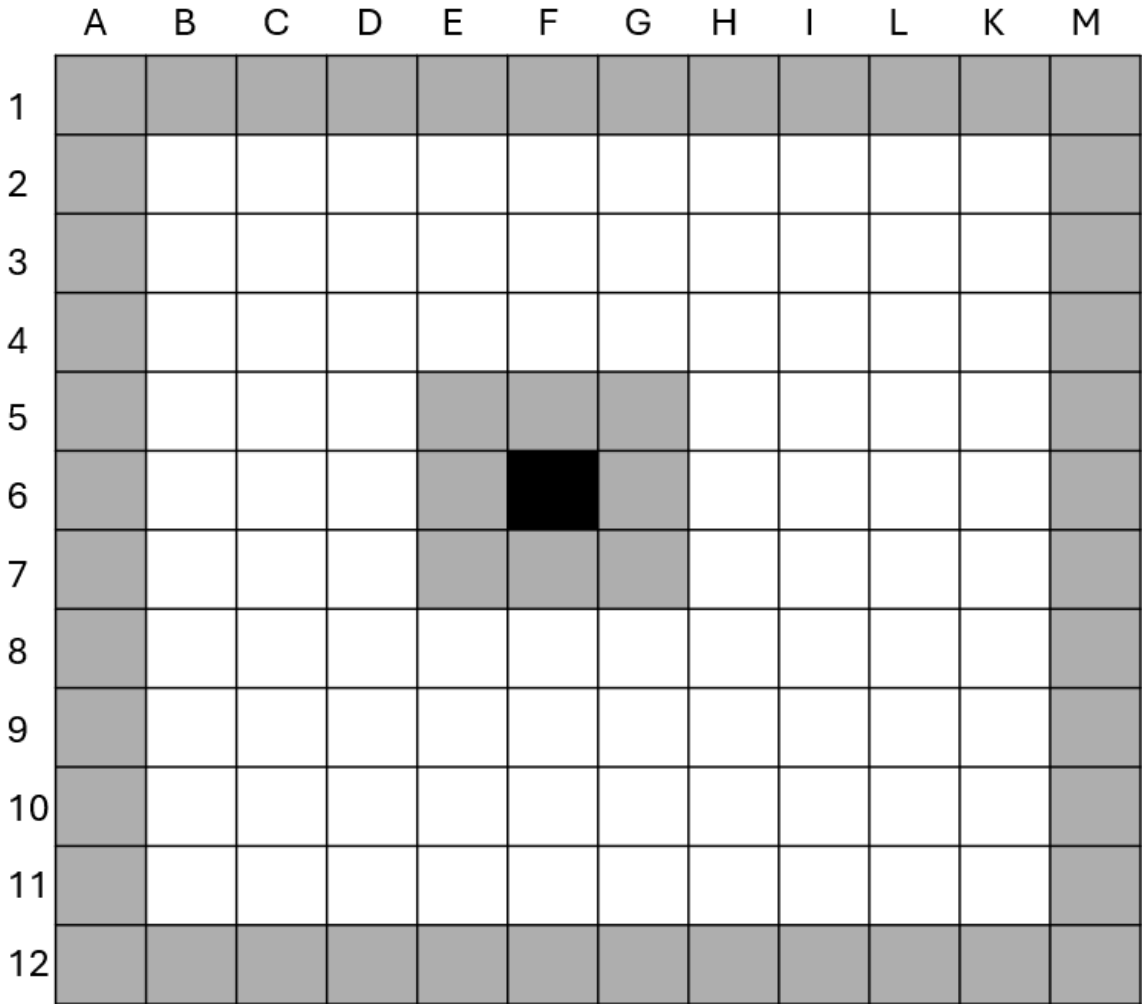
IACUC committee (Protocol 20-1).

Figure 1. Diagram of arena with labels for position identification. Edge squares shaded gray; position of cup marked in black. Fish did not approach the cup or enter the "edge" squares surrounding it in any behavioral trials.

Results

There was a significant difference in the number of lines crossed by solitary fish and those in groups (t_{17} = 2.882; $p < 0.05$, Table 1, Figure 2a). Individuals in groups crossed fewer lines than when alone. This contradicted my hypothesis that fish would move more with a group.

There was no significant difference in the number of edge squares entered by the fish depending on whether they were alone or in a group (t_{17} = 0.954; $p > 0.05$, Table 1, Figure 2b). This did not support my hypothesis that fish would move into the center of the arena more when in a group.

