



Sociable bluegill, *Lepomis macrochirus*, are selectively captured via recreational angling

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Individuals often show considerable variance in social behaviour and aggression, leading to defined social roles. Removal of individuals with particular roles from groups may have impacts on group function, leaving those groups less able to locate critical resources and avoid danger. In recreational fisheries, capture by humans constitutes a mortality risk, and therefore angling has the potential to fundamentally alter social structure in exploited populations if individuals with defined social roles are disproportionately captured. However, little work has examined the linkage between social behaviour and angling vulnerability. To address this gap, we conducted a study on bluegill, *Lepomis macrochirus*, a freshwater fish known to be socially gregarious, and a common target of recreational anglers in North America. Fish were angled in a naturalistic pond setting, and a subset of captured and uncaptured fish was then assessed for sociability in a shoaling assay and aggression/dominance in paired dyadic contests. Results showed a significant effect of time spent in the social zone on capture status, with captured individuals spending significantly more time near a transparent divider separating it from a shoal of conspecifics compared to uncaptured fish. Dominance was not associated with angling vulnerability, and sociability was not linked with dominance. Collectively, these results show that more social bluegill are more likely to be captured by anglers. This could in turn lead to decreased social functionality in exploited populations as a result of the removal of particularly social individuals, as well as possible evolution of social behaviour in exploited populations due to this selection.

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Interactions among individuals within a population are often dictated by overarching social structure. Many species form herds, shoals or loosely tied aggregations that provide for mutual protection and the acquisition of crucial resources to group members (Dyer, Croft, Morrell, & Krause, 2009; Krause, Croft, & James, 2003; Sih, Hanser, & McHugh, 2009). Social groups are often hierarchical, and group members may adopt specific roles based on their size, age, experience and behavioural tendencies (Croft, Darden, & Ruxton, 2009; Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014). The consistent behavioural tendencies of an individual are often collectively referred to as its 'personality', while the term 'behavioural syndrome' refers to sets of traits that are correlated across a population of individuals (Bell, 2007; Réale et al., 2010). An individual's sociability, defined as the tendency to associate with

conspecifics, is considered a major axis of animal behaviour and a significant determinant of social position within a hierarchy (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Within these social groups, certain individuals may be critical to group cohesion, and the loss of such individuals can lead to a cascading loss of social function for the entire group (Modlmeier et al., 2014). These critical individuals may be leaders that obtain that position as a result of their behavioural dominance (Burns, Herbert-Read, Morrell, & Ward, 2012; Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009), individuals that have acquired important knowledge that is of benefit to other group members (Franks & Marshall, 2013; Jolles et al., 2014), or highly social individuals that quickly spread such information throughout an entire group (Vital & Martins, 2013). Since individual behavioural characteristics (such as sociability and aggression) are likely to determine what role an individual occupies, understanding how these individual traits drive mortality risk is crucial in order to predict how group function may be impacted by the selective mortality of individuals with particular traits.

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Selective mortality for social species can come in the form of harvest, where individual characteristics predispose game animals to greater risk. For instance, more active elk, *Cervus canadensis*, have been found to be more vulnerable to hunters (Ciuti et al., 2012), while it has been posited that highly social spiny lobsters, *Panulirus argus*, are more likely to form tight congregations in traps, leading to capture (Childress, Heldt, & Miller, 2015). Indeed, the propensity for individuals with particular behavioural traits to be more likely to be captured in traps or other gear has been demonstrated in reptiles (Michelangeli, Wong, & Chapple, 2016) as well as fish (Olsen, Heupel, Simpfendorfer, & Moland, 2012; Pauli, Wiech, Heino, & Utne-Palm, 2015). Within the specific context of fishing, selective harvest of individuals with key behavioural, physiological or life history characteristics has been shown to lead to evolutionary change in exploited marine (Eikeset, Richter, Dunlop, Dieckmann, & Stenseth, 2013; Kuparinen & Merila, 2007) and freshwater (Kendall & Quinn, 2011; Philipp et al., 2009) recreational systems, a process known as fisheries-induced evolution (Diaz Pauli & Sih, 2017). Fisheries-induced evolutionary changes can lead to major impacts on the viability of exploited populations (Jørgensen et al., 2007). With regards to behaviour, studies examining links between angling vulnerability and individual traits have largely focused on two behavioural axes (Réale et al., 2007) that may evolve in response to selective capture – individual boldness and exploratory tendency (Alós, Palmer, Rosselló, & Arlinghaus, 2016; Härkönen, Hyvärinen, Paappanen, & Vainikka, 2014; Wilson, Binder, McGrath, Cooke, & Godin, 2011), with a typical finding that bolder and/or more exploratory individuals are more likely to approach lures and strike, leading to capture (Klefoth, Pieterek, & Arlinghaus, 2013; Klefoth, Skov, Kuparinen, Arlinghaus, 2017). A third behavioural axis, sociability, has rarely been studied in this context (but see Mourier, Brown, & Planes, 2017). Sociability is also often linked with aggression in individuals (Øverli et al., 2004; Weeks, Crowell-Davis, Caudle, & Heusner, 2000), another understudied behavioural axis in the context of angling vulnerability (but see Sutter et al., 2012). In the case of aggression, it might be expected that individuals that are aggressive towards other individuals could also be more aggressive in striking lures (Sutter et al., 2012). With regards to sociability, prior work has shown that social tendencies impact various aspects of an individual's ecology, such as its habitat choice (Budaev, 1997; Webster & Hart, 2006), which may in turn lead fish to be more vulnerable by causing them to frequent areas targeted by anglers (Matthias, Allen, Ahrens, Beard, & Kerns, 2014; Monk & Arlinghaus, 2018). Furthermore, intrinsic sociability may lead individuals to select differing social settings, for instance, large groups where intense competition for food (Stoner & Ottmar, 2004; Ward, Webster, & Hart, 2006) may leave individuals more likely to strike a baited hook. Collectively, social behaviour and/or aggression may well be linked to angling vulnerability, but work examining this potential relationship is currently scarce.

