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Influence of predation risk on individual spatial positioning and willingness to leave a safe refuge in a social benthic fish

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Abstract

Certain individuals tend to occupy frontal positions within social groups. Less is known about how predation risk can affect individual spatial positioning and group fidelity. We tracked individuals within groups goldfish (*Carassius auratus*) as they left a safe, covered, microhabitat to enter a risky, open-water, microhabitat over 2 days: one with and one without an avian predator (little egret—*Egretta garzetta*) present. For each day, an outing index was calculated to take into account both individual order of emergence from the refuge and the proportion of outings participated in. Prior to the experiment, fish were individually marked for identification, measured, and tested for boldness to enter a novel area. Body size did not predict individual outing index scores on either control or experimental days. Boldness index scores influenced outing index scores only on days with an egret present. We found individual outing index scores to be relatively consistent across both days, regardless of the presence of a predator. However, the presence of a predator increased the mean outing index score of the highest ranked fish and decreased the number of fish that occupied lead positions, suggesting that risk amplified the behaviour of the boldest fish. Furthermore, the presence of the predator decreased individual willingness to leave the safety of cover. Thus, we show that the introduction of a predator influenced social group movement and that the boldest individuals emerge at the front of the group under risk.

Significance statement

Within social species, some bold individuals tend to occupy positions at the front of the group. Groups of goldfish were provided a safe covered refuge, and we recorded the order in which individuals left the refuge to enter an open water environment over multiple outings. We examined fish behaviour over 2 days: with and without a predator present. We found that the predator decreased the probability the fish would leave the safe refuge; however, relative individual fish behaviour and positioning were consistent over the 2 days. Interestingly, the presence of the predator amplified the behaviour of the boldest fish. Our results demonstrate that predation risk can influence group and individual prey behaviour and illustrate that bold individuals emerge at the front of groups when risk is high.

Keywords Goldfish · Social group · Cohesion · Predator-prey · Consistency · Refuge

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Introduction

The spatial positioning of individuals within social groups can lead to different costs and benefits (Morell and Romey 2008). Generally, individuals located at the front or on the edges of moving groups have greater access to food items, but suffer higher risk whereas individuals located in safer positions will have less access to resources (Krause 1994; Bumann et al. 1997). Another important aspect of positioning is that those individuals in the front can influence the social group by initiating movement (Bumann and Krause 1993; Reebs 2001; King 2010; Petit and Bon 2010). In this way, certain individuals will tend to occupy forward positions, whereas others will respond to the individuals located at the front of the group (Couzin et al. 2005).

The variability and consistency of individual positioning within a group are dependent on social dynamics (King et al. 2009). In some species, group membership is fixed, and positioning within the group can be strictly regulated by hierarchies determined by sex (Ihl and Bowyer 2011), age (Sueur and Petit 2008; McComb et al. 2011), and previously established dominance structures (Squires and Daws 1975; Peterson et al. 2002). In such groups, a single individual will often occupy the front-most position and influence all group movements (e.g. Lusseau and Conradt 2009).

In contrast, in shoals of fish where membership is not always fixed, positioning within the group can be flexible (Pavlov and Kasumyan 2000). Individual positioning within fish shoals has been shown to be influenced by physiological traits associated with differences in metabolism and locomotor performance (Killen et al. 2017). Previous work has demonstrated that the largest (Krause et al. 2000; Reebs 2001; Ward et al. 2002) and boldest (Ward et al. 2004; Harcourt et al. 2009a) fish often occupy frontal positions. Furthermore, social feedback (Harcourt et al. 2009b; Nakayama et al. 2012) and external environmental factors (Giardina 2008; Ioannou et al. 2017) also influence individual positioning. For example, Burns et al. (2012) found that in a group, numerous individuals acted as the lead fish at various times, but the consistency of positioning within the group was influenced by the level of familiarity with the environment. Less is known about how external risk factors affect the consistency of individual positioning within groups of fish.

Predators provide the most direct risk to survival and influence the behaviour of prey species (Lima 1998; Brown et al. 1999; Clinchy et al. 2013). Most studies on anti-predator behaviour within a social group have focused on how individuals can reduce risk by moving into safer spatial positions (e.g. Hamilton 1971; Katz et al. 2010, 2014). However, few studies consider how predation may influence group fission-fusion dynamics and how individuals decide whether or not to synchronise their behaviour with a social group. To stay part of a coordinated group, an individual would not be able to stay in place while the rest of the group was out foraging. Conversely, an individual could not leave to forage when the group was resting (Conradt and Roper 2000). Nonetheless, although sociality and group formation provide the benefit of reduced individual mortality through collective vigilance, communal defence, and the dilution effect (Cresswell 1994; Lima 1995), it may not always be wise to join a group moving into a risky area when there is an option to stay in a safe refuge.

