

## Research



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### Author for correspondence:

Jesse Balaban-Feld

e-mail: [jbalaba2@gmail.com](mailto:jbalaba2@gmail.com)

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# Individual willingness to leave a safe refuge and the trade-off between food and safety: a test with social fish

Jesse Balaban-Feld<sup>1</sup>, William A. Mitchell<sup>2</sup>, Burt P. Kotler<sup>3</sup>, Sundararaj Vijayan<sup>1</sup>, Lotan T. Tov Elem<sup>1</sup>, Michael L. Rosenzweig<sup>4</sup> and Zvika Abramsky<sup>1</sup>

<sup>1</sup>Department of Life Sciences, Ben-Gurion University, Beer Sheva 8410501, Israel

<sup>2</sup>Department of Biology, Indiana State University, Terre Haute, IN 47809, USA

<sup>3</sup>The Jacob Blaustein Institute for Desert Research, Mitrani Department of Desert Ecology, Ben-Gurion University, Sde Boker 84990, Israel

<sup>4</sup>Department of Ecology and Evolutionary Biology, The University of Arizona, Tucson, AZ 85721, USA

JB-F, 0000-0002-5832-4513

Refuges offer prey animals protection from predation, but increased time spent hiding can reduce foraging opportunities. Within social groups, individuals vary in their refuge use and willingness to forage in the presence of a predator. Here, we examine the relative foraging benefits and mortality costs associated with individual refuge use and foraging behaviour within groups of goldfish (*Carassius auratus*) under predation risk from an avian predator (little egret—*Egretta garzetta*). We assessed individual order of emergence from the refuge and participation over 15 group foraging outings, and assigned each fish a daily outing index score. The individual fish that emerged from the refuge earlier than the other group members and that participated in more outings received high outing index scores and consumed more food compared with fish that tended to emerge in posterior positions and participate in fewer outings. However, individual fish that attained high outing index scores suffered a higher risk of predation. Furthermore, the amount of time the egret spent at the pool affected group foraging behaviour: as predation risk increased, groups of fish consumed significantly less food. Our results exemplify the trade-off between foraging success and safety from predation that prey species regularly experience.

## 1. Introduction

Prey animals maximize survival by enhancing energetic gains while at the same time reducing mortality risk [1,2]. In the presence of a predator, social prey can lessen the probability of being attacked by increasing time spent hiding in protected refuges [3]. Refuges provide protection from predators but offer little or no access to food resources; therefore, increased time spent hiding within a refuge reduces prey foraging opportunities [4,5]. As such, individuals must trade off energetic requirements and predation risk when considering when to leave a refuge and forage in dangerous locations that may contain predators [6–9].

Within social fish groups, individuals can differ in their willingness to forage in the vicinity of a predator [10,11], and in their refuge use [12]. Once inside a refuge, certain individuals in fish shoals can act as leaders that initiate group movement and influence others to follow them out of the safe refuge [13–16]. Previous work has considered the relative foraging benefits and mortality risks of different spatial positions within groups foraging in open areas, demonstrating that individuals occupying frontal and edge positions obtain higher energetic rewards [17,18], but also experience the greatest predation risk [19–21]. However, less is known about how the order of emergence of group members from a protected refuge can influence relative fitness costs and benefits among social prey living under predation risk.

When group members compete for access to limited food particles, those individuals that emerge from the refuge earlier than others and spend the most time foraging will have more opportunities to reach and consume food [22]. However, in the presence of an ambush predator employing a 'sit-and-wait' tactic, the first few individuals to emerge from the refuge are more likely to be spotted and attacked [23]. Thus, the most energetically rewarding positions of emergence from a refuge may be associated with an increased probability of being captured by a predator. On the other hand, cautious group members that choose to reduce risk by emerging from a refuge only after others have already left, or by simply not joining a group outing, will pay the cost of reduced foraging success [24,25]. In this way, individual willingness to forage in the presence of a predator and the order in which individuals emerge from a refuge can determine relative levels of food consumption and mortality among social group members.

Here, we assess individual order of emergence and willingness to leave a safe refuge within social fish groups, and simultaneously examine relative levels foraging success and survival. We predicted that the fish that were more willing to leave the safety of the refuge to forage, and that frequently were among the first few fish to emerge, would (i) consume more food and gain more weight, but (ii) also experience higher risk of capture by the predator.