To better understand whether individuals that differ in their vulnerability to angling also differ in their sociability or aggression, we conducted a laboratory study utilizing bluegill, *Lepomis macrochirus*. Bluegill are a semi-gregarious freshwater fish species that form social hierarchies based on aggressive interactions (Gaeta, Beardmore, Latzka, Provencher, & Carpenter, 2013; Lorenz, O'Connell, & Schofield, 2011) and are commonly targeted by anglers throughout much of North America. To define the relationship between angling vulnerability and social behaviours, we first subjected a population of bluegill to a series of angling trials in a natural pond environment. Next, we tested a subset of captured and uncaptured bluegill for sociability in a behavioural arena and for aggression in a dyadic contest. This work is among the first to examine the role of social behaviour broadly in driving angling

vulnerability, a relationship that could have evolutionary significance if these characteristics are indeed subject to angling selection in exploited systems.

METHODS

Study Site and Experimental Animals

We conducted all experiments at the Illinois Natural History Survey's Aquatic Research Facility using 151 adult bluegill acquired from Jake Wolf Fish Hatchery in Topeka, Illinois, U.S.A. on 4 June 2016. While bluegill were not aged over the course of this study, based on their lengths it is likely that all fish were at least 3 years old when they were acquired (Peterson, VanDeHey, & Willis, 2010). Mean (\pm SD) total length among study fish was 16.7 ± 6.5 , and mean weight was 80.4 ± 11.2 g. Bluegill acquired from the hatchery had been reared in a natural lake environment featuring natural forage and aquatic predators such as largemouth bass, *Micropterus salmoides*, and muskellunge, *Esox masquinongy*. While bluegill in this environment had to evade predators, they had not been previously exposed to angling pressure. Upon arrival at the Aquatic Research Facility, all fish were first implanted with a passive integrated transponder (PIT) tag (0.8 cm, 0.027 g, implanted in the body cavity) for individual identification before being stocked into a single 0.04 ha experimental pond. The pond featured an earthen bottom and native macrophytes for cover, and fish were able to forage on stocked mosquitofish *Gambusia* spp. as well as naturally occurring macroinvertebrates.

Angling Trials

We conducted angling sessions in the experimental pond over 5 days, on 13–15 and 20–21 June. All sessions were conducted by two experienced anglers. Each day of angling consisted of one 90 min session beginning at 0700 hours, followed by a second 90 min session beginning at 1730 hours. Both the morning session and the evening session were divided into three 30 min periods, and the shoreline of the angling pond was divided into two sections of equivalent length (approximately 40 m of shoreline). At the outset of the first period, an angler was randomly assigned to each of the two sections of the pond where they fished for 30 min, moving around the shoreline so as to target all possible areas of the pond within that section. After this period, the anglers switched sections and fished for a second 30 min period, and the process was repeated a third time for the third period. Both anglers used light-action spinning rods spooled with 1.8 kg Berkley® Trilene monofilament fishing line for all sessions, as is typical for bluegill anglers. The lure presentation consisted of a size 12 Eagle Claw® J-Hook baited with Berkley® Crappie Nibbles in one of three colours (chartreuse, pink, white). During each period, anglers used a different colour bait as determined by random selection. Upon capture, the hook was immediately removed from the fish, the identity of the individual fish was determined via PIT tag, and the fish was returned to the pond no more than 1 min after capture. All captured fish except one were hooked superficially in the mouth, allowing for easy dehooking; the one fish that was 'deep-hooked' was removed from the study to avoid the complications of a more prolonged dehooking time on its subsequent behaviour. A total of 40 fish were captured at least once, with only a single fish being captured twice.