The main motivation to leave a safe habitat and enter a dangerous location is to acquire resources (Brown 1999). An individual that chooses to stay in a refuge benefits by

avoiding the risk of predation, but pays the cost of reduced resource acquisition. On the other hand, an individual that joins a foraging party will benefit from increased access to resources, but will pay an increased cost of mortality risk (Brown et al. 1999). Thus, a fish inhabiting a location that provides certain protection from predators will need to determine whether to join or stay behind when other conspecifics move, as a group, into a risky, but energetically rewarding microhabitat.

Here, we assess individual spatial positioning and willingness to leave a safe refuge within a group and consider how group movement and fidelity are affected by predation risk. Specifically, we examine the total number of fish and the order of individuals leaving the safety of a covered microhabitat to enter an open, food-rich microhabitat in both the absence and presence of a predator. To do this, groups of goldfish were tested over two consecutive days in which an avian predator was introduced on the second day. We predict that (1) individual fish behaviour would be influenced by body size and boldness, (2) individual behaviour would be consistent regardless of the presence of a predator, but that (3) predation risk would diminish the likelihood of individuals leaving the safe microhabitat and thus reduce the average group outing size.

Methods

Study species

The common goldfish (*Carassius auratus*) is a social benthic fish that seeks cover from predation and forages as a coordinated group (Magurran and Pitcher 1983; Magurran 1984; Katz et al. 2013). Like other carp species that evolved in muddy water, goldfish do not use vigilance as their primary anti-predator behaviour. Instead, the fish manage risk largely by utilising time allocation and hiding when a predator is present (Katz et al. 2013). Other than colour, goldfish are little changed from their ancestral form (Holopainen et al. 1997). Consequently, a growing literature uses goldfish as a model study organism for behavioural research (e.g. Yoshida et al. 2005; Dunlop et al. 2006).

The little egret (*Egretta garzetta*) is a small heron of the Ardeidae family and provides the predator in our experiment. Adults range from 55 to 65 cm in length, possess an 88–106-cm wingspan, and weigh between 350 and 550 g. Little egrets are solitary, opportunistic hunters that ambush fish, amphibian, crustacean and insect prey in shallow water (Hafner et al. 1982). Our egrets were wild captured in northern Israel (Kibbutz Ma'agan Michael) and were released at the locations of capture following the experiment.

Pre-test: individual size and boldness

Individual fish were lightly anaesthetised using a diluted solution of MS-222, weighed, and measured from head to tail. Next, in order to identify individuals, each fish was individually marked with Biotouch micropigments. Fish body length ranged from 7.30 to 11.60 cm and weight varied between 5.01 and 13.42 g.

Two hours after marking the fish, we tested individual boldness to enter a novel environment. Preliminary observations indicated that after 60 min, fish activity levels returned to baseline levels. The boldness arena was a small tank ($35 \times$ 22×13 cm) that was split into two compartments by an opaque plastic barrier. We gently moved each fish into one side of the box and allowed 5 min for acclimation. After acclimation, a door (6 cm wide) was remotely raised using a string and pulley system, and the fish were free to move through the door. We recorded the time taken for the entire body of the fish to cross the threshold into the novel environment. We tested each fish individually, and if the fish did not emerge after 10 min, we terminated the trial and recorded the time to emerge as 600 s. We calculated a boldness index for each individual fish as 1 - (time to emerge / 600). With this index, the boldest fish scored close to 1, and the least bold fish (those that did not emerge for 10 min) scored 0. Each fish was tested once because fish have been shown to change their behaviour following a single exposure to a novel arena, which could have altered the outcome of our boldness assay (adapted from Brown et al. 2005; White et al. 2013).

Data availability statement The datasets generated and analysed during the current study are available from the corresponding author upon request.

Experimental design

We observed groups of eight goldfish and assessed individual positioning upon emergence from, and willingness to leave the safety of, a protected refuge. A cylindrical aviary (7 m diameter) was used as the experimental arena. The aviary contained three equally sized and spaced pools with a diameter of 1.5 m and a depth of 0.6 m. Each pool contained two microhabitats for the fish. A safe microhabitat in the centre of the pool provided a refuge in which the fish could shelter under a 23.75-cm radius opaque cover, but had no access to food. The open area outside of cover provided a risky microhabitat where fish could find food, but also would be exposed to risk from the egret predator. The fish were limited to the upper 15 cm of the water by a plastic 1 cm mesh. The egret predator was able to walk and hunt on this plastic mesh floor (see Katz et al. 2013).

