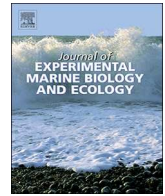




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Juvenile bonefish (*Albula vulpes*) show a preference to shoal with mojarra (*Eucinostomus* spp.) in the presence of conspecifics and another gregarious co-occurring species

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ABSTRACT

Grouping behavior occurs across a wide variety of taxa, both within and between species. While members are thought to obtain foraging and antipredator advantages, they can also experience costs in the forms of competition or increased conspicuity to predators. The mechanisms behind these costs and benefits can vary depending on group composition, ultimately influencing the choice of which groups to join. Mixed-species fish shoals are common in shallow nearshore habitats, where research has shown that juvenile bonefish (*Albula vulpes*) occur among similarly-sized mojarra (*Eucinostomus* spp.) at a rate far exceeding that predicted given the fishes overlapping habitat use, suggesting that bonefish may actively select to join mojarra. To evaluate this hypothesis experimentally, we assessed the shoaling preferences of bonefish when presented with shoals of conspecifics, mojarra, or another gregarious co-occurring fish (pilchard; *Harengula jaguana*) in a laboratory setting. Focal juvenile bonefish ($n = 25$) were given the choice between: (i) conspecifics or mojarra, and (ii) conspecifics or pilchard, tested in shoal sizes of one, two, four, and eight. Bonefish were also given the choice between a mixed shoal (two conspecifics, two mojarra) as an alternative to single species shoals of either: (iii) four conspecifics, or (iv) four mojarra. Juvenile bonefish exhibited a strong association with mojarra, spending significantly more time with them than conspecifics in all but one treatment. Moreover, focal fish showed no detectable preference between conspecifics or pilchard, regardless of shoal size. In mixed shoal treatments, focal fish spent significantly more time wherever there was a higher proportion of mojarra. These findings imply that the co-occurrence of bonefish and mojarra in nature is largely a product of bonefish shoal choice behavior, and likewise that any costs that bonefish might incur by joining mojarra (i.e., oddity effects) are likely outweighed by the putative benefits of doing so, which potentially include access to social information and/or reduced intraspecific competition.

1. Introduction

Sociality is an integral part of animal behavior, presenting itself across numerous taxa in the form of group living (Krause and Ruxton, 2002). Although most commonly considered in an intraspecific context, grouping behavior can also involve heterospecifics, with mixed-species groups occurring across nearly as many taxa as do single-species groups

(Hoare et al., 2000). Heretofore, the most widely researched aspects of both intra- and inter-specific group living pertain to the fitness advantages of joining others, with a particular emphasis on foraging and anti-predator benefits (Clark and Mangel, 1986; Krause and Ruxton, 2002; Sridhar et al., 2009).

Fishes are regularly used in the study of animal sociality, with shoaling or schooling behavior occurring in approximately 50% of all

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teleosts at some point in their developmental history, most often during the juvenile life stage (Radakov, 1973; Pavlov and Kasumyan, 2000; Hoare and Krause, 2003). Research seeking to elucidate the mechanisms which underly the organization of fish social groups suggest that, beyond the basic risks associated with not shoaling or the costs of moving between shoals (Krause and Godin, 1994; Ranta et al., 1994), individual grouping preferences are driven in large part by a tradeoff between two principal considerations; (1) the aforementioned foraging and/or antipredator benefits accrued through group participation, and (2) the corresponding costs of competition that arise when individuals share close proximities in space and time (Krause et al., 2000; Ward et al., 2002; Hoare and Krause, 2003).

The predominantly size and species-assorted nature of fish shoals observed in the wild (Krause et al., 1996; Hoare et al., 2000) has led many to theorize that the foraging and risk-related advantages of joining others are generally maximized when groups are phenotypically homogeneous (Krause et al., 2000; Hoare and Krause, 2003). This view has been reinforced by a number of experimental studies in which fishes have demonstrated a preference for shoaling with conspecifics, size-matched individuals, or those having similar body forms, colors, or patterns of pigmentation (reviewed in McRobert and Bradner, 1998; Krause et al., 2000; Saverino and Gerlai, 2008). Hypotheses offered to explain this apparent pressure for phenotypic homogeneity include that collective food-finding efficiency should be greatest when group members share analogous foraging tactics and resource use patterns, and likewise that size-or-species-matched shoals should help maintain an equitable distribution of resources by ensuring that grouped individuals are characterized by comparable levels of performance and/or competitive ability (Lindström and Ranta, 1993; Ranta et al., 1994; Peuhkuri, 1997). However, perhaps the most studied and broadly accepted motivation behind matched phenotype shoaling is the long-standing notion that “odd” individuals, or those of distinctive size, shape, color, or behavior, are more likely to be singled out for attack by predators (Wolf, 1985; Landeau and Terborgh, 1986), effectively neutralizing or at least diminishing the efficacy of key numerical benefits like risk dilution and predator confusion. Accordingly, the functionality of these intrinsic mechanisms is thought to be largely dependent upon being inconspicuous, or “blending in”, with respect to both physical appearance and behavior (Caro, 2005).

Yet mixed-phenotype or mixed-species groups of fishes, while less prominent than monospecific shoals or schools, are nonetheless widely documented in nature, implying that under certain circumstances this behavior confers adaptive benefits (Lukoschek and McCormick, 2000). Indeed, multispecies groups implicitly allow for greater maximum group sizes than single-species groups, theoretically enhancing the effectiveness of numerical benefits, particularly for rarer species among whom the availability of conspecific partners is limited (Ogden and Ehrlich, 1977; Pereira et al., 2011). Moreover, several contemporary works suggest that the processes giving rise to intrinsic numerical antipredator advantages can be more nuanced than previously thought and are not necessarily dependent on shoal homogeneity or coordinated behavior (Ruxton et al., 2007; Tosh et al., 2007; Rodgers et al., 2013), thus applying to heterospecific groups as well.

