Evolutionary Ecology Research, 2018, **19**: 319–332

Influence of manipulated risk of predation in a predator–prey foraging game in a patchy environment: egret and goldfish in experimental aviaries

Sundararaj Vijayan,[1] William A. Mitchell,[2] Burt P. Kotler,[3]
Michael L. Rosenzweig,[4] Jesse Balaban-Feld,[1]
Lotan Tamar Tovelem[1] and Zvika Abramsky[1]

[1]*Department of Life Sciences, Ben-Gurion University, Beer-Sheva, Israel,*
[2]*Department of Life Sciences, Indiana State University, Terra Haute, Indiana, USA,*
[3]*Department of Desert Ecology, Ben-Gurion University, Sde Boker Campus, Israel and*
[4]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA*

ABSTRACT

Background: Predator and prey engage in a behavioural game in which the behavioural decision of one affects that of the other. Behavioural games can be influenced by differential predation risk caused by habitat patchiness in the environment. Patches may provide prey with a differential risk of predation due to the size of area that provides refuge. The predator has to respond to the existence of patches with varying degrees of predation risk because this variable affects the time they spend foraging in each patch.

Question: Will the predator and the prey respond optimally to each other in a behavioural game?

Methods: We conducted behavioural experiments in two identical aviaries (7 m diameter), each with three separate pools (1.52 m diameter, 0.60 m deep, ~1000 litres capacity). Each pool had two habitats, one a horizontal cover in the centre of the pool (the refuge), the other open water (the risky patch). We used little egrets (one per experiment) and goldfish (15 fish per pool) as predator and prey respectively. We used small, medium, and large cover sizes as refuge, thus manipulating the predator's killing efficiency. We assigned a refuge size to each pool at random. We then observed the behavioural games of both players for 6 hours per experimental day. We recorded the time fish spent in the refuge; the time fish took to return to open water after being frightened into seeking cover (refractory time); the amount of food consumed by the fish; the time the egret spent in a single pool; the time it took the egret to return to that pool after leaving it; the number of fish caught by an egret during each phase of the experiment; and whether a fish was caught while it swam in open water or hid under a refuge,

Results: Contrary to our prediction, the fish were more active in the pools with smaller covers even though that is where they suffered the highest mortality. The egrets did not differentiate between cover sizes, spending a similar amount of time foraging at all three pools. However, the egrets timed their visits to the pools with the three sizes of covers in a way that matched the fish

---

Correspondence: Z. Abramsky, Department of Life Sciences, Ben-Gurion University, Beer-Sheva 84105, Israel. email: zvika@bgu.ac.il

refractory times in those pools. The egrets returned to a pool just when the fish were beginning to re-emerge from under the cover, thus maximizing their capture success.

Keywords: cover, differential risk, killing efficiency, optimal foraging, predator–prey behavioural games, refuge from predation, risk of predation.

INTRODUCTION

Predation is a major selective force in evolution. Almost all animal species are potential prey for others, at least during parts of their life cycle (e.g. Lima and Dill, 1990). Since predators must kill their prey or else die of starvation and the prey should protect themselves by trading off food and safety, various adaptations have evolved both among predators and prey (Brown and Mitchell, 1989; Brown, 1992; Lima, 2002). Some adaptations are morphological while others are behavioural, including apprehension, vigilance, and time allocation (use of cover and avoiding risky locations and times) (e.g. Lima and Dill, 1990; Luttbeg and Kerby, 2005; Preisser *et al.*, 2005).

Optimal foraging theory (e.g. MacArthur and Pianka, 1966; Stephens and Krebs, 1986) provides a theoretical framework for testing and understanding foraging decisions made by animals. Numerous studies have used this theory for studying different aspects of foraging behaviour such as diet selection (Brown and Mitchell, 1989; Mitchell, 1990; Lima *et al.*, 2003), habitat use (Fretwell and Lucas, 1969; Rosenzweig, 1981; Rosenzweig and Abramsky, 1997), patch use (Charnov, 1976; Brown, 1988, 1992), competition (Rosenzweig and Abramsky, 1997), and predation (Lima and Dill, 1990; Abramsky *et al.*, 2002; Kotler *et al.*, 2010).