Fish Holding

On 22 June, the pond was drained, 141 of the original 151 bluegill were recovered, and a subsample of 19 captured and 19 uncaptured

fish were haphazardly selected to be assessed for sociability and dominance. The remaining fish were used to populate stimulus shoals during sociability trials (see below). Initially, we selected 32 captured and uncaptured fish for behavioural testing, however, during the holding period, abnormally warm ambient temperatures over a 3-day period combined with an unexpected failure of the flow-through pump system led to the death of 19 of the 64 fish across a subset of the holding tanks. Following this event, we placed the remaining fish in the impacted tanks across the remaining holding tanks in order to ensure that each experimental fish experienced a tank environment that included a similar density of conspecifics. In the immediate aftermath of this event, we removed an additional two fish from the experiments due to listless behaviour in the tank and a lack of feeding motivation, indicating stress. An additional five fish showed no signs of stress, but they could not be paired successfully with an 'unfamiliar' fish during dyadic trials (see below), which began 6 days after the conclusion of the mortality event. Given that the remaining fish were feeding normally and displaying typical behaviour, and because this time frame has been found to be sufficient to allow for recovery in bluegill previously (McConnachie, O'Connor, Gilmour, Iwama, & Cooke, 2012), we did not expect that this event would have impacted the subsequent behaviour of the fish. Holding tanks for bluegill consisted of one of several circular 1135-litre outdoor holding tanks, where fish were fed daily with frozen bloodworms (Chironomidae). Holding tanks were equipped with a flow-through pump system that continuously circulated water from an adjacent pond into the holding tanks at a rate of approximately eight full water exchanges per tank per day. An equal number of captured and uncaptured fish were put into each holding tank prior to experimentation in order to avoid any possible tank effects that might lead to systematic differences in behaviour between captured and uncaptured fish. With regards to the possible impacts of angling stress on the captured fish, because fish typically recover from the stress of angling within 24 h (Cooke & Schramm, 2007; Cooke et al., 2003), we did not anticipate any impact of the angling event on the subsequent behaviour. Indeed previous studies have taken the approach of subjecting fish to angling prior to an assessment of individual behaviour or physiology (Härkönen, Hyvärinen, Niemelä, & Vainikka, 2016; Louison, Adhikari, Stein, & Suski, 2017; Wilson et al., 2011).

Shoaling Trials

The evening before shoaling trials were conducted, we placed focal fish individually into a 27-litre black plastic isolation box to prevent potentially confounding social interactions among trial subjects. Each isolation box was connected to a recirculation system that continuously provided oxygenated water from a common reservoir tank. Water temperature in the isolation tanks was maintained near 22 °C by a Teco® Heater-Chiller (Ravenna, Italy) that recirculated water within the reservoir tank. We designed shoaling trials to assess the willingness of an individual to associate near conspecifics on the opposing side of a transparent barrier, based on methods described in previous studies (Cote, Fogarty, & Sih, 2012; Jolles et al., 2014; Ward, Thomas, Hart, & Krause, 2004). Social behaviour was assessed only in the 38 focal fish (i.e. 19 captured and 19 uncaptured), while the remaining fish that were recovered from the pond were used to populate shoals for the purpose of this test. Trials were conducted in one of two behavioural arenas consisting of 565-litre (181 cm long × 65 cm wide) rectangular polyethylene stock tanks filled with water to a depth of 30 cm. Behavioural arenas were divided in half along their short axis by a clear Plexiglas divider that was punctured by a series of holes that allowed the exchange of water between the sides of the

arena (Fig. 1). A single 15 cm long piece of 7.6 cm diameter PVC piping was placed on one side of the arena to serve as a shelter item for the focal fish. On the day of the trial, a shoal of six conspecifics was drawn from the population of fish in the angling trials that had not been selected for behavioural assessments and placed in the side of the behavioural arena opposite of the focal fish. Over the course of the experiment, each nonfocal fish was used multiple times to populate shoals. By using a reasonably large shoal of nonfocal conspecifics, we increased our chances of having each shoal populated by a mix of behavioural types, preventing potential bias as a result of a focal fish desiring to interact more or less with shoals depending on the behavioural types present in the shoal (Harcourt, Sweetman, Johnstone, & Manica, 2009).