For this experiment, we focused on one of the three pools. The other two non-experimental pools contained 15 nonexperimental fish. It was important to offer multiple hunting locations so that the egret would be encouraged to move away from the experimental pool and return some time later. This allowed the fish to recover and act naturally after experiencing predation risk; otherwise, the fish would never leave the safe microhabitat. In the focal pool, we restricted access to the safe, covered microhabitat to one 20-cm-wide door so that we could observe the order in which the fish left the safe microhabitat to move into the risky microhabitat. We utilised an underwater camera placed under the opaque cover to track the movement and positioning of individual fish. Over the course of the experiment, floating food pellets were dispensed from a feeder into the open microhabitat at a constant rate of 15 pellets per hour. Plastic mesh blocked the food pellets from entering the covered microhabitat; thus, our design forced fish to trade-off access to resources and safety from predation.

Each group of eight fish was tested over two consecutive days. The first day was treated as a control day with no egret predator present. On the following experimental day, we examined the behaviour of the same group of fish under predation risk with a single egret allowed free movement throughout the aviary for 4 h. The experimental day began after the egret's first visit to the pool of interest. Considering that the egret was able to attack the fish, we were unable to randomise the order of control and experimental days. We analysed N= 19 groups of eight fish over 2 days for a total of N=152 individual fish.

Assessment of individual positioning—outing index

For each day, we examined individual fish group positioning over 15 outings. An outing began when the first fish left the safety of the cover to move into the risky microhabitat, and each outing ended when all of the fish participating in the outing returned to safety under the cover.

For each outing, we recorded the number of fish participating and the order in which each individual fish crossed through the door into the risky microhabitat. The first individual crossing the door was given an outing score of 8, the second a score of 7, the third a score of 6 and so on to the last fish that entered the risky area. Fish that did not participate in the outing were given a score of 0. To assess individual behaviour over each day, we calculated an outing index to take into account both spatial positioning and outing participation. The outing index for each individual fish was calculated as the average of the fish's outing scores (i.e. sum of scores/15 outings). The highest possible outing index was 8 and the lowest was 0. We calculated a separate outing index for each individual fish for the control (no predation risk) and experimental (predation risk) days. For each control and experimental day, the fish were given a daily outing rank based on their outing index scores, with the highest scoring fish receiving the top outing rank for that day. This allowed us examine and compare the mean behaviour of the top through lowest ranked fish over N = 19 days.

Statistical analysis

We used linear mixed models with group (N = 19) as a random effect to determine relationships between individual body size, boldness (pre-test) index scores and outing index scores on both control and experimental days (Table 1). Likelihood ratio tests were used to determine the significance of each regression. These analyses were done using the lme4 package (Bates et al. 2015) in R (R core team 2016). For the two analyses with boldness as the response variable, we transformed the data for a binomial regression (0 or 1) due to the fact that the majority of boldness scores tended to fall near the minimum and maximum values: the value was 0 if the boldness index score was below 0.5, and 1 if the boldness index score was above 0.5. For both of these analyses, the relationship was clearly non-significant, and we found this nonsignificant result for both the transformed and untransformed boldness data.

Over the 19 experimental days, the egret predator captured 31 (of 152 total) fish. Ten fish were eaten by the egret predator before 15 outings were recorded; thus, these fish did not receive an outing index score for the experimental day and were excluded from analyses involving outing index scores from experimental days. On average, these 10 fish were the fifth highest ranked fish on control days. Additionally, the 10 fish exhibited pre-test boldness index scores (mean \pm SE = 0.76 ± 0.14) similar to the average boldness index scores of the entire group (mean \pm SE = 0.74 ± 0.03).

Using group data to analyse the effects of predation on fish behaviour, we employed two-tailed paired t tests to compare control and experimental days. Next, examining

 Table 1
 Summary of regression comparisons

Response variable	Predictor		
Boldness index (0 or 1)	x	Weight	
Boldness index (0 or 1)	х	Length	
Outing index (control)	х	Weight	
Outing index (experiment)	х	Weight	
Outing index (control)	х	Length	
Outing index (experiment)	х	Length	
Outing index (control)	х	Boldness index	
Outing index (experiment)	х	Boldness index	
Outing index (experiment)	х	Outing index (control)	

Group (N=19) was added as random effect

only the experimental days, we calculated the level of predation risk as the proportion of trial time the egret spent at the experimental pool (via video analysis) and used a linear regression analysis to examine the effect of the level of predation risk on group outing size. Data were tested for normality and homoscedasticity in order to meet statistical assumptions. To minimise observer bias, blinded methods were used when all behavioural video recordings were analysed. All statistical analyses were conducted using R (R core team 2016).

Results

In general, the fish foraged as a coordinated group, with members observed to be swimming within touching distance. Group outings generally lasted for under 2 min, as the fish quickly returned to cover after searching for and consuming food pellets. On control days, 15 group outings were completed in (mean \pm SE) 139 \pm 40 min, compared with experimental days where 15 group outings were completed in 182 \pm 59 min; paired test (p > 0.05).