Game theory assumes that both predator and prey individuals forage so as to maximize their fitness. Since predators and their prey are engaged in a foraging game in which the behaviour of each species affects the optimal behaviour of the other, various behavioural adaptations have evolved both among predators and prey (e.g. Brown and Mitchell, 1989; Brown, 1992; Lima, 2002). Indeed, many studies have viewed predator–prey interactions as a game in which the decisions of each player are affected by the decisions of the other players (e.g. Sih, 1984, 1998, 2005; Hugie and Dill, 1994; Brown *et al.*, 1999; Kotler *et al.*, 2002, 2004; Hammond *et al.*, 2007).

Charnov (1976) developed the marginal value theorem (MVT) to predict optimal foraging time in a depletable food patch embedded in an environment with many food patches. The model assumes that the forager has evolved to maximize its average rate of energy intake, defined as the average rate of return from a patch divided by the average time to travel to and exploit that patch. The model predicts that the decisions taken by the forager are based on its perception of the quality of the environment. It was originally applied to a forager that eats a food resource, such as seeds or plants, that cannot respond behaviourally to the approaching predator. However, some predators do hunt for prey that can respond behaviourally to risk of predation through time allocation, vigilance, or a combination of the two (e.g. Hugie and Dill, 1994; Brown *et al.*, 1999; Kotler *et al.*, 2002, 2004; Hammond *et al.*, 2007). This results in a behavioural game between a predator and prey in which the optimal behaviours of each player might depend on those of the other. In such a behavioural game, rules other than MVT might govern foraging time in a patch.

But what happens when both players are free to respond behaviourally to each other and play a foraging game? We have developed a variation of the Charnov model in which the predator is allowed to respond to prey behaviour (Katz *et al.*, 2013, 2014a). It allows us to estimate the optimal foraging time in a patch in a game situation.

From the prey's point of view, it should trade off food and safety mostly by becoming vigilant and by shifting its activity, temporarily, to a safer microhabitat (time allocation). From the predator's point of view, it will maximize its capture success by adjusting its foraging strategy to the prey's anti-predatory behaviour so as to increase its success rate. Can both the predator and the prey simultaneously respond to one another, and if so, how?

To test such simultaneous responses, we previously (Katz *et al.*, 2010, 2013, 2014a, 2014b) developed a foraging game in an experimental setting of artificial pools with goldfish (*Carassius auratus*) as prey and little egrets (*Egretta garzetta*) as predators (Fig. 1). We conducted several experiments, in the first of which all pools contained 15 fish (Katz *et al.*, 2010). In a second experiment, pools were allocated different numbers of fish: 10, 15, and 20 (Katz *et al.*, 2013). In the third study, all pools contained the same number of fish, but that number was varied from 15 to 25 fish per pool (Katz *et al.*, 2014a). And in a fourth study, we varied the number of pools (Katz *et al.*, 2014b).

Our results showed that, in each case, fish and egret adjusted their behaviours quantitatively in ways that suggested that both species were adaptively responding to the rules of an interactive foraging game. Egrets responded adaptively to the behaviour of the fish by adjusting their visitation rates to pools and their foraging times within pools. The result was maximization of their capture success. In response to the egret behaviour, fish adjusted their behaviour by trading off food and safety. Thus, whatever adaptive responses these two species possess in natural environments would seem to be sufficiently plastic to transfer to the artificial circumstances of our experimental pools.

Researchers who have considered adaptations of predators have also recognized the probable importance of habitat patchiness (especially Lima, 2002). Predators ought to respond to the existence of patches with a varying degree of risk of predation because this variable affects the time predators spend foraging in each patch. Thus, we decided to investigate the importance of differential risk of predation between patches on the behavioural game of the two players. We set the number of fish to 15 in each pool. We varied the size of the refuge in each pool so that pools had either a small, a medium, or a large refuge (see Methods, below). The size of refuge influenced the predator's ability to attack and catch prey, thus modifying their killing efficiency. We examined the behavioural responses of both the egret and the fish to treatments with different refuge size. In all treatments, we distributed fish food only in the riskier of the two habitats, so that the fish had to leave the refuge in order to forage and eat the food in the risky open water.