## 2. Methods

### (a) Study species

The prey species was the goldfish (*Carrassius auratus*), a small domesticated cyprinid. The goldfish were acquired in northern Israel (Ma'agan Michael, Hof HaCarmel), where they are raised in large (4000–40 000 m<sup>2</sup>) outdoor pools. Goldfish are related to darkly coloured carp species that inhabit streams, ponds and lakes in their native range in eastern Asia [26]. Other than colour, *C. auratus* have changed little from their ancestral form, and exhibit normal carp behaviours including seeking cover and foraging as a social group [27]. Similar to other carp species that evolved in muddy water environments, goldfish do not exhibit vigilance behaviour, but rather manage risk through the use of time allocation and by taking cover when a predator is in the area [28]. There is a growing body of literature that uses goldfish as a model fish species for behavioural research [29–31]. Furthermore, prior experiments in our laboratory have shown that goldfish naturally school, seek refuge from predation and later re-emerge to forage [28,32].

The predator in our experiment was the little egret (*Egretta garzetta*), a small heron in the Ardeidae family. Little egrets stalk prey in shallow water and are opportunistic foragers of small fishes, amphibians, crustaceans and insects [33]. Our egrets were wild captured in northern Israel (Kfar Ruppin, Beit She'an Valley), and were released at the location of capture following the experiment.

### (b) Housing of experimental animals, measurement of fish body size and individual fish marking

Prior to use in experiments, fish are housed in a main 1880 l cylindrical holding pool (2.0 m diameter × 0.6 m height) and fed 1 g of fish food pellets per fish per day. Fish are given a minimum of one week acclimation in the main holding pool before being used in experiments. The day before the experiment, individual fish were moved to a temporary 840 l tank (1.2 × 1.0 × 0.7 m).

Next, individual fish were randomly removed from the temporary holding tank with a net, lightly anaesthetized with a diluted solution of MS-222, weighed and measured from head to tail. Next, to allow for individual identification, the fish were marked with black Biotouch micropigment ink using electric tattooing needles (see electronic supplementary material, figure S1 for examples of fish markings). Individual fish were tested once for willingness to enter a novel area, but we did not find any significant relationship with this behaviour and our experimental variables; therefore, the results are not presented.

Prior to use in experiments, egrets were held in a main rectangular holding cage (4 × 4 × 3 m) and fed 100 g of fish per day. Egrets are given a minimum of one week in the main holding cage, and one week in the experimental aviary for acclimation. During experimentation, the egret was held in a rectangular cage (3 × 2 × 1.7 m) that is connected to the outside of the experimental aviary (see below). Following each 4 h experiment, the egret was placed back into the holding cage, and provided a sufficient amount of fish to reach the required daily 100 g of food.

### (c) Experimental design

Experiments were conducted in a specially designed outdoor aviary (7 m diameter) containing three equally spaced 1060 l pools (1.5 m diameter × 0.6 m depth) (electronic supplementary material, figure S2). The water in the experimental pools was kept at a constant temperature of 25°C. The pools contained a plastic 1 cm mesh floor that limited the fish to the upper 15 cm of the pool and provided a surface for the egret to walk and forage on. Each pool included two distinct microhabitats for the fish. In the centre of each pool, an opaque disc (0.47 m diameter) mounted flat on the water surface offered a safe refuge under which to hide from predators, but no access to food. The surrounding open water provided an area in which the fish were at risk of predation but had access to food. Floating food pellets were dispensed from a conveyor belt into the risky microhabitat at a constant rate of one pellet every 4 min (electronic supplementary material, figure S3). In this open-water habitat, the fish experienced a gradient of risk as the predatory egret was not always present at the focal pool, and did not always succeed when attempting to capture fish. Additionally, individual fish located close to the refuge could reach the safety of cover quicker than individuals located far from the refuge. Our experiment was designed to simulate the trade-off between food and safety that prey experience. Organisms have safe locations (e.g. refuges) and/or behaviours (e.g. remaining motionless) in which they cannot forage, and other less secure locations and active behaviours that expose them to predation but allow them to forage [3,4].