Body size, boldness, and outing index

Our pre-test of individual boldness revealed no significant relationship between boldness to enter a novel area and either measure of body size (boldness-weight: $\chi^2(1) = 0.03$, p = 0.86; boldness-length: $\chi^2(1) = 1.20$, p = 0.27).

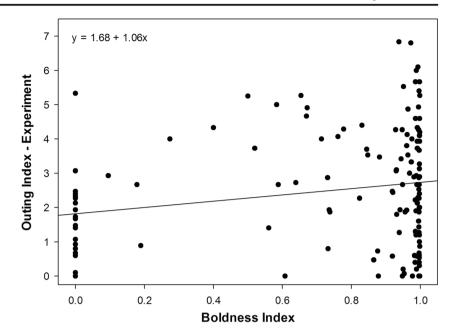
Additionally, we found no significant relationship between individual body size and outing index in either control (outing index-weight: $\chi^2(1) = 0.27$, p = 0.61; outing index-length: $\chi^2(1) = 0.03$, p = 0.87) or experimental days (outing indexweight: $\chi^2(1) = 0.06$, p = 0.80; outing index-length: $\chi^2(1) =$ 0.01, p = 0.95).

We did not observe a significant correlation between individual boldness and outing index on control days ($\chi^2(1) =$ 2.76, p = 0.10). However, we did find a significant relationship between individual pre-test boldness and outing index under predation risk ($\chi^2(1) = 7.60, p < 0.01$), with bolder individuals tending to score higher in outing index over 15 group outings on experimental days (Fig. 1).

Fish behaviour on control and experimental days

Overall, individual outing index scores ranged from 0 to 6.83 and were relatively consistent regardless of the presence of a predator. Individual outing index scores significantly correlated across the control and experimental days ($\chi^2(1) = 69.55$, p < 0.001) (Fig. 2).

For each control and experimental day, the fish were ranked based on their outing index scores, with the highest scoring fish receiving the highest daily rank. Outing index **Fig. 1** Relationship between (pretest) boldness index scores and outing index scores on experimental days. Each black dot represents one individual fish. Linear fit line represents average for N = 19 groups



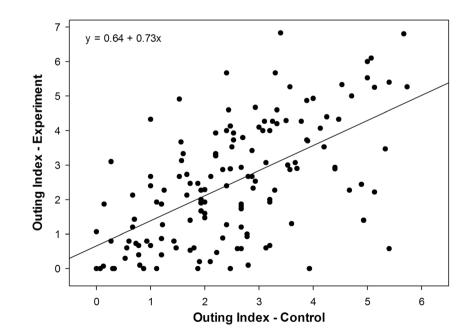
scores, which take into account both spatial positioning and the proportion of outings participated in, varied significantly among the ranks (ANOVA-control: $F_{7,144} = 97.63$, p < 0.001; experiment: $F_{7,134} = 31.27$, p < 0.001) (Fig. 3a). Spatial positioning when leaving the safe microhabitat was significantly variable: higher ranked fish left the safety of cover in positions at or near the front of the group while lower ranked fish generally occupied posterior positions (ANOVA-control: $F_{7,144} =$ 56.97, p < 0.001; experiment: $F_{7,134} = 38.66$, p < 0.001) (Fig. 3b). Additionally, higher ranked fish participated in significantly more group outings compared with lower ranked fish (ANOVA-control: $F_{7,144} = 18.33$, p < 0.001; experiment: $F_{7,134} = 7.17$, p < 0.001) (Fig. 3c).

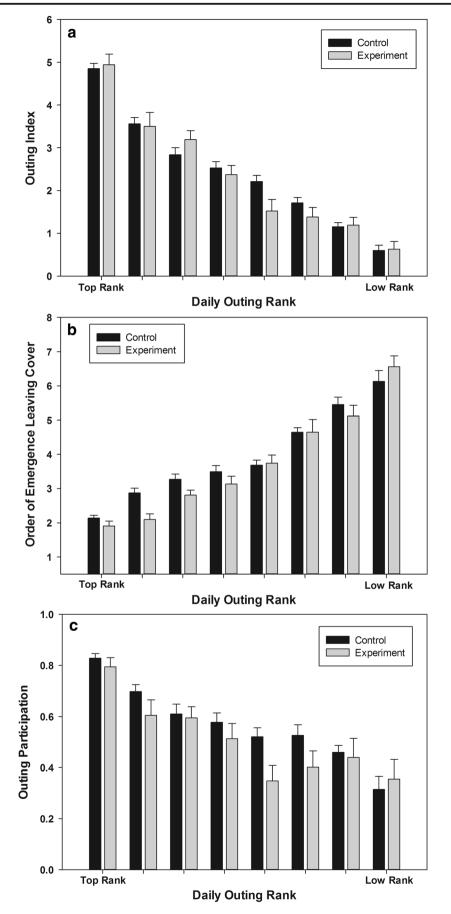
Egret effects

The presence of an egret predator had an effect on how often individual fish left the safety of cover. Individuals participated in significantly fewer outings on experimental compared to control days. However, the presence of a predator did not significantly influence overall group outing size or the total number of fish that led at least one outing (Table 2).