Since there was never more than a single foraging egret at a time, fish in treatments with a large refuge should experience a smaller per-capita predation risk than those in treatments with a medium or small refuge. One would expect that the decreased risk would lead fish in treatments with a large refuge to spend more time in the riskier microhabitat, eat more food, yet suffer a reduced predation rate compared with fish in treatments with a medium or small refuge. One would also expect fish offered the smallest refuge to show the opposite behaviour, rarely emerging into the riskier habitat. The reader will soon see that fish did not behave as expected.

The asset-protection principle (Clark, 1994) predicts that the magnitude of a prey's response to predation risk varies with the energy state of the prey. Prey with a higher energy state are expected to show stronger avoidance of predation risk than prey with a lower energy state. Such prey may reduce their activity in high-risk habitats to such a degree that the overall expected benefit to the predator of hunting in that habitat is actually less than in habitats where its killing efficiency is less, and prey show less avoidance of the predator.

Furthermore, the predator in such a pool will have a lower expected value than in a pool with lower killing efficiency.

Our predictions were as follows:

1. Fish will reduce their foraging activity in pools with predation risk compared with control pools without predation risk.
2. In pools with higher predator killing efficiency (smaller prey refuges):
   - fish will reduce foraging activity;
   - fish will leave more food uneaten;
   - predators will spend less time hunting.
3. The egret will use a Charnov-like rule (Katz *et al.*, 2014b) to choose the combination of foraging time in a pool and return time to a pool that results in the most fish captured.

METHODS

The predator and forager in our experimental treatments was the little egret, *Egretta garzetta* (Ardeidae), a small heron. Little egrets stalk their prey in shallow water, often standing still in ambush. They are opportunistic hunters of fish, amphibians, crustaceans, and insects. Without alternative food, each little egret must eat 15–20 (about 100 g) goldfish per day to meet its daily energetic demands (Kushlan, 1978). Egrets were caught in the wild (Ma'agan Michael, Kibbutz Ma'agan Michael D.N. Menashe, Israel, 32°33′20″N, 34°54′51″E). After participating in the experiments, egrets were returned to and released at the location of capture.

The prey comprised the 'comet' variety of common goldfish, *Carassius auratus*, a relatively small cyprinid. Goldfish are a domesticated variety of a dark, greyish-brown carp native to eastern Asia. The species was introduced to Europe from its original source in China in the early sixteenth century and today the olive-green phenotype inhabits most natural lakes, streams, and natural ponds there (Holopainen *et al.*, 1997). Other than colour, comet goldfish are little changed from their ancestral form (Holopainen *et al.*, 1997). Consequently, a growing literature has used goldfish as a model study organism for behavioural research (e.g. Pitcher and Magurran, 1983; Vargas *et al.*, 2004; Weir and Grant, 2004; Amano *et al.*, 2005; Stenberg and Persson, 2005; Yoshida *et al.*, 2005; Dunlop *et al.*, 2006; Ingrum *et al.*, 2010). We used goldfish ranging in size from 6 to 7 cm (6 to 7 g). Such individuals are easily captured and handled by egrets.

The experimental system

We conducted the experiment in two specially designed aviaries (each 7 m in diameter; Fig. 1) at the Ben-Gurion University Bergmann Campus, in Beer Sheva, Israel (31°15′5.2″N, 34°47′59.2″E). Each of the two aviaries contained three pools (patches), equidistant from each other, with a diameter of 1.52 m and a depth of 60 cm (Fig. 1). A plastic wire mesh placed horizontally in each pool created a false bottom that restricted fish to the top 15 cm of water.