Fishes in mixed-species groups may also accrue fitness gains through altogether distinct mechanisms. One such advantage is enhanced access to resources, often obtained through the exploitation of food-related social cues or knowledge acquired by observing the foraging behaviors of others (Ryer and Olla, 1992; Laland and Williams, 1997), including “nuclear” heterospecifics that possess unique prey-finding abilities (Sazima et al., 2006; Krajewski, 2009). Similarly, such “social information” (Dall et al., 2005) sourced from heterospecifics may also serve to mitigate predation risk for mixed-species group members, conveying the riskiness of given foraging area (Gil and Hein, 2017; Hein et al., 2018) or providing early warning of predators via collective detection (Ward et al., 2011). Finally, given the presumably lesser niche overlap between heterospecifics (as compared to

conspecifics), partnering with other species may help to alleviate costs of intraspecific competition and the agonistic or aggressive interactions that can accompany it (Debrot and Myrberg, 1988; Overholtzer and Motta, 2000), while still permitting assortment by other aspects of phenotype, such as body size, that can influence competitive ability.

Mixed-species associations between marine fishes are particularly well-described in tropical nearshore systems, where they are notably more prevalent among juveniles (Lukoschek and McCormick, 2000; Moland and Eagle, 2005). The shallow littoral zones of such systems often function as nurseries (Beck et al., 2001; Laegdsgaard and Johnson, 2001), leading to spatio-temporal overlap in the distributions of various species (Nagelkerken et al., 2000; Layman and Silliman, 2002) as juveniles presumably seek to exploit the access to resources and refuge from predators offered by these habitats (Paterson and Whitfield, 2000; Munsch et al., 2016). Among said fishes, bonefish (*Albula vulpes*), the focal species in this study, support economically important catch and release fisheries throughout the tropical and sub-tropical Northwest Atlantic (Fedler, 2010, 2013). While patterns of habitat and resource utilization are relatively well understood for adult bonefish, the ecological requirements of early life stages have proven to be more enigmatic (Adams et al., 2007; Adams et al., 2014). Recent work has revealed that unlike more advanced stages (adults and subadults) which typically associate in large schools (Murchie et al., 2013), juvenile bonefish occur alone or in small conspecific groups, dispersed among much larger shoals of similarly-sized mojarras (*Eucinostomus* spp.) (Haak et al., 2019). Moreover, the near-obligate rate at which bonefish cooccur with mojarras greatly exceeds that expected by chance (even when considering the species' shared environmental preferences), suggesting juvenile bonefish may selectively associate with mojarras shoals, whose “attractiveness” has been attributed to their manifestation of several ecological characteristics that confer a unique capacity for the production of social information, in the form behavioral cues about shared predators and/or prey (Haak et al., 2020).

Our study presents a lab-based behavioral examination of the relationship between juvenile bonefish and mojarras, seeking to assess whether the small conspecific group sizes and persistent co-occurrence of bonefish with mojarras in the wild may in fact reflect the outcome of active shoal selection on the part of bonefish. To this end, we employed a well-established experimental protocol to quantify and compare the propensities of juvenile bonefish to affiliate with conspecifics and mojarras across a range of shoal sizes and mixed-species group combinations. Moreover, because experimentally-determined shoaling preferences can be sensitive to the choice of stimulus species considered (Keenleyside, 1955; Krause et al., 2000), we quantified the inclination of bonefish to join another sympatric, gregarious, and abundant inhabitant of tropical nearshore habitats, pilchards (*Harengula jaguana*), which despite occurring in the same general areas, exhibit relatively little ecological overlap with bonefish. By evaluating bonefish shoaling behavior over these varying contexts, we hoped to gain additional insights on the mechanisms or tradeoffs behind observed shoaling preferences.

Based on the hypothesis that bonefish actively choose to associate with mojarras, we predicted that focal individuals would exhibit an affinity for mojarras stimulus shoals at least comparable to that displayed for conspecific shoals. Such an outcome would be inconsistent with basic notions regarding pressure for shoal homogeneity, instead implying that the costs of oddity played a limited role in driving shoal choice or were offset by some yet-to-be-identified advantages of joining mojarras. We furthermore expected that bonefishes' predilection for mojarras would substantially exceed that for pilchards, whose pronounced ecological incompatibilities would likely serve to increase the oddity of focal individuals while also reducing the potential for them to profit through antipredator or foraging-related mechanisms. On the other hand, the absence of a discernable preference for mojarras (over pilchards) might suggest that bonefishes' willingness to associate with heterospecifics is not necessarily motivated by access to benefits that

are unique to joining mojarras, but may rather reflect an effort to limit exposure to conspecifics and subsequent costs of intraspecific competition. Finally, a notable preference for conspecifics over other stimulus species would align more closely with the traditional hypothesis that numerical benefits (i.e., risk dilution and/or predator confusion) were the primary drivers behind group choice, making it less likely that juvenile bonefishes' occurrence among mojarras in nature is a result of active choice on the part of bonefish.

Because the oddity or conspicuity of an individual is a function of the proportional representation of their phenotype within a group, and because other costs and benefits of joining others (e.g., competition or resource-scrounging) can also be affected by group size (Barnard and Sibly, 1981; Grand and Dill, 1999; Hoare et al., 2004), shoaling preferences may be sensitive to the number of individuals in stimulus shoals. To address this eventuality, we examined the interaction between stimulus species and group size, replicating the shoal choice experiments across a range of different stimulus shoal sizes (i.e., groups of 1,2,4, and 8 individuals). Frequency-dependent processes may likewise be mediated through the species composition of stimulus shoals; for example, we surmised that by joining a mixed shoal comprising similar proportions of conspecifics and mojarras, bonefish might obtain any benefits conferred by mojarras while also limiting their own oddity, a seemingly optimal scenario. Accordingly, we conducted an additional experiment to determine whether focal bonefish preferred a mixed shoal (with equal numbers of conspecifics and mojarras) versus a shoal comprised entirely of either stimulus species. In this case, a preference for the mojarra shoal over the mixed shoal would further underscore the limited weight placed on oddity and/or the unattractiveness of conspecifics as partners, possibly intimating that any gains to be had by joining mojarras may decline with the increasing presence of conspecifics.