For this experiment, we focused on just one of the three pools. The two non-experimental pools contained 15 non-experimental fish and provided the egret with multiple places to forage. This encouraged the egret to spend time moving among multiple locations to hunt, importantly providing time for the groups of focal fish to recover and school naturally following the departure of the predator from the focal pool. In the focal pool, we observed groups of eight individually marked fish, and restricted access to the covered refuge to one 20 cm wide door in order to observe the order and positioning of individual fish leaving the safety of the refuge to move into the risky microhabitat. We used an underwater camera placed below the refuge, and two other identical cameras placed above the surface of the water near the edge of the focal pool, to assess individual order of emergence from the refuge and food consumption (cameras: Geovision model GV-EVD2100). Plastic mesh stopped the food pellets from entering the covered refuge in order to force fish to trade off food and safety. Additionally, thin plastic barriers placed 2 cm under the surface of the water were used to contain

the floating food particles within the view of our camera array (see electronic supplementary material, figures S1 and S3).

We tested each group of eight fish over two consecutive days. The first day was treated as a control with no egret predator present, and fish behaviour was recorded for 4 h. On the following experimental day, an egret was released into the aviary, and allowed free movement for 4 h during which time we recorded the behaviour of fish and egret. After 4 h, the egret was removed and returned to the adjacent holding cage. Control and experimental days were each recorded for 4 h in the same manner. A new set of eight fish was used for each 2 day control–experiment sequence. We analysed  $n = 19$  groups of eight fish, for a total of  $n = 152$  individual fish. As individual egret hunting style and aggressiveness is highly variable, a single egret was used as the predator throughout the experiment in order to ensure that the different groups of goldfish experienced the same predator hunting mode and general level of risk.

#### (d) Daily outing rank and food consumption

On each day, we observed individual order of emergence and food consumption over the first 15 foraging outings out of the safe refuge. The first outing on a given day was able to be examined only after all fish were observed to be under the covered refuge. On experimental days, recording of fish outing behaviour began only after the egret first visited the focal pool. Throughout the day, outings commenced when the first fish crossed through the door into the risky open-water microhabitat. Each outing ended when all of the participating fish returned to the covered refuge.

To assess relative individual outing behaviour over each day, we developed an outing index to take into consideration both spatial positioning and outing participation. The outing index was calculated in the following manner. For each outing, the first individual leaving cover was given an outing score of 8, the second a score of 7 and so on to the last fish that crossed through the door. Any fish that did not participate in a given outing was given a score of 0. We calculated a daily outing index for each individual fish as the average of each fish's outing scores (i.e. sum of scores divided by 15). Following each control and experimental day, the fish were ranked based on their outing index scores, with the highest scoring fish receiving the top daily outing rank (1) and so on to the lowest ranked fish (8). Separate daily outing ranks were calculated for control and experimental days.

During each outing, we recorded individual pellet consumption in order to measure foraging success. At the end of each experimental day, we removed the surviving fish, recorded which fish had been captured by the egret and counted the number of uneaten food pellets. All surviving fish were then weighed to determine overall weight change (%) from the beginning to the end of the experiment as an additional indicator of foraging success.

#### (e) Statistical analysis

Data were tested for normality and homoscedasticity in order to meet statistical assumptions. To minimize observer bias, blinded methods were used when all behavioural video recordings were analysed. A linear mixed model was used to determine the influence of body length on overall weight change (%). We employed generalized linear mixed models (GLMMs) to analyse the relationships between body length and food pellet consumption on control and experimental days. Control and experimental days were analysed separately. When the response variable in our GLMM was a count (e.g. number of food particles eaten), we performed a residual analysis using the R package DHARMA. Using this package, we generated 250 simulations assuming a GLMM with Poisson-distributed error, and tested whether the actual

residuals differed significantly from the simulated residuals with a Kolmogorov–Smirnov test. We also performed a dispersion test. In those cases in which the residuals did deviate significantly owing to overdispersion, we used a GLMM with a negative binomial distributed error. Individual ID ( $n = 152$ ) was added as a random effect, with Individual ID nested within Group ID ( $n = 19$ ), and likelihood ratio tests were used to determine the significance of each relationship. The analyses were performed using the lme4 package [34] in R [35].