Each pool had two microhabitats:

- The *safe microhabitat* was formed by a circular opaque cover over the centre of the pool. The radius of the three different sized covers used was as follows: small (18.75 cm), medium (22.75 cm), or large (36.75 cm). The fish could shelter under the cover. We hoped

Fig. 1. Panorama of the experimental arena as viewed from one of the digital cameras, showing the three equally spaced pools, each 0.76 m in radius. The three pools had protective central covers of different size that formed a refuge for fish: small (18.75 cm radius), medium (22.75 cm radius), and large (36.75 cm radius). Note the egret in the pool on the right.

that smaller covers would increase the killing efficiency of the egret by forcing the goldfish to swim farther away from the cover.

- The *risky microhabitat* consisted of open water in the rest of the pool. There the fish had a high risk of predation by the egret.

In our experiments, goldfish schooled naturally, seeking cover and re-emerging largely as a coordinated group (Pitcher and Magurran, 1983; Magurran, 1984).

The experiment

We placed one egret in each of the two aviaries with 15 fish per pool. The control treatment involved 15 fish per pool without an egret. We conducted the experiment in all four seasons from July 2015 to February 2017. During the winter, we heated the water to 20°C to maintain normal goldfish activity. Most egrets were given five days of acclimation in the aviary and the pool setup. In contrast, fish were given one day of acclimation. We used 12 different egrets in the course of the experiments. The actual size of the cover was assigned at random to each of the three pools for each of the 12 participating egrets.

Egrets were captured in the wild and were kept for at least 6 weeks in an acclimation cage before participating in the experiments. We have come to recognize that after this amount of time they forget any previous hunting experience. Since we used egrets captured from the wild, we wished to minimize handling them during the short time they spent with us in captivity. Therefore, using a continuous, randomized design, we assigned each egret to one or the other aviary during experimental treatments. Experiments lasted 6 hours per day and consisted of two days without an egret (control) followed by two days with an egret (experiment). For the days with an egret, we counted leftover fish food particles at the end of the experiment. Thus, we measured the number of particles and percentage of food consumed by the fish. The fish consumed all the food on control days. At the end of the first experimental day of an egret treatment, we counted the fish in each pool. We replaced missing fish with naïve fish, and placed the egret in a holding cage for the night. At the end of the second day, we replaced all fish with naïve ones.

In each aviary, we used four high-resolution cameras, one above each pool and one that was able to view the entire aviary arena. These cameras recorded every event in the experimental arenas, producing a permanent record of egret and fish behaviours for analysis and archiving. We entered (into an Excel spreadsheet) the behavioural data for each minute of the 360-minute daily experiments. We analysed these data using Python programming and SPSS. In particular, we recorded where the egret was (one observation per minute), and any fish captured during that minute. From these data we could measure the total and mean foraging time in a pool and the average return time to a pool. Return time is simply how long it takes an egret to return to a specific pool after leaving it. We also counted (one observation per minute) how many fish in each pool were outside the sheltered habitat. We then calculated the mean number of fish that were outside cover as well as their mean and total time outside cover on each experimental day.

For each day, we also calculated fish re-emergence time (refractory time). This was defined as: after an egret visit, the mean time between the state of 'all-fish-under-cover' and that of 'one-fish-emerging-outside-cover'. We counted the number of surviving fish at the end of each experimental day. Then, by following egret behaviour continuously on the recorded videos, we could tell when each fish was captured. Thus we were able to measure the number of fish alive during each minute of an experiment. We used the data for each of the three pools in an aviary, both separately and in combination, to calculate the measured variables. Since much of our data is not normally distributed, we used non-parametric tests for analysis. (In most of the figures, however, we use means and standard errors to show trends in the data.)

We found no significant differences between experimental days 1 and 2, and therefore did not use 'experimental day' as a variable in analyses. We present all results and statistical analyses for $n = 24$, thus combining the results for the two experimental days. Some extreme points were removed from some of the analyses (e.g. a foraging time of 6 hours in one pool – the entire length of the experiment).