2. Methods

2.1. Study species

Although juvenile bonefish, mojarras, and pilchards overlap broadly in their utilization of shallow nearshore environments, interspecific differences in several fundamental ecological characteristics yield divergence in their distributional patterns at finer scales (Sogard et al., 1989; Layman and Silliman, 2002). Obtaining a greater maximum size and occupying a higher trophic position, juvenile bonefish are relatively uncommon compared to the much more abundant and gregarious mojarras and pilchards, which often comprise schools of hundreds to thousands of individuals. As demersal benthivores, juvenile bonefish and mojarras share a mutual foraging guild, preying primarily on benthic infauna and epifauna from shallow intertidal waters that are often less than 1 m in depth (Vega-Cendejas et al., 1994; Layman and Silliman, 2002; Griffin et al., 2018). In contrast, the principally zooplanktivorous pilchard differs markedly in its foraging microhabitat use, typically occupying the upper reaches of the water column in areas of 1 to 5 m total water depth (Modde and Ross, 1983; Vega-Cendejas et al., 1994). Nonetheless, despite these fine-scale differences, all three fishes have been found to co-occur sporadically within the same comparatively small areas sampled by beach seining (Haak et al., 2020). From a gross morphological perspective, all three fishes share a superficial resemblance, displaying the typical piscine body form associated with subcarangiform modes of propulsion, although both mojarras and pilchards are considerably deeper-bodied than the more elongate bonefish. Contributing to their outward similarity, bonefish, mojarras, and pilchards are all characterized by crypsis, achieved primarily through a highly reflective, mirror-like appearance paired with countershading (darker dorsal and lighter ventral) pigmentation, characteristics that are common among fishes that occupy relatively unstructured environments (Denton, 1971; Johnsen and Sosik, 2003; Johnsen, 2014).

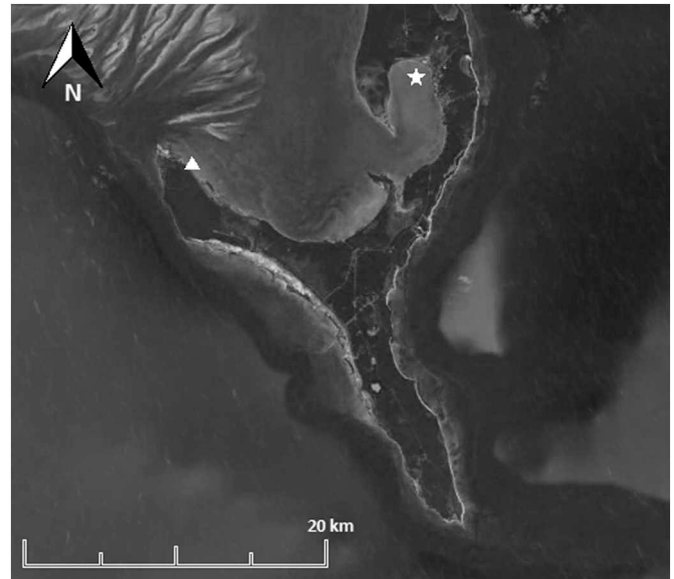


Fig. 1. Map of southern Eleuthera, The Bahamas. The star denotes the capture and collection site of juvenile bonefish and mojarra in Rock Sound, and the triangle denotes the location of the Cape Eleuthera Institute and the location of pilchard capture.

2.2. Capture, transport, and holding

The study was conducted in south Eleuthera, The Bahamas (N 24°50'05" and W 76°20'32") at the Cape Eleuthera Institute (CEI) during June and July of 2015 (Fig. 1). Twenty-five juvenile bonefish (mean = 70.2 ± 15 mm SD fork length; range 50–110 mm) were collected from Rock Sound to be the 'focal fish' in the shoaling study. Mojarra (mean = 67.8 ± 7.5 mm SD fork length; range 58–81 mm), juvenile pilchard (mean = 73.2 ± 7.1 mm SD fork length; range 62–90 mm), and additional juvenile bonefish (mean = 70.5 ± 9 mm SD fork length; range 55–85 mm) were similarly collected; these three species made up the respective 'stimulus shoals'. Juvenile bonefish and mojarra were caught using spot seining techniques, whereby nearshore habitats (< 1 m depth) in Rock Sound were visually assessed, and when the species of interest were identified, a seine net (15.25 m length × 1.22 m height, 0.6 cm mesh size) was used to capture them. Pilchard were caught using a cast net (0.6 cm mesh) on-site at CEI. Captured fish were transferred into flow-through net pens (1.50 m length × 0.7 m width × 1.20 m height) and left in shallow water while more fish were collected, before being relocated to coolers (0.9 m length × 0.35 m width × 0.2 m height; 63 L) on the boat for transportation (in the case of juvenile bonefish and mojarra). All fish transfers were done with care to limit exposing fish to air or causing net abrasion (Murchie et al., 2009; Cook et al., 2015). Upon arrival at the wet lab facility at CEI, the juvenile bonefish focal fish (herein referred to as 'focal fish') were held in individual pens (0.35 m length × 0.3 m width × 0.2 m height; 0.3 cm mesh size) for researchers to follow the same individuals throughout the entire study without needing to excessively handle or mark these fish. The individual holding pens were set in tanks (1.55 m diameter × 0.25 m height; 472 L) that were aerated and continuously supplied with fresh seawater (10 L/min) at ambient water temperatures (28.6 ± 2.4 °C SD), thus did not induce visual or olfactory isolation, similar to (Wright and Krause, 2006). There were up to eight individual holding pens per tank. The three species of stimulus fish (bonefish, mojarra, and pilchard) were held in separate tanks with their conspecifics in larger pens (0.90 m length × 0.3 m width × 0.2 m height; 0.3 cm mesh size). Focal fish and stimulus fish received the same level of handling and overall had the same treatment and level of care. All fish were held for a minimum of 48 h prior to experimentation. All fish

Table 1

Combinations of species and shoal sizes that each focal juvenile bonefish was exposed to in independent trials. BF = bonefish, MO = mojarra, PI = pilchard.