First, using regression analyses, we examined relationships between daily outing rank and both measures of foraging success (pellets eaten and weight change (%)). Control and experimental days were again analysed separately. To confirm that the variance in individual average outing index scores was greater than would be expected by chance, we employed a randomization analysis [36] (electronic supplementary material, appendix SA). Next, considering only experimental days, we analysed the effect of daily outing rank and body length on fish survivorship with a GLMM using the binomial family with a logit link. We performed our analysis using the lme4 package of R to be able to take into account group effect. We considered Survival (0 or 1) to be the response, daily outing rank (1 through 8) and body length to be the fixed effects, and group ( $n = 19$ ) to be the random effect. The logit values predicted by the regression were back-transformed to determine the predicted probability of survival associated with each of the eight daily outing ranks. Examining 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). We then used a linear regression analysis to assess how the amount of time the egret spent at the focal pool (predation risk) influenced group fish feeding rates. The paired two-tailed  $t$ -tests were used to compare the mean fish group outing size, and outing duration between control and experimental days. Finally, we subsampled  $n = 10$  experimental days, and recorded the total time out of cover for each individual fish ( $n = 80$ ) over the 15 recorded outings. We then used a linear regression to determine the correlation between 'outing index' and time spent outside of the refuge.

Data available on figshare: 10.6084/m9.figshare.6507056.

### 3. Results

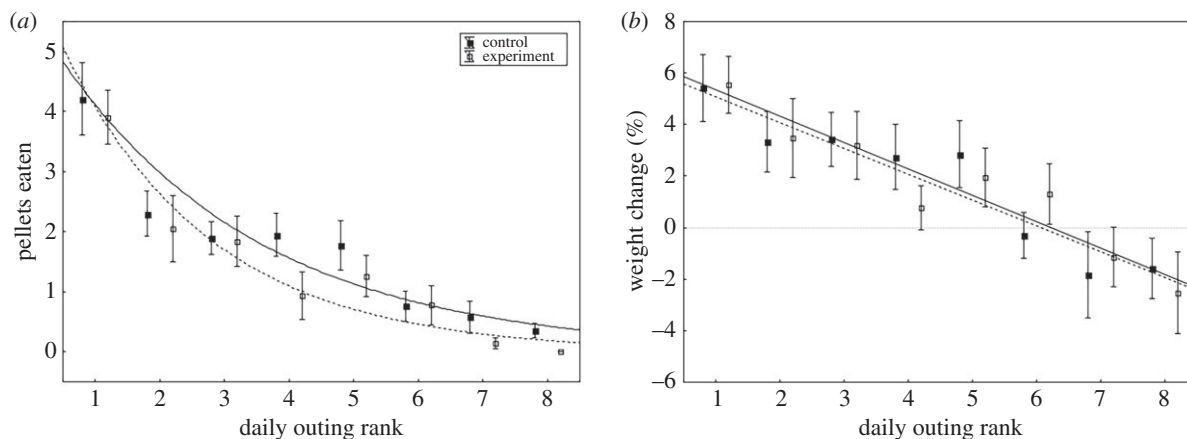
#### (a) Body size and food consumption

The initial goldfish body length from head to tail varied between 7.30 and 11.60 cm. We found no relationship between body length and the number of food pellets eaten on either control or experimental days (control— $\chi^2(1) = 0.98$ ,  $p = 0.32$ ; experiment— $\chi^2(1) = 0.07$ ,  $p = 0.79$ ). Additionally, we found no relationship between body length and overall weight change ( $\chi^2(1) = 0.00$ ,  $p = 0.98$ ). The initial body weight ranged from 5.01 to 13.42 g, and there was no relationship between initial body weight and weight change (%) ( $\chi^2(1) = 0.07$ ,  $p = 0.79$ ).

#### (b) Foraging benefits and mortality costs

Individual outing index scores ranged between 0 and 6.83 and we observed that certain fish spent more time leading the group out of cover and participated in more outings compared with others (electronic supplementary material, appendix SA). A subsample analysis found that outing index scores were positively correlated with time spent outside of the refuge ( $F_{1,78} = 62.4$ ,  $r = 0.67$ ,  $p < 0.001$ ).