Ethics

Protocols for animal maintenance and experimental treatments were conducted in accordance with the ethical guidelines for animal research established and approved by the University Committee for the Ethical Care and Use of Animals in Experiments at Ben-Gurion University of the Negev (Authorization No. IL-49-10-2010). A license to catch the egrets was obtained from the Israel Nature and National Parks Protection Authority (Authorization No. 39323). The fish and the egrets were kept under strict veterinary supervision in accordance with all necessary regulations.

RESULTS

The foraging times of the egrets in the pools on the first and the second days did not differ statistically (Wilcoxon signed test: $P = 0.78$). Recalling that naïve fish were introduced into the experimental pools after day 1, we expected more fish to be captured on day 2 than on day 1. Instead, approximately the same number of fish were captured by egrets on the two experimental days (paired t-test = 0.83, $df = 35$, $P = 0.41$). We believe that schooling caused this result as the fish were moving in and out of cover together. Thus, naïve fish were simply following the experienced fish. Therefore, we concluded that there was no day effect, and treated each day as an independent result.

Fish

As predicted, fish spent less time feeding in the egret treatment than in the control. In the absence of the egret (control), the total activity of fish was similar in all pools. But fish activity was significantly higher (Freidman $P = 0.000$) when the egret was absent (282 ± 16.79, 260.00 ± 16.86, and 249.79 ± 19.73 minutes for the small, medium, and large covers respectively).

We had expected that cover size would correlate with fish behaviour, i.e. that fish would expose themselves to predation in the riskier habitat (away from cover where they could feed) in proportion to cover size. But although we found a significant relationship, it was the reverse of that we expected. That is, when the egret was present, fish spent significantly more time in the open area of the pool with the smallest cover size (Freidman $P = 0.04$). The mean total time was 76.6 ± 17.19, 61.00 ± 14.98, and 39.67 ± 9.56 minutes for the small, medium, and large covers respectively.

On experimental days, mean time out of cover was similar for all three cover sizes: 2.96 ± 0.52, 2.95 ± 0.52, and 2.74 ± 0.42 minutes for the small, medium, and large covers respectively. On control days, mean activity time of the fish was significantly higher than on experimental days (Freidman $P = 0.000$); but it was similar between the three pools (16.68 ± 3.21, 16.07 ± 5.01, and 10.81 ± 1.83 minutes for the small, medium, and large covers respectively). The absence of a cover-size effect goes against our expectations.

The mean refractory times of the fish after an egret visit were somewhat variable but not significantly different. Values were 34.54 ± 9.8, 23.17 ± 4.3, and 31.17 ± 12.28 minutes for the small, medium, and large covers respectively (average = 28.23 ± 4.33 minutes).

Although fish in the treatment pools spent time in the riskier habitat in inverse proportion to cover size, the fish in all pools left a similar number of food pellets: 26.38 ± 5.48, 24.25 ± 5.71, and 29.75 ± 6.74 pellets in pools with a small, medium, and large cover respectively. In addition, the mean number of active fish per minute was similar for the three cover sizes: 6.38 ± 0.63, 7.58 ± 0.70, and 7.69 ± 0.76 for pools with a small, medium, and large cover respectively So fish must have consumed similar amounts of food in the three pool types.

Egrets

The egrets captured 6.33 ± 0.82, 2.83 ± 0.42, and 1.25 ± 0.29 fish in pools with small, medium, and large covers respectively. The difference between numbers of captured fish was significant between all cover sizes (Wilcoxon $P = 0.001$). Indeed, the number of fish captured by the egret was significantly higher in pools with small covers (Freidman $P = 0.0001$). The ratio of captures was $(6.33/2.83) = 2.2$ and $(6.33/1.25) = 5.1$ for small/medium and small/large, respectively. It appears that the fish were paying a high price for their risky behaviour.

Contrary to our prediction, the egret spent similar average foraging time per visit (10.89 ± 2.51, 12.12 ± 1.66, and 11.27 ± 2.22 minutes) and similar total time/pool (65.33 ± 9.31, 74.43 ± 10.00, and 70.77 ± 11.81 minutes) in pools with small, medium, and large covers respectively.