Experiment 1								
Species combinations	BF or MO	BF or PI	BF or MO	BF or PI	BF or MO	BF or PI	BF or MO	BF or PI
Shoal size	1 × 1	1 × 1	2 × 2	2 × 2	4 × 4	4 × 4	8 × 8	8 × 8
Experiment 2								
Species combinations	4 BF or 2 BF + 2 MO			4 MO or 2 BF + 2 MO				
Shoal size	4 × 4			4 × 4				

were fed cut up shrimp ad libitum at the end of trials each day and were monitored for health including consistent levels of activity, feeding, and body coloration.

2.3. Shoaling trials

Each focal fish ($n = 25$) was observed in two experiments, made up of a total of ten different stimulus shoal combinations/trials (Table 1). Due to the length of time required to complete all trials, there were three sets of focal fish run through all trials consecutively. Individuals 1–10 were tested between June 12–29, individuals 11–17 were tested between July 10–20, and individuals 18–25 were tested between July 27–August 5, 2015 – each focal fish had ten days of experimentation, with every fish in each set tested in a random order on each of the 10 days. There were two experiments conducted; the first examined shoaling preference when given the choice between two single-species shoals of four different shoal size (eight trials total), and the second examined the tendency to shoal with a mixed shoal or a single-species shoal (two trials total). Each focal fish's shoaling response was tested by giving the option of shoaling with the following groups of fishes: Experiment 1 – (i) conspecifics or mojarra; (ii) conspecifics or pilchard; Experiment 2 – (iii) conspecifics or a mixed shoal with equal mojarra and bonefish; and (iv) mojarra or a mixed shoal with equal mojarra and bonefish. Experiment 1 included eight trials with the above species and shoal size combinations. Focal fish shoaling preference was examined with four stimulus shoal combinations (one combination per trial), with either one-, two-, four-, or eight- fish in each stimulus shoal (i.e., 1×1 , 2×2 , 4×4 , 8×8); that is, each focal fish in a trial was given the choice between one mojarra or one bonefish, two mojarra or two bonefish, one pilchard or one bonefish, and so on. Therefore, focal fish were tested in four shoal size combinations with conspecifics or mojarra, as well as four shoal combinations with conspecifics or pilchard (Table 1).

Experiment 2 aimed to determine the shoaling tendencies of focal fish when given the opportunity to shoal with a single-species shoal or a mixed shoal. The focal fish was given the choice of either: (iii) four conspecifics or a mixed shoal of two conspecifics and two mojarra (i.e., a 4×4 design) in one trial; and (iv) four mojarra or a shoal of two conspecifics and two mojarra (herein referred to as a 'mixed shoal') in the other trial.

A single Y-maze (0.7 m arm lengths × 0.18 m width × 0.25 m height) was utilized as the experimental arena. Methods were modified from Wright and Krause (2006). One arm of the Y-maze was the focal fish release area, with the other two arms housing the two stimulus shoal options. Each stimulus shoal was in a one-way glass transparent bin (18 cm length × 18 cm width × 20 cm height; 6.5 L) at the end of each respective arm, with a daylight emulating light bulb (Lighting Science Group, Satellite Beach, Florida, United States of America; 60 watt) 30 cm above each stimulus fish bin for greater efficacy of the one-way glass (modifications made from Wright and Krause, 2006). There

was no olfactory exchange between the focal fish and stimulus shoals; due to the one-way glass, focal fish were able to see the stimulus shoals without the opposite occurring (see Wright and Krause, 2006). Stimulus shoals were given 1 h to acclimate to holding bins prior to experimentation. A focal fish was removed from its individual holding pen and first placed in an opaque beaker (14 cm diameter × 15 cm height; 2.3 L) with water from the test tank and left to acclimate for 10 min. After 10 min, the fish was gently poured into a transparent cylinder (15 cm diameter × 30 cm height) in the empty arm of the Y-maze and left to acclimate for another 5 min. Following this final acclimatization period, the focal fish was released and observed via live video feed for 20 min (DVR9–4200 9 Channel 960H Digital Video Recorder and PRO-642 Cameras; Swann Communications U.S.A Inc.; Santa Fe Springs, California, United States of America). The observer recorded seconds spent close-shoaling with either stimulus shoal, quantified as being within approximately two body lengths (20 cm) of the stimulus shoal (Pitcher 1986). After the 20 min trial, the focal fish was moved back to its individual pen and the process was repeated with another randomly selected focal fish. Stimulus shoal position in the Y-maze was changed every five trials, with stimulus shoal individuals also being changed occasionally to prevent shoaling bias (Wright and Krause, 2006).

2.4. Statistical approach

All analyses were conducted using R version 3.3.1 (R Core Team 2016). For both (i) bonefish or mojarra treatments, and (ii) bonefish or pilchard treatments, linear mixed effects models (LME) were fit to square root transformed time (sec) spent with each species to meet statistical assumptions. Stimulus shoal species (bonefish or mojarra; bonefish or pilchard) and shoal size (1×1 , 2×2 , 4×4 , 8×8) were included as predictors, as was the interaction between shoal species and shoal size. Focal individual was included as a random effect to account for interdependence in the behaviors exhibited by a given fish across observations. A backward model selection approach was used to determine significant predictors by comparing full models to those with reduced terms with likelihood-ratio tests (Zuur et al., 2009). When significant predictors were identified, a Bonferroni post-hoc test was used to determine which stimulus shoal species and shoal sizes were significantly different. An analogous approach was also used to compare the time that focal fish spent alone, or not shoaling, between the two different heterospecific stimulus shoal alternatives presented in Experiment 1 (i.e., mojarra and pilchards). For the mixed shoal experiments, time focal bonefish spent with (iii) conspecifics or a mixed shoal with equal mojarra and bonefish, and (iv) mojarra or a mixed shoal with equal mojarra and bonefish were analyzed using paired t -tests. Parametric assumptions were checked prior to analysis and the data were square root transformed to meet the assumption of normality. Statistical comparisons were considered significant at an alpha level of 0.05, with the exception of cases where Bonferroni correction was applied.