Table 1. Results of a two-tailed t-test comparing the lines crossed (over a 15-minute period) and edge squares recorded (observed cases of being in an edge square during the 15-minute period) for both social treatment groups, alone and with conspecifics.

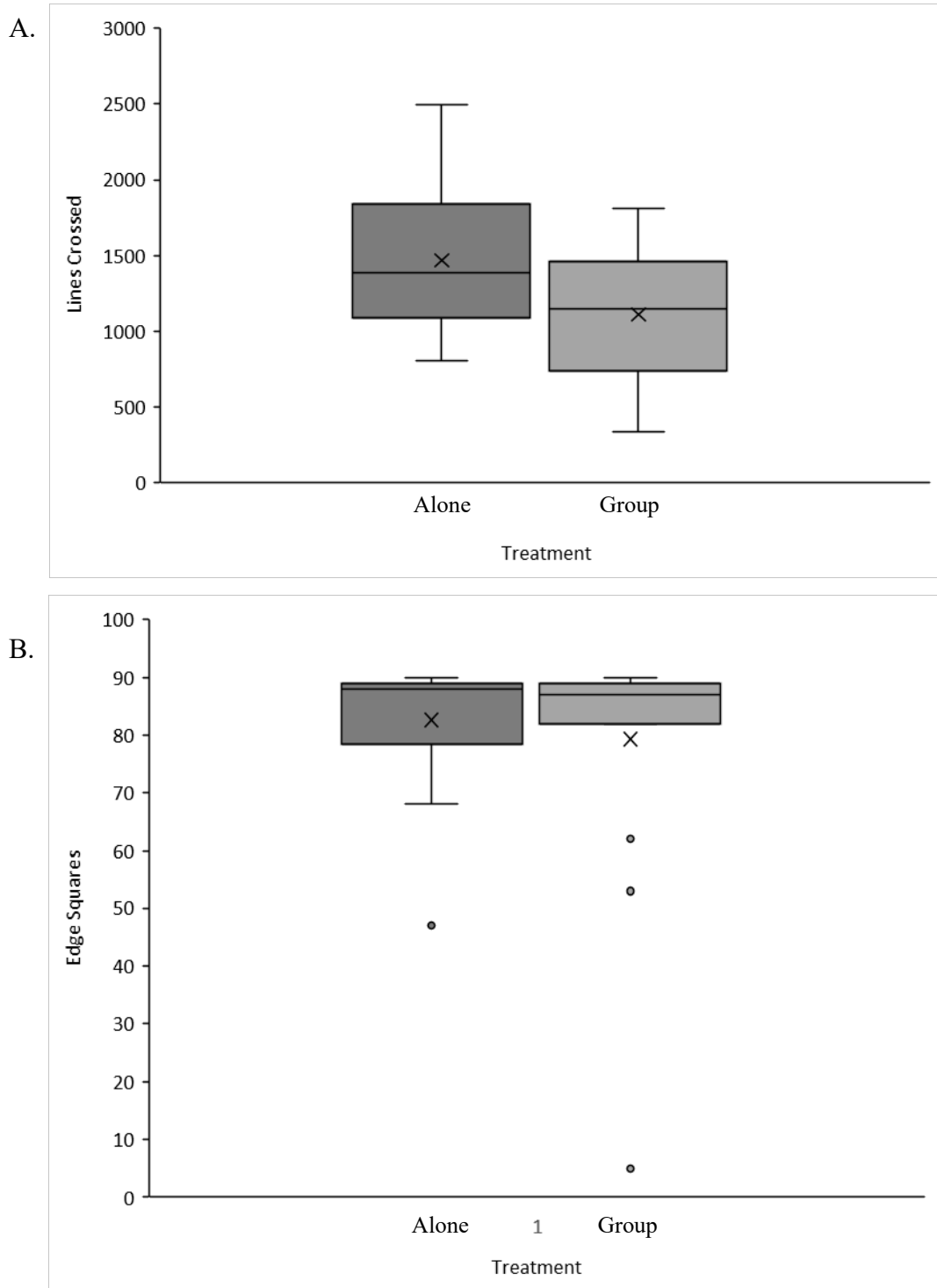|	Lines Crossed		Edge Squares	
	Alone	*Group*	*Alone*	*Group*
Mean	1468.11	1112.67	82.61	79.28
Variance	208303.99	164930.00	116.49	443.15
n	18.00	18.00	18.00	18.00
df		17.00		17.00
t Stat		2.88		0.95
t Critical		2.11		2.11
p		0.01		0.35