Consistent with our prediction, the egret's estimated optimal mean foraging time in a patch, obtained using our Charnov-like technique (Katz *et al.*, 2014b), was similar to that observed for the small, medium, and large covers and for the three pools combined (Table 1).

In Fig. 2 we provide an example calculation of Charnov-like optimal foraging times (estimated foraging times). The Charnov-like optimality technique is different from the original Charnov model (Charnov, 1976) because, using the Charnov-like technique, the egret chooses the mean return time as part of the game.

Table 1. Comparison of estimated and observed optimal patch residency calculated using the Charnov-like technique of Katz *et al.* (2014)

	Small cover	Medium cover	Large cover	All pools
Egret mean return time (minutes)	34.5 ± 2.49	33.2 ± 7.52	38.6 ± 5.93	35.4 ± 3.76
Egret observed mean foraging time (minutes)	10.99 ± 2.55	12.12 ± 1.66	11.27 ± 2.22	11.43 ± 1.25
Estimated foraging time (minutes)	14.3	12.26	19.40	11.46
t-test (observed vs. estimated)	1.36	0.09	1.79	0.03
P-value	0.19	0.93	0.09	0.98

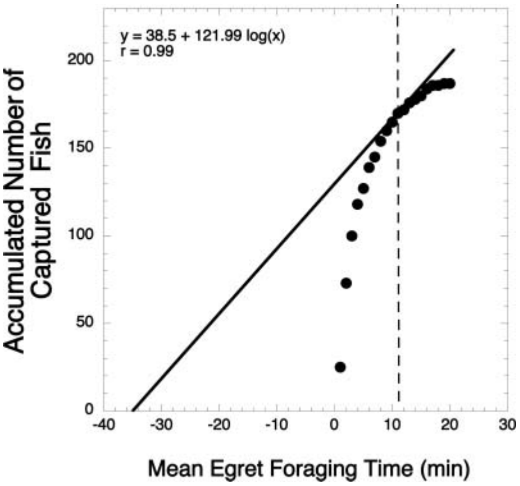

Fig. 2. Using our Charnov-like technique (Katz *et al.*, 2013), we were able to show that the estimated mean optimal foraging time in a pool (11.46 min) was similar to the mean observed time (11.43 min).

DISCUSSION

Predator and prey are engaged in a behavioural game (e.g. Brown *et al.*, 1999; Lima, 2002; Sih, 2005; Wolf and Mangel, 2007). The predator has to capture and eat prey to survive, and the prey has to avoid being eaten by trading off food and safety. Almost every aspect of prey decision-making, from foraging behaviour to mate choice, is influenced by the risk of predation (e.g. Lima and Dill, 1990; Lima, 1998; Sih, 1998).

Our experimental procedures arranged for common goldfish (the prey) and little egrets (their predators) to interact in a setting consisting of three artificial pools with two habitats, one safe and with no food, the other risky but with the food goldfish require. The size of the safe habitat varied between the three pools. Both predator and prey responded behaviourally to the predation interaction as they should have done (Sih, 1984, 2005; Lima, 2002; Schmitz, 2005).

Can fish respond to predator visitation rate and adjust their visits to the risky and productive microhabitats according to the presence or absence of the egret? The prey's behaviour in each patch may indirectly influence the resulting pass-along effect, i.e. transferring the risk to other individuals or other patches (Lima, 2002). Many prey species can only trade off food and safety through time allocation among microhabitats to reduce their risk of predation. Namely, when risk of predation is high, the prey should hide in protected areas and refuges, entering the risky and productive habitats only when the predator is absent. Such feedback between predator and prey has dynamic consequences for their interactions (Brown *et al.*, 1999) and may enhance their stability (Krivan, 1997, 2007).

Katz *et al.* (2010) showed that time allocation is the major anti-predatory behaviour of goldfish. The fish respond to the presence of the egret by reducing significantly the time the fish spend foraging out of cover in the open water. This behaviour is in line with the general theoretical predictions of trade-off models: risky foraging behaviour will vary inversely with increased predation risk and general food availability (Abrams, 1993).