3. Results

3.1. General behavior of stimulus shoals

During experimental trials, species comprising stimulus shoals exhibited differing behaviors that were largely consistent with their varying ecologies and habits in the wild. Shoals of all three species were loosely aggregated, with individuals moving haphazardly around the tank space and displaying little in the way of clear directionality or coordinated movement. Nonetheless, pilchard shoals tended to be more tightly organized and densely clustered than those of bonefish or mojarra, maintaining smaller intra-individual distances. Marked differences in activity level were evident across the three species; mojarra were the most passive, exhibiting a “stop and go” pattern of movement that included long periods of hovering in place. Bonefish, in contrast, swam more continuously, and pilchards were by far the most active, swimming constantly and at a notably faster rate. Individuals of all three species were present throughout the water column, however bonefish and mojarra were more concentrated near the bottom of the tank, while pilchards showed a more even vertical distribution.

3.2. Bonefish or mojarra stimulus shoals

In treatments with bonefish or mojarra as the stimulus shoal choices, focal bonefish spent significantly more time shoaling with mojarra than conspecifics (Fig. 2a); focal fish spent over three quarters of the 20 min trial observation period engaged in a shoal, with 73% of that time spent shoaling with mojarra. In many instances, focal fish would explore the experimental arena (i.e., investigate both shoal options) and then choose to shoal closely with mojarra. There was a significant interaction between stimulus shoal species and shoal size (LME; $X^2 = 19.3, p < .001$). Bonefish spent significantly more time with mojarra in shoal sizes of one, four, and eight (Tukey’s HSD; $p < .001$); however, despite also spending marginally more time with mojarra in shoal sizes of two, the difference in this treatment was not significant (Tukey’s HSD; $p = 1.0$; Fig. 2a).

3.3. Bonefish or pilchard stimulus shoals

Juvenile bonefish generally tended to spend a similar amount of time with conspecifics, pilchard, and non-shoaling during the 20 min trial (Fig. 2b). It was common for focal fish to swim around the experimental arena to all of the arms several times (i.e., entering and exiting shoaling zones), often without making a discernible choice to join either stimulus shoal for any substantial period. When comparing focal fish shoaling tendencies between conspecifics or pilchard, there was no significant interaction between shoal species and shoal size ($X^2 = 2.8, p = .42$), nor was there a significant effect of shoal species ($X^2 = 0.06, p = .8$) or shoal size ($X^2 = 0.5, p = .9$) on juvenile bonefish shoal choice (Fig. 2b). From the perspective of time spent not shoaling (i.e., not within the shoaling zone of either stimulus species), when comparing the mojarra and pilchard treatments, there was no effect of shoal size ($X^2 = 0.36, p = .95$), nor was there an interaction between stimulus species and shoal size ($X^2 = 1.14, p = .77$). However, there was a highly significant effect of stimulus species overall ($X^2 = 45.8, p < .001$), with focal bonefish spending nearly twice as much time not shoaling in the pilchard treatments (mean = 497 ± 258 s SE) than in the mojarra treatments (mean = 272 ± 251 s SE).

3.4. Bonefish or mixed stimulus shoals

When given the choice between bonefish or mixed shoals, focal fish preferred to spend more time shoaling with the mixed shoals of bonefish and mojarra than with the conspecific shoal (Fig. 3a); focal fish were engaged with a shoal nearly three quarters of the 20 min observation period, with 66% of that time spent shoaling with the mixed shoal. There was a significant difference between time spent shoaling with bonefish (mean = 263 ± 63 s SE) and time spent shoaling with the mixed shoal (mean = 619 ± 79 s SE). Focal fish spent significantly more time shoaling with the mixed shoal than with conspecifics ($t = -2.6, df = 24, p = .02$).

3.5. Mojarra or mixed stimulus shoals

Contrary to the results of the bonefish or mixed shoal treatments,

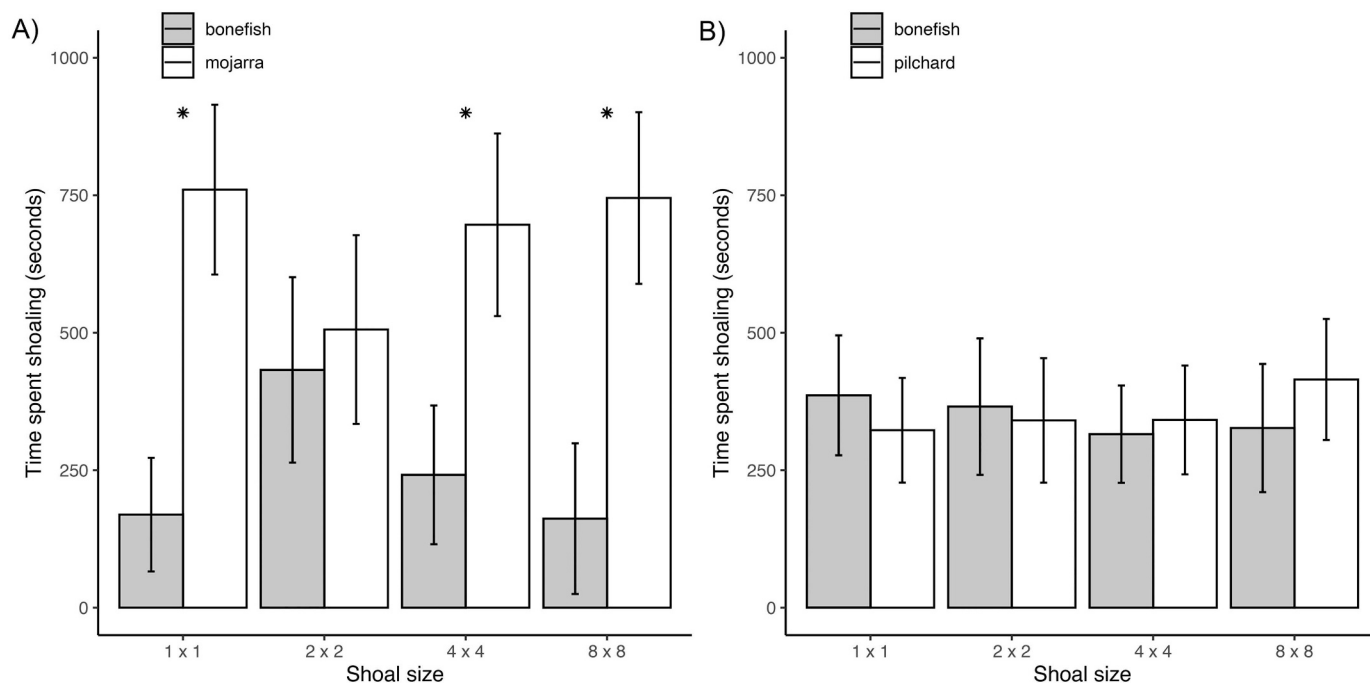


Fig. 2. Mean responses (\pm SE) of time focal bonefish spent (in seconds) shoaling with other bonefish or mojarra (2a), and time spent (in seconds) shoaling with bonefish or pilchard (2b) in stimulus shoal sizes of $1 \times 1, 2 \times 2, 4 \times 4, 8 \times 8$. Asterisks (*) denote significant differences between species in each shoal size.