With the exception of 1 day that was removed as a possible outlier where the egret spent 73% of the day at the focal pool, the proportion of egret foraging time at the experimental pool ranged between 2 and 38%. We found that the relative level of predation risk marginally decreased the mean number of fish

Fig. 2 Outing index scores for control and experimental days. Each black dot represents one individual fish. Linear fit line represents average for N = 19groups





◄ Fig. 3 Mean (+SE) a outing index, b spatial positioning when leaving the safe microhabitat, and c proportion of outings participated in. For each control and experimental day, individual fish were ranked based on their outing index scores, with the highest scoring fish receiving the top daily outing rank. Black bars represent control days; grey bars represent experimental days. N = 19 groups

participating in each outing, but did not significantly affect group outing size ($F_{1,17} = 1.70, r = -0.31, p = 0.21$).

Discussion

We examined the spatial positioning of goldfish leaving the safety of a covered microhabitat to enter an open and risky microhabitat and observed that certain individuals repeatedly occupied frontal positions and participated in more outings, while other fish consistently occupied posterior positions and participated in fewer group outings.

Individual (pre-test) boldness predicted outing behaviour under predation risk, supporting previous work demonstrating that, within a group, a fraction of intrinsically bold individuals move into forward positions (Kurvers et al. 2009; Schuett and Dall 2009; Johnstone and Manica 2011; Nakayama et al. 2016). Bold individuals that are more likely to take risks benefit from improved access to resources (e.g. Short and Petren 2008), but enhance the probability of being killed by a predator (e.g. Belgrad and Griffen 2016). The fact that boldness predicted outing index scores when an egret was present, but did not for control days in the absence of a predator, suggests that under predation risk, bolder individuals were most likely to initiate movement out of the safety of cover. However, considering that the fish in our experiment were satiated prior to testing, it is unclear why certain individuals would exhibit such risky behaviour when the potential cost of death should seemingly outweigh the short-term benefits of foraging. Perhaps, inter-individual differences in metabolic rate and aerobic capacity influence risk-taking behaviour and determine relative spatial positioning within a group (Killen et al. 2012a). For example, fish with higher metabolic rates have been shown to occupy forward positions as they are able to withstand drag in order to take advantage of the foraging benefits associated with frontal group locations. In contrast, fish with inferior metabolic capacities swim in the rear of groups and benefit from hydrodynamic forces that reduce swimming costs, but pay the cost of reduced foraging opportunities (Killen et al. 2012b). Thus, theory suggests that differences in metabolic rate and personality syndromes associated with boldness, aggression, and overall activity level may be linked to life history trade-offs (Wolf et al. 2007). Highly active, bold individuals trade-off immediate success with a shorter lifespan while less bold individuals live longer but have lower average fitness levels (Wolf and Weissing 2012).

Our findings that the presence of a predator significantly decreased individual outing rates and tended to lower the average group outing size support the idea that predators can influence prey behaviour through indirect effects. Much prior work on predator effects considered only the lethal effects of direct predation (e.g. Smith et al. 2010; Fletcher et al. 2010). However, the results of our experiment add to the burgeoning field examining nonlethal predator effects on prey behaviour and fitness (e.g. Lima 1998; Brown and Kotler 2004; Palacios et al. 2016; Voelkl et al. 2016). As we have shown, the presence of a predator can reduce prey foraging activity (Preisser et al. 2005). Such nonlethal effects have been shown to strongly influence prey populations, and prey responses to risk have been shown to influence growth rates and mortality at the same level or higher than the effect of direct predation (Pangle et al. 2007; Creel and Christianson 2008).

Although the presence of a predator generally decreased individual willingness to leave the covered refuge, individual behaviour relative to the rest of the group was consistent across control and experimental days. The likelihood that an individual fish would leave cover, and its positioning within the group, remained relatively consistent regardless of the presence of a predator. Prior work on the consistency of leadership in fish shoals found individual positioning to be consistent over multiple repeated trials, but that the identity of the lead fish was more variable in a novel environment. As the group gained familiarity in the environment over time, positioning became more consistent (Burns et al. 2012). In our study, even though the introduction of a predator altered the external environment, outing index scores remained stable and consistent. In fact, the presence of a predator slightly increased the mean outing index score of the highest ranked fish and marginally decreased the number of fish that occupied the front-most spot, suggesting that the introduction of risk actually enhanced the consistency of the forward positioning of the boldest fish.