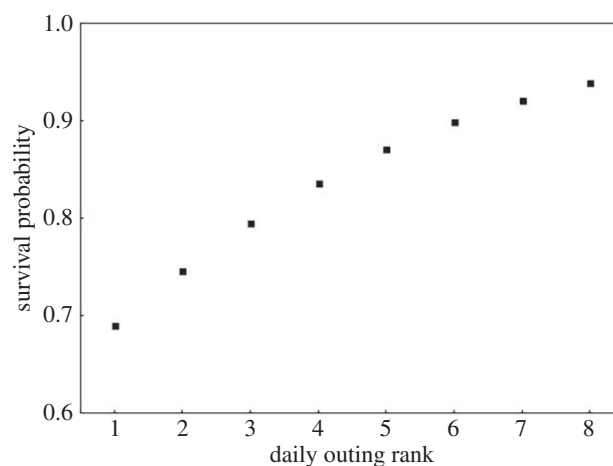




**Figure 1.** Mean ( $\pm$  s.e.) (a) pellets eaten and (b) weight change in relation to daily outing rank for both control and experimental days. For each day, individual fish were ranked based on their outing index scores, with the highest scoring fish receiving the top daily outing rank (1). Black squares and solid lines represent control data; open squares and dashed lines represent experimental data. Each data point represents the mean values for each rank taken from  $n = 19$  days (e.g. mean of 19 fish ranked 1). In (b), data points above the dotted horizontal reference line indicate weight gain, and points below the reference line indicate weight loss.

For both control and experimental days, we found that the fish with higher daily ranks ate more pellets (control— $F_{1,7} = 75.50$ ,  $r = 0.96$ ,  $p < 0.001$ ; experiment— $F_{1,7} = 111.66$ ,  $r = 0.97$ ,  $p < 0.001$ ; figure 1a). Furthermore, higher ranked fish gained significantly more weight compared with lower ranked fish as weight change was positively related to daily outing rank (control— $F_{1,7} = 51.32$ ,  $r = 0.95$ ,  $p < 0.001$ ; experiment— $F_{1,7} = 50.59$ ,  $r = 0.95$ ,  $p < 0.001$ ; figure 1b).

Regarding mortality risk, we analysed the influence of outing index and body length on fish mortality with a GLMM with binomial error term, and group as a random effect. We found that mortality increased with daily outing rank. The coefficient of the log odds ratio of the probability of being eaten was positive and significant ( $0.277 \pm 0.121$ ;  $\chi^2(1) = 5.81$ ,  $p = 0.02$ ). We observed that the top ranked fish that scored high daily outing scores were more likely to be killed by the egret (figure 2). Furthermore, on the fatal outings, the preponderance of fish captured were either the first or second fish to emerge out of the protected refuge (figure 3). Body length had no significant effect on the probability of being captured when it was the only predictor variable ( $0.060 \pm 0.309$ ,  $\chi^2(1) = 0.038$ ,  $p = 0.85$ ), or when it was included in a model containing outing rank ( $0.072 \pm 0.308$ ,  $\chi^2(1) = 0.054$ ,  $p = 0.82$ ).



**Figure 2.** Effect of daily outing rank on fish survivorship. The logit values predicted by the GLMM regression were back-transformed to determine the predicted survival probabilities (black squares). There was a significant interaction between daily outing rank and survival probability (intercept = 0.78,  $CI_{0.95} = -0.17-1.84$ ; slope = 0.28,  $CI_{0.95} = 0.05-0.53$ ; regression:  $\chi^2(1) = 5.81$ ,  $p = 0.02$ ).

As predation risk increased (more egret time at focal pool), the groups of fish ate significantly less food ( $F_{1,17} = 8.76$ ,  $r = -0.60$ ,  $p < 0.01$ ; figure 4).