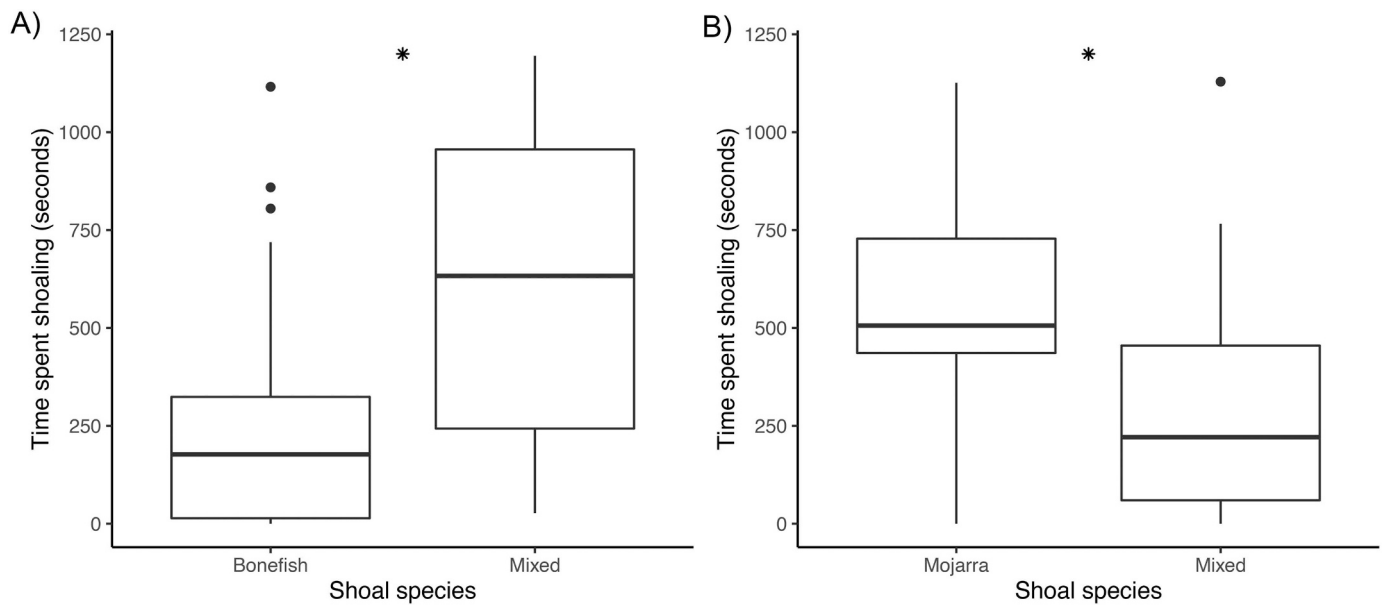


Fig. 3. Box-and-whisker plot of time focal bonefish spent (in seconds) shoaling with four bonefish or a mixed shoal of two bonefish and two mojarra (3a), and time focal bonefish spent (in seconds) shoaling with four mojarra or a mixed shoal of two bonefish and two mojarra (3b). The horizontal bold line within the box indicates the median of the data, while the boundaries of the box indicate the 25th and 75th percentiles, and the whiskers denote upper and lower data points outside the middle 50th percentile. Asterisks (*) denote significant differences between single species and mixed species shoals.

focal fish preferred to shoal with the mojarra stimulus shoal, rather than spending their time with the mixed shoal (Fig. 3b); similarly focal fish spent nearly three quarters of the 20 min trial engaged with a shoal, with 70% of that time spent shoaling with mojarra. There was a significant difference between the time focal fish spent shoaling with mojarra (mean = 581 ± 62 s SE) and time spent shoaling with the mixed shoal (mean = 291 ± 56 s SE). The focal fish in this treatment spent significantly more time with mojarra than with the mixed shoal ($t = 2.8$, $df = 24$, $p = .01$).

4. Discussion

Our experiments demonstrate that *A. vulpes* juveniles prefer to join mojarra over conspecifics across a variety of different social contexts, providing compelling behavioral evidence that their small conspecific group sizes and habitual co-occurrence with mojarra in nature are not artifacts of chance, but rather reflect the active selection of shoaling partners by bonefish. Although prior observations (Haak et al., 2019; Haak et al., 2020) led us to surmise that bonefish would display a discernable affinity for mojarra (certainly exceeding that for ecologically-distinct pilchards), we did not necessarily expect that the strength of this attraction would so conclusively surpass that for members of their own species. Examples of such behavior are rare in the literature, which shows that fish almost invariably favor conspecifics over heterospecific shoalmates (Krause et al., 2000; Ward et al., 2002), making *A. vulpes*' predilection for mojarra over conspecifics somewhat anomalous and implying that this behavior carries a unique adaptive significance, presumably conferring fitness advantages. Although we did not explicitly evaluate the nature of these putative benefits, when viewed within the context of previous research our findings nonetheless permit some reasonable inferences regarding the likely tradeoffs that drove observed grouping preferences.