Figure 2. A (top) boxplot of lines crossed with solitary vs group treatment ($t_{stat} = 2.882$; $t_{crit} = 2.110$; df = 17; $p < 0.05$). B (bottom) boxplot of the number of edge squares recorded in relation to social context, outliers represented as solid points ($t_{stat} = 0.954$; $t_{crit} = 2.110$; df = 17; $p > 0.05$). For both, lower and upper box boundaries represent 25th and 75th percentiles respectively, line inside box represents median, X inside box represents mean, lower and upper error lines represent local minimum and local maximum respectfully, filled circles are outliers.

Discussion

I investigated variation in exploratory and risk-aversion behaviors of striped killifish, *F. majalis*, as influenced by the presence of conspecifics. I found a significant difference in the number of lines crossed; that fish crossed significantly fewer lines when with conspecifics than when alone. These findings contradicted my hypothesis that the presence of conspecifics would facilitate movement within the arena. For the solitary fish, more movement could indicate the fish trying to find shelter in the arena since in both treatments the fish stayed in the edge of the arena showing risk aversive behavior (Maximino et. al. 2010; Treit & Fundytus 1988; Tkaczynski 2014). It is also possible the solitary fish moved more in an effort to find conspecifics; *F. majalis* are schooling fish that are rarely found alone in the wild. The observed activity level decrease could also imply a collective latency to move throughout the arena which may allow them to avoid predators more effectively (Treit & Fundytus 1988; Maximino et. al. 2010; Tkaczynski 2014).

I also found no significant difference in the number of edge squares occupied depending on whether a fish was observed alone or in a social group. This did not support my hypothesis that the presence of conspecifics would increase the likelihood for an individual to approach the interior, and riskier, area of the arena. However, in both treatment groups these fish stayed in the edge squares, rarely going into the center areas of the arena. The number of edge squares entered was meant to determine if individuals changed their preference for the outside edge of the arena vs the center open sections when conspecifics were present. I hypothesized that the open spaces in the center of the arena would be perceived as risky; and would be avoided by solitary fish, whereas the presence of conspecifics would encourage movement into the center areas. This predicted response could have resulted from reduced perceived predation risk or increased

competition while foraging (Treit & Fundytus 1988; Tkaczynski 2014). During both treatments fish remained in the edge squares of the arena, rarely going into the center squares a handful of times. If group size does impact this behavior, it is possible the relatively small groups tested (3-4 individuals) may not initiate the predicted group behaviors and fish instead behaved the same as when alone (Landeau & Terborgh 1986). The smaller groups in our study may still remain highly vulnerable to predation and experience less competition than larger wild groups. *F. majalis* are observed with 20-30 individuals minimum (personal observation of Dr. Isaac Ligocki).

The findings of this study did not support my original prediction, that individuals in groups would increase their activity level and tendency to move in the internal areas of the arena. The use of the novel environment was meant to place an emphasis on the observed behaviors resulting from the presence of conspecifics being the sole variable changed. However, this may have impacted the behavior of the fish if a longer acclimation period was needed for the new environment, a factor that has not been studied in most species (Pazmino et. al. 2020). Future studies could further delineate whether behavioral shifts resulted from differences in perceived predation risk or differences in foraging behavior by including treatments in which fish are exposed to predator or food cues. Additionally, it is possible fish would have been more acclimated to the arena with a longer acclimation period. If indeed individual fish displayed higher activity levels because they were trying to find conspecifics, this hypothesis could be tested by immediately following the solitary behavioral trial with a group trial to determine if activity levels decreased.

In this study I found that when housed with conspecifics, fish displayed less exploratory behavior, but did not adjust their behavior in the context of a measure of risk aversion. This

change in behavior may indicate a motivation by solitary fish to find conspecifics; this motivation may result from perceived predation risk, increased foraging success within a group, or potentially other factors. Generally, *F. majalis* are highly social fish, and the many possible hypotheses regarding why sociality has evolved in this, and other species, are not mutually exclusive. It is possible and likely that sociality is maintained as a behavioral strategy in *F. majalis* for a number of reasons. Teasing apart the relative impact of factors such as predation, foraging success, and reproduction will allow for deeper insights into how sociality may vary within and between species, and what impact this variation might have on organisms and the communities they live in.

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