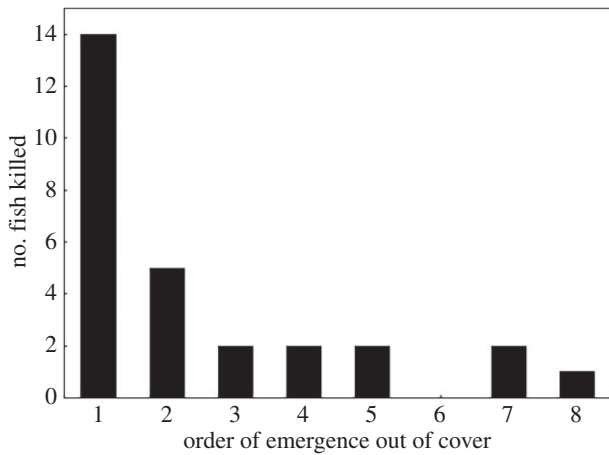
### (c) Effect of predation risk on group foraging behaviour and food consumption

The average fish group outing size was significantly smaller on experimental days compared with control days (mean  $\pm$  s.e. number of fish: control— $4.56 \pm 0.16$ ; experimental— $3.76 \pm 0.42$ ; paired  $t$ -test— $t_{18} = 2.16$ ,  $p = 0.04$ ). Additionally, the presence of the egret on experimental days significantly decreased the average length of fish foraging outings (mean  $\pm$  s.e. outing duration: control— $3.18 \pm 2.23$  min; experimental— $0.65 \pm 0.10$  min; paired  $t$ -test— $t_{18} = 4.76$ ,  $p < 0.001$ ).

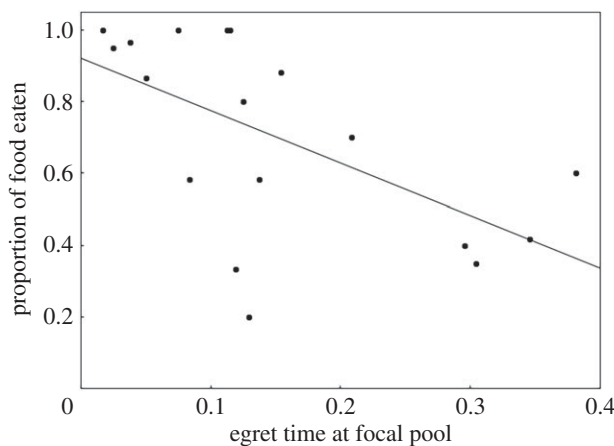
The groups of fish consumed 100% of the pellets on all control days. On experimental days, with the exception of one day that was removed as a possible outlier where the egret spent 0.73 of the day at the focal pool, the proportion of egret foraging time at the focal pool ranged between 0.02 and 0.38, and significantly affected fish food consumption.

## 4. Discussion

We simultaneously observed the foraging benefits and mortality costs associated with refuge use and willingness to forage under predation risk. At the individual level, group members that took more foraging risks enjoyed the most foraging success, but experienced the highest probability of being killed by the egret predator. On the other end of the spectrum, individuals that took few risks had a very low probability of being captured, but rapidly lost weight. At the group level, the presence of the egret significantly reduced overall foraging behaviour and consumption, as the fish foraged in smaller groups and spent considerably more time in the refuge in response to perceived predation risk. Taken as a whole, our results exemplify the trade-off



**Figure 3.** Order of emergence leaving covered refuge on fatal outing for fish captured by egret predator ( $n = 28$ ). Three fish were killed by egrets before the first recorded outing and were thus excluded.



**Figure 4.** Relationship between predation risk (time egret spent at focal pool) and total group fish food consumption (proportion of food pellets eaten). Each black dot represents data from one of  $n = 18$  experimental days (one experimental day was excluded as an outlier).

between foraging success and safety from predation that prey species regularly experience [4,6,37].

Individual willingness to forage, and the order of emergence from the refuge, influenced relative foraging success among group members. The fish that emerged earliest and most often consumed significantly more food than the fish that followed. Our results support earlier work that has shown individuals more willing to take risks leaving a refuge to move into an open environment benefit from increased foraging success [38]. In our system, single pellets were dropped onto the surface of the water at a constant rate of one pellet every 4 min. Consequently, food resources were limited and, in most cases, only one or two fish would consume food pellets on a given outing. In such a situation, the first few fish to enter the risky habitat enjoyed an immense advantage as they were able to reach the scarce food pellets before the other fish following behind. We have demonstrated that in an environment where food resources are scarce, those individuals that take the most risks secure early access to the limited food. By contrast, if food is abundant, relative order of emergence from a refuge becomes less important as the majority of individuals will be able to find and consume a sufficient amount of food. Thus, the

resource density in a given habitat may partially determine the value of risky foraging behaviour [39].