Table 2Comparison ofindividual and group behaviouracross control and experimentaldays

	Control	Experimental	Paired t test		
	Mean (SE)	Mean (SE)	N	t	р
Individual outing participation	0.58 (0.02)	0.52 (0.02)	142	3.05	< 0.01
Group outing size	4.57 (0.22)	3.77 (0.40)	19	1.60	0.13
Number of outing leaders	4.89 (0.30)	4.47 (0.28)	19	1.14	0.27

In testing fish individually prior to the experiment, we found no relationship between fish size (weight or length) and boldness. Furthermore, body size did not influence individual outing behaviour within a social group. These results are in line with prior work on fishes (Harris et al. 2010; Ingley et al. 2014), but contrast with other studies that have found negative and positive correlations between body size and boldness (Brown and Braithwaite 2004; Wilson et al. 2010). Larger fish, who are often in good condition, have been shown to exhibit boldness in terms of the length of time to emerge from cover (Brown et al. 2007a). Alternatively, as smaller fish have reduced capacity to escape predators and tolerate starvation, predation pressure and metabolic requirements can force individuals to act bold in order to find sufficient food and quickly grow into a larger, less vulnerable size class (Sogard 1997; Dowling and Godin 2002; Brown et al. 2005). In our study, the lack of a significant correlation between size and bold behaviour may be explained by the fact that all of the fish were lab-raised and well fed prior to testing, rendering it less likely that boldness was influenced by hunger or other immediate metabolic requirements (see also Brown et al. 2007b).

A few aspects of our experimental design warrant discussion. First, ideally we would have been able to randomise the order of our control and experimental days. However, the predator in our experiment was able to attack and kill the fish. Further, prior work in our system has documented clear longterm carryover effects of predation risk on fish behaviour (sensu Diaz-Uriarte 2002), as fish exposed to an egret predator significantly reduce activity the following day. Additionally, previous experiments conducted in our system have shown that fish behaviour remains similar over 2 days without a predator (pers. obs. ZA). Thus, we are confident that our results from the experimental days represent effects of predation risk rather than the effects of time spent in the experimental arena.

Second, although we were interested in examining how certain fish occupy frontal group positions and are more willing to leave the safety of a protected location, we did not distinctly assess relative levels of individual leadership. We observed which fish initiated movement out of the refuge as we recorded the order of emergence, but we did not assess specific interactions and synchronicity among individuals as has been done in other studies more focused on the comparative leadership influence among group members (e.g. Harcourt et al. 2009b; Schaerf et al. 2016; Jolles et al. 2017).

Nonetheless, we have shown that certain individuals consistently position themselves near the front of a group and that external risk factors can influence the frequency of movement out of cover. Furthermore, individual outing behaviour was relatively consistent in the presence and absence of predation risk. Given that many studies examining individual spatial positioning within a group have focused on either foraging success (e.g. Di Bitetti and Janson 2001) or mortality risk (e.g. Bumann et al. 1997), future work is needed to simultaneously examine such costs and benefits of spatial positioning and willingness to forage under predation risk. Such studies will provide a better understanding of the decisions individuals make when trading-off safety from predators and foraging opportunities.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The experiments were conducted in full accordance with the animal care and ethical guidelines of Ben-Gurion University of the Negev, and the Abramsky lab was granted permission to use egrets and goldfish in this study by the committee for the ethical care and use of animals in experiments (Authorization number: IL-37-07-2017).

Conflict of interest The authors declare that they have no conflict of interest.

References

- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixedeffects models using {Ime4}. J Stat Softw 67:1–48
- Belgrad BA, Griffen BD (2016) Predator–prey interactions mediated by prey personality and predator hunting mode. Proc R Soc B 283: 20160408
- Brown JS (1999) Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res 1:49–71
- Brown C, Braithwaite VA (2004) Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. Anim Behav 68: 1325–1329
- Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014
- Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399
- Brown C, Jones F, Braithwaite VA (2005) In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. Anim Behav 70:1003–1009
- Brown C, Jones F, Braithwaite VA (2007a) Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*. J Fish Biol 71:1590–1601
- Brown C, Burgess F, Braithwaite VA (2007b) Heritable and experiential effects on boldness in a tropical poeciliid. Behav Ecol Sociobiol 62: 237–243
- Bumann D, Krause J (1993) Front individuals lead in shoals of threespined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*). Behaviour 125:189–198
- Bumann D, Krause J, Rubenstein D (1997) Mortality risk of spatial positions in animal groups: the danger of being in the front. Behaviour 134:1063–1076
- Burns AL, Herbert-Read JE, Morell LJ, Ward AJ (2012) Consistency of leadership in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments. PLoS One 7:e36567