If one accepts the common assumptions that risk dilution and predator confusion are among the primary motivators of grouping, and likewise that these numerical benefits are diminished by oddity effects and thus maximized when shoals are phenotypically homogenous, then, holding all other factors equal, conspecifics should generally be favored over morphologically distinct heterospecifics as shoal partners (Mathis and Chivers, 2003; Rodgers et al., 2011). Given their low relative

abundance within mixed shoals, juvenile bonefish inherently take on a degree of conspicuity by joining mojarra, however focal individuals demonstrated an unequivocal preference for mojarra in all but one (i.e., the 2×2) of six different experimental treatments (Fig. 2a; Fig. 3). This routine choice to join phenotypically distinct individuals implies either that the risks associated with oddity are relatively small, or that they are outweighed by the (yet unknown) advantages of joining mojarra. Indeed, mixed shoal treatments presented juvenile bonefish with the opportunity to participate in groups containing both conspecifics and mojarra, theoretically providing “the best of both worlds” by permitting access to any benefits obtained from being in the company of mojarra while also serving to reduce the focal individual's conspicuity by allowing them to remain among the dominant phenotype in the group (Ruxton et al., 2007). Notwithstanding, bonefish in this treatment still elected to join shoals containing the greatest proportion of mojarra and/or the smallest possible contingent of conspecifics, reinforcing the notion that oddity was not an overriding consideration in group choice.

An equally unforeseen experimental outcome was focal fishes' apparent indifference for conspecifics versus pilchards, between which they tended to divide their time uniformly (Fig. 2b). While not in itself remarkable when contrasted with bonefishes' atypical preference for mojarra, the lack of a detectable bias is made noteworthy by the pronounced ecological discrepancies that exist between the focal species (bonefish) and pilchards. Other instances of such ambiguity in shoal choice typically involve phenotypically-similar stimulus species with whom the focal species is known to affiliate in nature (e.g., Quattrini et al., 2018). However, bonefish are not known to join pilchard shoals in nature and (beyond a coarse superficial resemblance) share very little in common with pilchards, whose disparate resource use regimes, patterns of water column utilization, and general social behaviors likely served only to magnify the phenotypic oddity of focal individuals. It thus goes without saying that conspecifics should make far more attractive partners from the perspective of maintaining shoal homogeneity, yet observed behaviors did not follow this expectation. Accordingly, it may be inferred that bonefish experience relatively little of the strong selective pressure for phenotypic homogeneity that is conventionally thought to give rise to a preference for conspecifics, or likewise that this pressure is superseded by other more pressing

considerations.

As much as the shoaling preferences revealed here might be perceived as reflecting an affinity for mojarras on the part of juvenile bonefish, they may likewise be interpreted as manifesting the absence of an attraction to (or possibly even an avoidance of) conspecifics. Focal individuals' partiality towards mojarras over members of their own species, and even more so their seeming ambivalence when presented with a choice between conspecifics and morphologically-and-ecologically-distinct pilchards, may signal that conspecifics are particularly unappealing partners, offering little in terms of group-related fitness benefits for juvenile bonefish. Indeed, the much greater amount of time that focal fish spent not shoaling (i.e., alone) in the pilchard stimulus treatments (versus the mojarra treatments) indicates an increased willingness on the part of bonefish to accept the risks of being solitary and/or the costs of switching shoals, perhaps in exchange for the chance of encountering better partners (Krause and Godin, 1994; Ranta et al., 1994).

The relative unattractiveness of conspecific partners might indicate the presence of vigorous intraspecific food competition between *A. vulpes* juveniles, which can in turn give rise to aggression and other costly agonistic interactions (reviewed by Ward et al., 2006). In this event, assuming that resource use overlap is lesser between heterospecifics than conspecifics, juvenile bonefishes' participation in mojarra shoals may represent an adaptation which serves to help circumvent or mitigate the basic competitive costs of joining others. In fact, analogous mechanisms have been offered to explain an apparent preference for heterospecifics and/or avoidance of conspecifics in other marine fishes (Robertson et al., 1976; Debrot and Myrberg, 1988; Overholtzer and Motta, 2000). The above assumption regarding trophic niche overlap is likely to hold true in the case of bonefish and mojarras, which exhibit notable differences in their foraging behaviors, the predominant sensory modes they employ for prey detection, and in the functional morphology of their feeding apparatuses, factors that commonly mediate niche partitioning between other soft-sediment benthivores (Labropoulou and Eleftheriou, 1997; Zahorcsak et al., 2000; Schwalbe and Webb, 2014).

What unique fitness benefits might juvenile bonefish accrue by affiliating with mojarras? As proposed by Haak et al. (2020), the attraction of bonefish to mojarras may be motivated by the exploitation of risk or resource-related social cues generated by the latter, whose ecological traits imply a high propensity for the detection and conveyance of information (following Goodale et al., 2010). For example, bonefish may more efficiently locate patchily-distributed benthic prey by taking advantage of cues produced by foraging mojarras, who possess specialized auditory physiology which permits them to detect buried or otherwise obscured benthic organisms (Green, 1971; Parmentier et al., 2011). As likewise suggested by Haak et al. (2020), bonefish may also reduce their vulnerability to predation by "eavesdropping" on threat-related cues produced by mojarras, whose sensory abilities and intermittent search strategy together connote a high potential for antipredator awareness (McAdam and Kramer, 1998; Kramer and McLaughlin, 2001). The collective shoal choice preferences displayed by focal fish in this study provide support for the prospective role of information in driving observed association patterns (Haak et al., 2020), aligning well with theoretical predictions that functionally similar heterospecifics, with overlapping but not identical niches, should be the most profitable sources of socially acquired knowledge (Seppänen et al., 2007). Moreover, the large conspecific schools in which adult bonefish regularly participate mark a pronounced departure from the grouping preferences documented among juveniles in the present study, an ontogenetic shift in social behavior that may be explained by the greater relevance of information on predators and prey between heterospecifics as juveniles, when size-related ecological constraints lead to greater niche overlap between the species (Haak et al., 2020).