High daily outing ranks were positively related to both foraging success and mortality risk. This was expected owing to the fact that high daily outing scores were assigned to individuals that tended to be among the first few fish to emerge from the refuge and that participated in a high proportion of foraging outings. Such fish were more likely to be exposed and captured when the egret predator was present, compared with the other, more risk-averse group members [40]. Additionally, on a single outing basis, the first fish to emerge from the protected habitat experienced considerably more mortality risk than all other trailing group members. This was probably owing to the fact that egrets are ambush predators that quickly strike at the sight of suitable prey [41].

The reason why some fish in our study were more likely to leave the safety of cover than others in order to forage remains unclear. In contrast with prior work on fishes [22], we did not find a significant relationship between individual body length and foraging success. Other studies have shown that internal state variables related to body size, such as metabolic capacity and energetic state, motivate individuals to take risks [16,42–44]. However, in our study, all fish were well fed prior to testing, so hunger differences were most likely not a factor that should have influenced risk-taking behaviour. Theory suggests that contrasting behavioural tactics are maintained within populations via the trade-off between short-term success and long-term survival [45,46]. The results of our study illustrate how individuals that take more risks achieve greater immediate fitness gains over a shorter life-span, while more cautious individuals have less short-term success but live longer [47]. Nonetheless, more work is needed to better understand how individual differences interact with external factors, including interactions among conspecifics and between predator and prey, to ultimately motivate certain individuals to take more risks when foraging for resources.

Overall, our study illustrates both the lethal [48] and non-lethal effects [49,50] that predators have on prey. In addition to generating mortality risk, the activity of the predator significantly influenced fish refuge use and foraging success. The presence of the egret on experimental days drastically reduced overall fish foraging behaviour compared with control days that lacked a predatory threat. Furthermore, on experimental days, the duration of time the egret spent at the focal pool directly influenced how much time the fish spent hiding under the refuge. The groups of fish spent less time foraging in response to increased predation risk, illustrating how access to a safe refuge can enhance the impact of predation risk via increased missed foraging opportunities [51]. Our results add to the literature demonstrating how fear from predation can stimulate defensive behaviours that reduce the risk of mortality, but also reduce time spent foraging, and thus lower fitness [52–54].

Although the results of our study demonstrate how variation in individual refuge use and risky foraging behaviour influence relative levels of foraging success and mortality within social groups, certain limiting aspects of our experimental set-up warrant discussion. Owing to the fact that our camera array was fixed and lacked coverage of the entire open-water microhabitat within the experimental pool, we could only record discrete events (e.g. in/out of refuge, order of emergence from refuge). As a result, we

could not record the spatial positioning of the individual fish in the open-water microhabitat (cf. [55,56]) and were unable to reveal much regarding the group-level processes linked with the trade-offs between foraging and safety. Previous work suggests that social interactions and feedback among conspecifics can influence group movement and decision-making [57]. As such, it is not necessarily the case that order of emergence from a refuge is indicative of spatial positioning within freely foraging groups [58]. Accordingly, future experiments are needed to clarify how individual decisions regarding leaving a refuge may or may not correlate with spatial positioning and foraging success within social groups foraging in the open under predation risk.

Nevertheless, our study explicitly characterizes the trade-off between foraging success and mortality risk that social prey encounter, and illustrates links between prey refuge use, foraging success and mortality risk in an environment containing a real, active predator. Live predators have frequently been restrained, confined separate from prey, or replaced by models and/or kairomones in experiments

examining prey anti-predator behaviour; however, this study demonstrates how incorporating freely moving, ecologically relevant predators can provide important insights into predator–prey interactions [59].

**Ethics.** All applicable international, national and 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).

**Data accessibility.** Data available in the electronic supplementary material and at: <https://doi.org/10.6084/m9.figshare.6507056>.

**Authors' contributions.** J.B.-F. conceived the experiment and wrote the manuscript; W.A.M. contributed to statistical analyses; B.P.K., S.V., L.T.T.E., M.L.R. and Z.A. contributed to experimental design, video analyses and edited early drafts of the manuscript.

**Competing interests.** The authors declare no competing interests.

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