Each trial was filmed with a GoPro® Hero 3 camera positioned directly over a line marking 8 cm from the divider on the focal side of the arena. This area within 8 cm of the divider was referred to as the 'social zone' for the purpose of the experiment. A second line was drawn 24 cm from the divider, the area from that line to the end of the arena away from the divider was designated as the antisocial zone, with the space in-between labelled the 'neutral zone' (Fig. 1). Each trial consisted of a 15 min acclimation period followed by a 15 min trial when behaviours were observed and recorded. During the trial, we determined the total amount of time that each focal fish spent in the social and antisocial zones. Time spent in the social zone was considered a measure of sociability in that greater time spent in the social zone indicated a more social focal fish (Cote et al., 2012). Four days after the first trial, we subjected each focal fish to a second trial to assess the short-term repeatability of shoaling behaviour. Following their second shoaling trial, each fish was returned to their original outdoor holding tank, where they were held until assessment for dominance in dyadic trials.

Dyadic Trials

To quantify social dominance and aggression as it relates to angling vulnerability, we subjected experimental fish to paired dyadic trials conducted in one of eight 37-litre glass aquaria (50 cm long × 28 cm wide × 33 cm high) that were initially divided in half by a removable opaque plastic barrier. Three sides of the aquarium were blocked with opaque plastic sheeting to avoid startling of the fish by observers, and scoring of all trials was conducted by a single observer (lead author M.J.L.) looking in through a small slit in an opaque plastic blind positioned in front of each aquarium. Trials began on 24 July and were conducted and scored based on previously described methods (DiBattista, Anisman, Whitehead, & Gilmour, 2005; Jeffrey, Esbaugh, Vijayan, & Gilmour, 2012). In each trial, two focal fish (one captured, one uncaptured) were size-matched within 5% total length and placed into opposing sides of the divided aquarium. Previous work on the closely related pumpkinseed sunfish, *Lepomis gibbosus*, has demonstrated that, while size is a major predictor of dominance, differences in size of the magnitude used in this study are unlikely to be determiners of dyadic outcomes (Beacham, 1988). Each fish was given a differentiating caudal fin clip (a small clip to either the upper or the lower lobe of the caudal fin) prior to loading to identify it during observations, however, the observer was unaware of which fish was captured and uncaptured when making observations during the trial. We selected pairs of fish for dyadic trials from different holding tanks to ensure that each pair had no prior opportunity to interact with each other during holding. Upon being placed into the aquarium, both fish were immediately fed with bloodworms and allowed to acclimate to the aquaria overnight.

The following morning the divider was removed, and, after a 30 min acclimation period, we initiated behavioural observations.

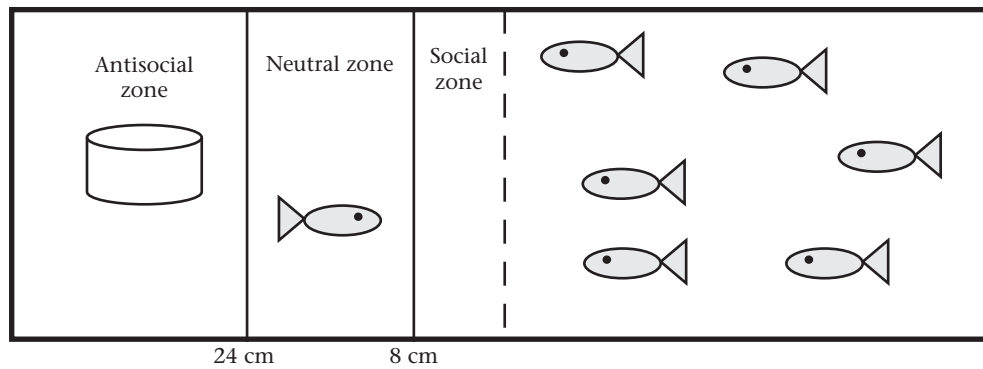


Figure 1. Diagram of the arena used in shoaling trials. The time that the focal fish spent in the social, neutral and antisocial zones was recorded from videos taken during each 15 min trial. The dashed line represents the transparent divider; the area within 8 cm of the divider on the focal's side was the social zone; the area more than 24 cm from the divider on the focal's side was the antisocial zone; the area in between was the neutral zone. A cylinder of PVC piping was used as a cover item for focal fish in the antisocial zone. One focal fish is shown in the neutral zone, with six nonfocal fish in the social zone.

The divider was not replaced over the 2 days of study, allowing the fish to continuously interact. The first behavioural observation for each pair took place between 0830 and 1000 hours, with the second observation taking place between 1430 and 1700 hours. This pattern of a morning and afternoon observation was repeated the following day for each pair, for a total of four behavioural observations over a period of 2 days. Categorical scores describing tank position, feeding, aggressive acts and coloration were recorded during each observation using a scoring method developed based on pilot observations (Table 1). At the outset of the observation, we noted the position of the fish in the tank was noted and categorized it according to one of three possibilities: a 'dominant' position where the fish was actively moving in the centre of the tank, a 'subordinate' position where the fish was found immobile in a corner facing one of the sides of the tank (i.e. skulking) and a 'neutral' position where the fish was found near the bottom but was not in the corner and was still facing inwards, towards the centre of the tank. Next, a small amount of frozen bloodworm was dropped into the tank, and the first fish to feed was noted. Over the next 5 min, we counted aggressive interactions (chases, bites, gill flares, yawning displays) for each fish, and followed that with a second assessment of tank position. Finally, at the conclusion of the observation, we noted the colour of the fish. Because brighter coloration in centrarchids is an indicator of high social status (Howard, 1974), and because subordinate fish featured far darker coloration during the dyadic trial, the fish displaying brighter coloration (especially more prominent orange coloration on the breast and more vivid coloration on the rest of the body) compared to the opponent received one point. If no obvious difference in coloration was present, no points were awarded for either fish. It