- Clinchy M, Sheriff MJ, Zanette LY (2013) Predator-induced stress and the ecology of fear. Funct Ecol 27:56–65
- Conradt L, Roper TJ (2000) Activity synchrony and social cohesion: a fission-fusion model. Proc R Soc Lond B 267:2213–2218
- Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433: 513–516
- Creel S, Christianson D (2008) Relationships between direct predation and risk effects. Trends Ecol Evol 23:194–201
- Cresswell W (1994) Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. Anim Behav 47:433–442
- Di Bitetti MS, Janson CH (2001) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Anim Behav 62:47–56
- Diaz-Uriarte R (2002) Incorrect analysis of crossover trials in animal behaviour research. Anim Behav 63:815–822
- Dowling LM, Godin J-GJ (2002) Refuge use in a killifish: influence of body size and nutritional state. Can J Zool 80:782–788
- Dunlop R, Millsopp S, Laming P (2006) Avoidance learning in goldfish (*Carassius auratus*) and trout (*Oncorhynchus mykiss*) and implications for pain perception. Appl Anim Behav Sci 97:255–271
- Fletcher K, Aebischer NJ, Baines D, Foster R, Hoodless AN (2010) Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. J Appl Ecol 47:263–272
- Giardina I (2008) Collective behaviour in animal groups: theoretical models and empirical studies. HFSP J 2:205–219
- Hafner H, Boy V, Gory G (1982) Feeding methods, flock size and feeding success in the little egret *Egretta garzetta* and the Squacco heron *Ardeola ralloides* in Camargue, southern France. Ardea 70:45–54
- Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295-311
- Harcourt JL, Sweetman G, Johnstone RA, Manica A (2009a) Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. Anim Behav 77:1501–1505
- Harcourt JL, Ang TZ, Sweetman G, Johnstone RA, Manica A (2009b) Social feedback and the emergence of leaders and followers. Curr Biol 19:248–252
- Harris S, Ramnarine IW, Smith HG, Pettersson LB (2010) Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia reticulata*. Oikos 119:1711– 1718
- Holopainen IJ, Tonn WM, Paszkowski CA (1997) Tales of two fish: the dichotomous biology of crucian carp (*Carassius carassius* (L.)) in northern Europe. Ann Zool Fenn 34:1–22
- Ihl C, Bowyer RT (2011) Leadership in mixed-sex groups of muskoxen during the snow-free season. J Mammal 92:819–827
- Ingley SJ, Rehm J, Johnson JB (2014) Size doesn't matter, sex does: a test for boldness in sister species of Brachyrhaphis fishes. Ecol Evol 4: 4361–4369
- Ioannou CC, Ramnarine IW, Torney CJ (2017) High-predation habitats affect the social dynamics of collective exploration in a shoaling fish. Sci Adv 3:e1602682
- Johnstone RA, Manica A (2011) Evolution of personality differences in leadership. Proc Natl Acad Sci USA 108:8373–8378
- Jolles JW, Boogert NJ, Sridhar VH, Couzin ID, Manica A (2017) Consistent individual differences drive collective behaviour and group functioning of schooling fish. Curr Biol 27:2862–2868
- Katz MW, Abramsky Z, Kotler BP, Alteshtein O, Rosenzweig ML (2010) Playing the waiting game: predator and prey in a test environment. Evol Ecol Res 12:793–801
- Katz MW, Abramsky Z, Kotler BP, Rosenzweig ML, Alteshtein O, Vasserman G (2013) Optimal foraging of little egrets and their prey in a foraging game in a patchy environment. Am Nat 181:381–395
- Katz MW, Abramsky Z, Kotler BP, Roth I, Alteshtein O, Rosenzweig ML (2014) A predator–prey behavioural game: how does number of food patches influence foraging tactics? Evol Ecol Res 16:19–35