One might interpret the seemingly limited weight placed on

phenotype matching as evidence that basic numerical grouping benefits like risk dilution or predator confusion (which are often thought to depend on shoal homogeneity) were not among the foremost likely advantages to be obtained by joining mojarras. Nevertheless, others have shown that heterogeneous shoals and loosely associated participants (i.e., those not exhibiting coordinated behaviors) can still profit from the predator confusion effect (Ruxton et al., 2007), so that access to such benefits may still play a role in driving the observed grouping preferences. Likewise, recent developments in the understanding of the sensory mechanisms behind the predator confusion effect suggest that shoal heterogeneity may even benefit some group members; specifically, cryptic fishes may further diminish their own detectability by joining more conspicuous ones (Tosh et al., 2006; Tosh et al., 2007; Rodgers et al., 2013). Although bonefish and mojarras are characterized by outwardly similar forms and degrees of crypsis, subtle asymmetries may nonetheless exist, potentially promoting bonefish's association with mojarras.

It is also possible that mojarras experience fitness costs imposed by the presence of bonefish in mixed shoals. Such penalties often come in the forms interference competition or kleptoparasitism (e.g., Webster and Hart, 2006); however the aforementioned evidence of niche partitioning between bonefish and mojarras, and the lack of discernable agonistic interactions among heterospecific shoal participants (in video surveys) together suggest that any such losses are not large (Haak et al., 2020). Furthermore, given the nominal representation of bonefish in free-ranging mojarra shoals (i.e., 1% of individuals), any such costs of interspecific competition are probably negligible compared to the costs of intraspecific competition among mojarras. Alternatively, all shoal members may face an increased threat of predation due to the presence of an odd individual such as a bonefish (Landeau and Terborgh, 1986; Quattrini et al., 2018).

Our findings with respect to the seeming absence of attraction to conspecifics are partly at odds with observations from in-situ underwater video surveys, which showed that although occurring in very low frequencies, juvenile bonefish were often present in small, loosely clustered conspecific groups of 2 to 5 individuals nested within much larger mojarra shoals (Haak et al., 2020). This apparent incongruity may be related to the maximum shoal sizes used in our study, which were limited by practical considerations (i.e., fish availability, handling concerns, and arena size) to a maximum of 8 individuals and therefore, while within the range of those encountered in nature, were still small compared to the typical size of wild shoals (which often comprise tens to hundreds of individuals). It thus seems probable that bonefish may grow increasingly tolerant of the presence of conspecifics when mojarras are more abundant, a pattern of behavior that is loosely consistent with theorized group-size constraints on producer-scrounger relationships (Barnard and Sibly, 1981; Vickery et al., 1991), perhaps lending further support to the potential role of information in driving observed patterns.

It is likewise plausible that discrepancies in shoal structure as observed in the laboratory and in nature reflect the influence of "familiarity" (Ward and Hart, 2003) between *A. vulpes* shoalmates. Regular interactions among bonefish in the wild may lead to individual-level recognition between certain fish, which can subsequently affect shoaling choices by reducing aggression or even promoting affiliation between familiar conspecifics, facilitating larger group sizes. Meanwhile, our focal individuals were obtained from many distinct collection efforts and held in isolation, largely precluding the development of such relationships. With that said, the overall low observed abundances of juvenile bonefish and their correspondingly small group sizes in nature suggest familiarity would regardless play a limited role, however the fission-fusion dynamics of these groups 'within' a (mojarra) shoal are still unknown.

Other challenges associated with studying wild fish populations (Ostrander, 2000) influenced our experimental design and possibly our observed outcomes. Among these, juvenile bonefish tend to be highly

dispersed and thus present in low densities, making their capture unusually challenging and time-consuming, and placing constraints on overall sample size as well as stimulus shoal sizes. The reduced statistical power resulting from sample size limitations may offer an explanation for the incongruity presented by the 2×2 treatment of experiment 1, in which, despite significant differences for all other group sizes, we did not detect a significant preference for mojarras over conspecifics. Alternatively, there may be an unknown ecological implication associated with this treatment (i.e., stimulus shoal individuals in the 2×2 were less social, or group sizes of two are unattractive; e.g., Cote et al., 2012; Laskowski and Bell, 2014), and as such future investigation of this phenomenon is warranted.

Shoal choice decisions can be influenced by both visual and olfactory cues which can sometimes elicit distinct or conflicting responses (Ward et al., 2004; Webster et al., 2007). Our experimental design exposed focal fish only to visual cues, and therefore it is possible that distinct shoaling preferences could emerge in response to other forms of stimuli. Likewise, several previous works have found that shoaling preferences are influenced by extrinsic factors and can vary across contexts, such as differing levels of perceived predation risk or resource availability (Allan and Pitcher, 1986; Mathis and Chivers, 2003). Moreover, the same factors have been shown (theoretically) to affect the fitness gains obtained through social information, with consequences for optimal grouping behavior (Gil et al., 2017). Accordingly, future studies may consider manipulating these variables to evaluate how observed preferences covary (e.g., Ward et al., 2003).

Collectively, the grouping preferences elucidated in this study corroborate inferences drawn from field-based observations and permit limited insights on the relative importance of different factors in producing observed shoal structure, however the underlying mechanisms that govern these decisions remain unclear. Even so, it seems obvious that bonefish derive some fitness advantages by joining mojarras, of which socially acquired information on shared predators and/or prey appears to be one likely candidate (Haak et al., 2020). On the other hand, mojarras might simply serve as a convenient, phenotypically similar and readily available surrogate through which bonefish procure more basic numerical benefits while also limiting their costs of competition. Yet the strong positive associations documented in the wild between several other species and eucinostomids (Sazima, 2002; Haak et al., 2020) insinuate that mojarras may confer unique benefits. Similar shoal choice experiments involving a broader range of focal species may aid in unraveling the nature of these relationships. More broadly, this work mirrors findings of other recent studies which show that pressure for shoal homogeneity is perhaps less universal than previously thought, because oddity may interact with or be overridden by other concerns (Mathis and Chivers, 2003; Rodgers et al., 2013; Quattrini et al., 2018).

Author statement

Szekeres and Haak contributed to experimental design, data collection, data analysis, and manuscript preparation. Wilson contributed to study design, data collection, and manuscript preparation. Brownscombe contributed to study design, data analysis, and manuscript preparation. Danylchuk, Shultz, and Cooke contributed to study design and manuscript preparation.

Declaration of Competing Interest

None.

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