should be noted here as well that no differences in coloration were present between any paired fish prior to interactions, meaning differences in colour almost certainly represented differences in social status and stress between the paired individuals. The overall social dominance score of the fish was determined by adding the scores from the four individual observations, with higher scores indicating more dominant individuals. Within this scoring system, position in the tank is weighted heavily, which reflects prior work that shows that commanding the centre position of a tank is the best indicator of dominance (Sloman, Gilmour, Metcalfe, & Taylor, 2000; Sloman, Metcalfe, Taylor, & Gilmour, 2001). Following the conclusion of dyadic trials, the fish were removed from the tanks and returned to the outdoor holding tanks overnight before being stocked into an onsite pond.

Ethical Note

All procedures for experimentation with vertebrate animals adhered to the Institutional Animal Care and Use Committee (IACUC) Protocol no. 16039 at the University of Illinois Urbana-Champaign. Animals were acquired from Jake Wolf State Fish Hatchery in Illinois, where they had been held in a natural lake setting up to the point of acquisition. A total of 151 bluegill were used in the study. The individuals were not sexed specifically, but prior work using fish acquired from the source we did for this study indicates that the population was likely to be roughly 50% male and 50% female. Bluegill were held in 1135-litre outdoor holding tanks, at a density of up to 16 fish per tank. Each tank was hooked to a recirculating water system that changed out the water in the tank at a rate of approximately eight full water exchanges per day. Following the conclusion of the experiment, all remaining fish were stocked into a 0.12 ha pond at the Illinois Natural History Survey's Aquatic Research Facility, where they had access to stocked minnow forage as well as naturally occurring macroinvertebrate forage, in addition to access to natural cover items. The procedures of this experiment included multiple instances of fish handling, including implanting the fish in the body cavity with 0.8 cm, 0.027 g passive integrated transponder (PIT) tags for individual identification (each tag was approximately 0.03% of the weight of the average bluegill used in this study); these tags were kept in the fish following the study, as they are highly unlikely to impact further behaviour and vitality (both during the experiment and afterwards). The tags were quickly injected into the fish (10 s of total handling time), a rapid procedure that did not require anaesthesia. In addition, the procedures involved a potentially stressful situation during dyadic trials, where aggressive

Table 1
Summary of scoring system used for bluegill in dyadic trials for dominance

Behaviour	Score	Description
Tank position	0	'Skulking' in a corner of the tank facing outwards
	2.5	Near the bottom of the tank but not in a corner
	5	In the centre of the tank, patrolling
Feeding	0	Not first to feed
	1	First to feed
Aggressive acts	0	0 aggressive acts
	1	1–4 aggressive acts
	2	≥5 aggressive acts (bites, chases, gill flares, side displays)
Coloration	0	Darker overall coloration
	1	Brighter overall coloration

Trials consisted of four 5 min observations over a 2-day period.

interactions were observed as part of the experimental design. Given that the monitoring of aggression was necessary to achieve the goals of the study, avoidance of this situation was impossible within this framework.

Statistical Analysis

We performed a chi-square test to determine whether fish had any preference for the three zones in the shoaling assay and did not simply move about the tank at random, regardless of whether or not a fish was captured. This was done to validate the shoaling assay design, as it would be expected that fish on average would show a preference for the social zone, where they could associate with conspecifics. For this analysis, the null hypothesis of random movement was tested based on the expectation that the proportion of the trial time spent in each zone was proportional to the area of each zone within the arena, for each individual trial. We used Spearman rank correlations to determine the repeatability of times spent in each of the three zones between the first and second trials. This rank-based approach (McGhee & Travis, 2010; Wilson & Godin, 2009) was used to account for the fact that across all fish, time spent in the social zone was higher in the second trial compared to the first (Student *t* test: $t_{37} = -2.81$, $P = 0.007$). The difference in social behaviour across trials was likely due to acclimation to the testing procedure (Dingemanse et al., 2009), requiring that repeatability be evaluated based on an individual's zone occupancy across trials relative to other fish, independent of the mean level change in behaviour among all fish across trials (Bell, Hankison, & Laskowski, 2009).