- Killen SS, Marras S, Steffensen JF, McKenzie DJ (2012a) Aerobic capacity influences the spatial position of individuals within fish schools. Proc R Soc Lond B 279:357–364
- Killen SS, Marras S, Ryan MR, Domenici P, McKenzie DJ (2012b) A relationship between metabolic rate and risk-taking behaviour is revealed during hypoxia in juvenile European sea bass. Funct Ecol 26:134–143
- Killen SS, Marras S, Nadler L, Domenici P (2017) The role of physiological traits in assortment among and within fish shoals. Philos Trans R Soc Lond B Biol Sci 372:20160233
- King AJ (2010) Follow me! I'm a leader if you do; I'm a failed initiator if you don't? Behav Process 84:671–674
- King AJ, Johnson DD, Van Vugt M (2009) The origins and evolution of leadership. Curr Biol 19:911–916
- Krause J (1994) Differential fitness returns in relation to spatial position in groups. Biol Rev 69:187–206
- Krause J, Hoare D, Krause S, Hemelrijk CK, Rubenstein DI (2000) Leadership in fish shoals. Fish Fish 1:82–89
- Kurvers RH, Eijkelenkamp B, van Oers K, van Lith B, van Wieren SE, Ydenberg RC, Prins HH (2009) Personality differences explain leadership in barnacle geese. Anim Behav 78:447–453
- Lima SL (1995) Back to the basics of anti-predatory vigilance: the groupsize effect. Anim Behav 49:11–20
- Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48:25–34
- Lusseau D, Conradt L (2009) The emergence of unshared consensus decisions in bottlenose dolphins. Behav Ecol Sociobiol 63:1067–1077
- Magurran AE (1984) Gregarious goldfish. New Sci 103:32-33
- Magurran AE, Pitcher TJ (1983) Foraging, timidity and shoal size in minnows and goldfish. Behav Ecol Sociobiol 12:147–152
- McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J, Moss C (2011) Leadership in elephants: the adaptive value of age. Proc R Soc Lond B 278:3270–3276
- Morell LJ, Romey WL (2008) Optimal individual positions within animal groups. Behav Ecol 19:909–919
- Nakayama S, Harcourt JL, Johnstone RA, Manica A (2012) Initiative, personality and leadership in pairs of foraging fish. PLoS One 7: e36606
- Nakayama S, Harcourt JL, Johnstone RA, Manica A (2016) Who directs group movement? Leader effort versus follower preference in stickleback fish of different personality. Biol Lett 12:20160207
- Palacios M, Warren DT, McCormick MI (2016) Sensory cues of a toppredator indirectly control a reef fish mesopredator. Oikos 125:201– 209
- Pangle KL, Peacor SD, Johannsson OE (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology 88:402–412
- Pavlov DS, Kasumyan AO (2000) Patterns and mechanisms of schooling behaviour in fish: a review. J Ichthyol 40:S163–S231
- Peterson RO, Jacobs AK, Drummer TD, Mech LD, Smith DW (2002) Leadership behaviour in relation to dominance and reproductive status in gray wolves, *Canis lupus*. Can J Zool 80:1405–1412
- Petit O, Bon R (2010) Decision-making processes: the case of collective movements. Behav Process 84:635–647
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org
- Reebs SG (2001) Influence of body size on leadership in shoals of golden shiners, *Notemigonus crysoleucas*. Behaviour 138:797–809
- Schaerf T, Herbert-Read JE, Myerscough MR, Sumpter DJ, Ward AJ (2016) Identifying differences in the rules of interaction between individuals in moving animal groups. arXiv:1601.08202

- Schuett W, Dall SR (2009) Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. Anim Behav 77:1041–1050
- Short KH, Petren K (2008) Boldness underlies foraging success of invasive *Lepidodactylus lugubris* geckos in the human landscape. Anim Behav 76:429–437
- Smith RK, Pullin AS, Stewart GB, Sutherland WJ (2010) Effectiveness of predator removal for enhancing bird populations. Conserv Biol 24:820–829
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60:1129–1157
- Squires VR, Daws GT (1975) Leadership and dominance relationships in merino and border Leicester sheep. Appl Anim Ethol 1:263–274
- Sueur C, Petit O (2008) Organization of group members at departure is driven by social structure in Macaca. Int J Primatol 29:1085–1098
- Voelkl B, Firth JA, Sheldon BC (2016) Nonlethal predator effects on the turn-over of wild bird flocks. Sci Rep 6:33476
- Ward AJ, Hoare DJ, Couzin ID, Broom M, Krause J (2002) The effects of parasitism and body length on positioning within wild fish shoals. J Anim Ecol 71:10–14

- Ward AJ, Thomas P, Hart PJ, Krause J (2004) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). Behav Ecol Sociobiol 55:561–568
- White JR, Meekan MG, McCormick MI, Ferrari MC (2013) A comparison of measures of boldness and their relationships to survival in young fish. PLoS One 8:e68900
- Wilson AD, Godin J-GJ, Ward AJ (2010) Boldness and reproductive fitness correlates in the eastern mosquitofish, *Gambusia holbrooki*. Ethology 116:96–104
- Wolf M, Weissing FJ (2012) Animal personalities: consequences for ecology and evolution. Trends Ecol Evol 27:452–461
- Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history tradeoffs favour the evolution of animal personalities. Nature 447:581–584
- Yoshida M, Nagamine M, Uematsu K (2005) Comparison of behavioural responses to a novel environment between three teleosts, bluegill *Lepomis macrochirus*, crucian carp *Carassius langsdorfii*, and goldfish *Carassius auratus*. Fish Sci 71:314–319