We used binary logistic regression to determine whether dominance, social behaviour and/or fish length predicted whether or not a fish was captured during angling trials. Because the three measures of social behaviour taken from the shoaling assay (time spent in antisocial, social and neutral zones) were compositional (i.e. not independent) and autocorrelated (i.e. a fish that spent more time in the social zone automatically spent less time in the antisocial zone), we included only time spent in the social zone as the predictor variable of interest. Effect sizes of dominance score, fish length and time spent in the social zone were then tested for significance. Because each fish was assessed twice for sociability and only once for aggression/dominance, for the purpose of the model, time spent in the social zone was summed between the two shoaling trials. Simple linear regression was used to determine whether dominance score and the total time spent in the social zone over both shoaling trials were related to each other. All statistical analysis was performed in R 3.2.2 (R Core Team, Vienna, Austria) with alpha values for significance set at $P = 0.05$.

RESULTS

Fish showed a disproportionate affinity for particular zones (trial 1: $\chi^2_2 = 832.9$, $P < 0.001$; trial 2: $\chi^2_2 = 1712.6$, $P < 0.001$), indicating that fish position within the shoaling arena was not random. Specifically, fish spent significantly more time in the social zone than expected if distribution were random, and significantly less time in the antisocial zone, although as described above, the time spent in each zone changed between trials 1 and 2 (mean time in social, neutral and antisocial zones: trial 1: 311.1 s, 234.6 s and 354.1 s; trial 2: 427.1 s, 197.3 s and 275.6 s). Rank order of time spent in each of the three zones was significantly repeatable between trials (social zone time: $r_s = 0.38$, $P = 0.01$; neutral zone time: $r_s = 0.39$, $P = 0.01$; antisocial zone time: $r_s = 0.37$, $P = 0.01$).

Time spent by bluegills in the social zone of the behavioural arena emerged as a significant predictor of whether or not an individual was captured during angling. Captured fish spent, on

average, 422 s in the social zone during shoaling trials, while uncaptured fish averaged 315 s in the social zone (Figs. 2 and 3). Although uncaptured fish emerged from dyadic trials with a higher dominance score in 12 of 19 trials, dominance in dyadic trials was not significantly associated with capture status (Table 2). Furthermore, no relationship was found between time spent in the social zone and dominance score (linear regression: $F_{1,36} = 0.1$, $P = 0.75$).

DISCUSSION

Sociability is a critical factor in determining fitness for many species through its role in mate selection, predator avoidance, habitat selection and knowledge transfer (Krause et al., 2003; Wilson, Croft, & Krause, 2014). The results of this study indicate that increased sociability, one of five major axes of behaviour (Réale et al., 2007), is associated with increased vulnerability to recreational angling in bluegill. In this study, bluegill that were captured by anglers spent 34% more time engaged with conspecifics on average when compared to fish that were not captured. Rank order of time spent in the three zones of the behavioural arena were repeatable across trials, indicating that experimental measures of sociability were indicative of social behaviour tendencies that are intrinsic (Bell et al., 2009; van Oers, Drent, de Goede, & van Noordwijk, 2004). While tests assessing the role of sociability in driving angling vulnerability are scarce, Arlinghaus et al. (2016) argued that extensive angling selection on other behavioural axes (primarily boldness) can impact crucial social behaviours such as shoal cohesiveness and nest defence. The results of the present study, however, indicate that sociability itself as a behavioural axis may be under selective pressure, rather than being impacted via proxy through selection on other related behaviours. If selection favouring less social behavioural types is indeed occurring in the wild, there may be nonnegligible ecological impacts. Cohesive social behaviour is necessary for accomplishing crucial tasks such as foraging (Dyer et al., 2009; Morrell et al., 2008; Webster & Hart, 2007) and avoiding predators (Croft, Krause, et al., 2009; Lacasse & Aubin-Horth, 2014). If fishing mortality rates of highly social individuals are high due to angler harvest, the ability of fish groups to perform functions that rely on highly social group members may indeed be reduced; however, further work will be necessary to determine the extent of this selection in natural systems.

Along with sociability, aggression is another major axis of personality (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Réale et al., 2007) that has been posited to be a driver of angling vulnerability under the prediction that highly aggressive and dominant individuals would tend to aggressively strike fishing lures and baits (Suski & Philipp, 2004; Sutter et al., 2012). In contrast to sociability, dominance was not associated with capture vulnerability in bluegill. Predictions regarding the ecological implications of fisheries selection on aggression have been studied largely within the context of changes in nest defence behaviour following removal of especially aggressive individuals. For example, work on artificially selected lines of largemouth bass, *M. salmoides*, demonstrated that 'low-vulnerability' fish were less aggressive, albeit within the specific context of defending their nests against potential brood predators (Cooke, Suski, Ostrand, Wahl, & Philipp, 2007; Sutter et al., 2012). The present results indicate that, outside the context of nest defence, intraspecific aggression is not associated with capture likelihood in bluegill. Based on this study and previous work, we postulate that for centrarchids, selective capture of aggressive individuals may primarily occur during the reproductive period when nest-guarding males are angled off nests (Suski & Philipp, 2004; Sutter et al., 2012). Alternatively, differences in selection may relate to the ecology of the individual species. Bluegill are known to be more socially gregarious than largemouth

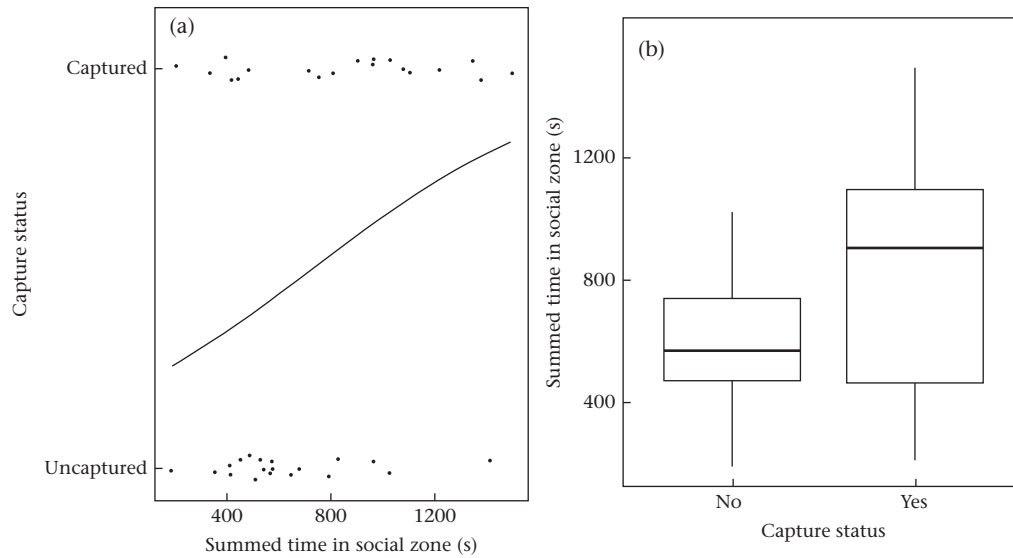


Figure 2. Summary of the relationship between social behaviour in a shoaling test and angling vulnerability in bluegill. (a) Logistic regression line describing a significant effect of social time on capture status. Data points have been jittered to account for overlap. (b) Box plots showing time spent in the social zone during shoaling trials, for captured ($N = 19$) and uncaptured ($N = 19$) bluegill. Boxes show 25% and 75% quartiles, median (line within box) and $1.5\times$ interquartile range (whiskers).

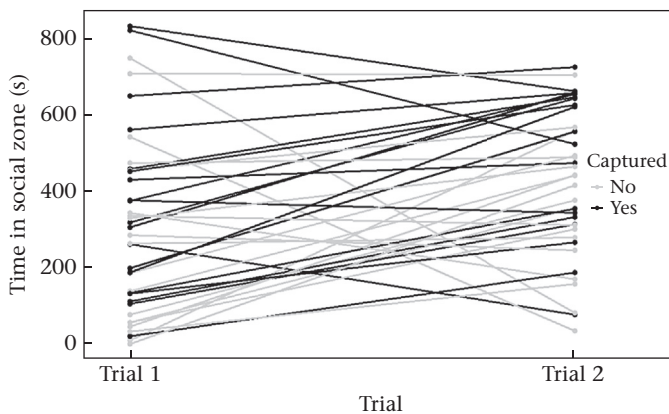


Figure 3. Time spent in the social zone by individual bluegill during each of the two shoaling trials.

Table 2

Summary of a logistic regression model assessing the effects of fish length, dominance score and time spent in the social zone on whether or not a bluegill was captured during angling trials

Factor	Estimate	SE	Z	P
Fish length (cm)	-0.02	0.07	-0.33	0.74
Dominance score	-0.03	0.02	-1.58	0.11
Time spent in social zone (s)	0.002	0.001	1.97	0.04

Because bluegill were assessed twice for time spent in the social zone, the total time spent in the social zone between both trials was used as the predictor variable. Significant main effects within any model are given in bold.

bass, and form social groups to facilitate foraging and predator avoidance (McCartt, Lynch, & Johnson, 1997; Savino & Stein, 1982). Perhaps social behaviours drive angling vulnerability only in species that are highly social, whereas in species where individuals are more solitary, social behaviours are rendered irrelevant. If this is the case, we could expect that, in exploited populations, the impacts of fisheries selection on behaviour may differ depending on the species in question. While conceptual models predicting increased timidity as a result of selective capture of bold/aggressive

phenotypes have been put forward (Arlinghaus et al., 2016), the present results indicate that, in bluegill, increased timidity resulting from fisheries-related selection is unlikely to occur, as elevated aggression and dominance were not associated with angling vulnerability.

In studies of selective harvest mortality, linkages between behaviours are of interest because selection based on one characteristic can also lead to evolutionary change in the linked characteristic. A behavioural syndrome describes a suite of behaviours that are linked together across individuals in a population (Bell, 2007; Réale et al., 2010). While it may be expected that sociability and aggression are correlated with each other within this framework, previous work examining the link between sociability and aggression has been met with mixed results. On one hand, a negative relationship between the two axes has been found whereby more social individuals were less aggressive in American eels, *Anguilla anguilla* (Geffroy, Bru, Dossou-Gbété, Tentelier, & Bardonnnet, 2014), as well as in the social spider *Anelosimus studiosus* (Pruitt & Riechert, 2011). By contrast, a positive relationship between sociability and aggression has been demonstrated in graylag geese, *Anser anser* (Kralj-Fišer, Weiß, & Kotschal, 2010), and threespine sticklebacks, *Gasterosteus aculatus* (Laskowski & Bell, 2014). In the current study, dominance score was not a significant predictor of time spent in the social zone, indicating that a behavioural syndrome linking sociability and aggression (whether positively or negatively) either does not exist or is not especially strong in bluegill. If sociability and aggression are not linked in bluegill, this may allow for fisheries-induced selection to alter levels of sociability without changing aggression/dominance (Dochtermann & Roff, 2010). If angling selection is indeed capturing bluegill based on the characteristics observed in this study, we should therefore expect a decline in social tendencies in bluegill from heavily fished systems, with no corresponding change in mean aggression levels.

Prior work on bluegill may provide clues as to why, in this species, we found that sociability, but not dominance, was associated with angling vulnerability. While sociability has not been heavily studied with respect to angling vulnerability (but see Mourier et al., 2017), many studies have found a positive relationship between boldness and angling vulnerability (Alós et al., 2016; Härkönen et al., 2014; Klefoth et al., 2013; Lennox et al., 2017), with

an expectation that more aggressive individuals will be more vulnerable to capture as well (Wilson et al., 2011). Conversely, Wilson et al. (2011) found that for bluegill, shy (i.e. less bold) individuals were more vulnerable to capture. Combining these results with the present study, it appears that shy and social individuals are more likely to be captured. While there is currently little direct study as to the specific mechanisms that might underlie the connection between shyness/sociability and angling vulnerability, perhaps this finding is due to social individuals being among the first to explore novel food sources, leading to capture on baited hooks (Modlmeier et al., 2014; Vital & Martins, 2013). Or, perhaps social bluegill tend to form more densely packed groups, leading to a density-driven increase in feeding motivation and competition when a baited hook is placed nearby a large group of social individuals (Stoner & Ottmar, 2004). Regardless of the mechanism, the oft-reported connection between high boldness, aggression and capture vulnerability does not appear to apply to bluegill, and, in fact, angling may be expected to selectively capture more social phenotypes in exploited populations.

Conclusion

Recreational angling is a popular activity throughout much of the world, having a massive cultural and economic impact (Post, 2013). The maintenance of healthy recreational fisheries is the primary mission of fisheries managers, and research has examined the possibility of fisheries collapse as a result of recreational harvest (Cooke & Cowx, 2004; Post, 2013; Post et al., 2002). A relatively new emphasis has been placed on the role of individual behaviour in driving vulnerability to capture, which could lead to evolutionary shifts in the behavioural characteristics of populations (Diaz Pauli & Sih, 2017; Uusi-Heikkilä, Wolter, Klefoth, & Arlinghaus, 2008; Ward et al., 2016). The negative impacts of such shifts are largely a matter of speculation, with a major concern being the disruption of social functioning in exploited populations (Arlinghaus et al., 2016). While other work has speculated on impacts on social behaviour through other behavioural mechanisms, we show here that social behaviour in and of itself may be under selection in recreational fisheries, with more social individuals being more vulnerable to capture. Given the relatively small sample size for the present study, however, it is clear that more work will be required to determine whether selection based on sociability is widespread in this species. Even if sociability is indeed a primary driver of angling vulnerability in bluegill, it remains possible that the selective capture of social phenotypes may apply only to the study species; currently very little additional work has examined the role of social behaviour in driving vulnerability to capture (Mourier et al., 2017). Therefore, if we are to form more concrete conclusions about the impact of fishing on population functioning, more investigation will be required that examines the behaviours of interest more directly, both through laboratory as well as field-based observations of behaviour.

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