However, in the present study goldfish did not respond to the different sized covers as we had expected. The time they spent in the open water habitat varied inversely with cover size. They did so despite the fact that they suffered a predation cost inversely proportional to cover size. Clearly, our results suggest that we did not correctly anticipate the effects of cover size. We assumed the smaller the cover, the greater the predation pressure. Although true, fish either paid no attention to cover size or actually behaved as if pressure varied inversely with cover size. We believe this result to be a failure of our imaginations rather than a failure of fish to behave optimally.

First, we observed no crowding under the covers. All 15 fish could retreat to a cover at the same time. Second, we did not take the refraction of light into account. Light is refracted when it travels between air and water, so the smallest cover would actually provide more limited protection than would be indicated by the relative sizes of the covers (figure 5 in Katz *et al.*, 2016). In fact, in pools with the smallest covers, a significantly higher proportion of the fish were captured under the cover ($\chi^2 = 9.06$, $df = 2$, $P = 0.01$; Fig. 3). So fish remaining under the smallest covers were not getting the degree of protection provided by the medium and large covers. That would certainly change the trade-off relationship. In particular, it would reduce the protection value of the smallest covers, thus reducing the amount of time an optimal goldfish ought to use them.

We also did not consider the instantaneous per capita reward actually present in pools. Because egrets captured the most fish in pools with the smallest covers, the pools contained most leftover food. On average, the surviving fish in the pools had 15.2 (132/8.67),

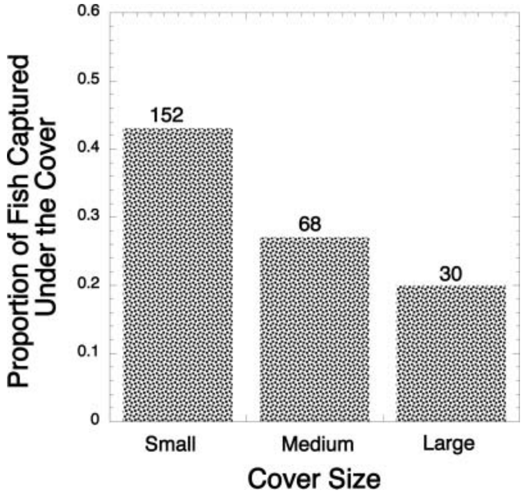

Fig. 3. Proportion of individuals captured under cover in pools with refuges of three sizes. The number above each bar represents the total number of fish caught in that pool.

10.85 (132/12.17), and 9.6 (132/13.75) food pellets in the pools with the small, medium, and large covers respectively. Could it be that fish in pools with a small cover were attracted to the extra food present in the riskier microhabitat?

We turn now to the egrets' behaviour. Can an egret use tactics that maximize its capture success when it is faced with a prey that inhabits a patchy environment whose patches differ in the magnitude of predation risk? Lima (2002) hypothesized that a top predator may have the spatial and temporal cognitive abilities to manage prey fear via its movement among patches in a way that maximizes its capture success. Predators may make foraging decisions in order to take advantage of the behaviour of their prey (Brown *et al.*, 1999; Lima, 2002). Namely, a predator might adjust its patch-visitation schedule to the anti-predatory behaviour of the prey in its home range and do so in a way that leaves prey less wary and easier to capture during its next visit (Wolf and Mangel, 2007; Katz *et al.*, 2010). By so doing, the predator, using time allocation, would be spreading the risk of predation over its hunting patches.

Contrary to our expectation, the egret spent similar foraging times in the pools with the three different cover sizes and returned to each pool with similar mean return times. Thus, it would appear that the egrets' tactics in our experimental setting was to allocate equal times to all pools. Were these tactics successful? Did they yield the best capture success?

The egrets timed their visits to the pools with the three sizes of covers in a way that matched the fish refractory times in those pools. For all three comparisons between cover size specific refractory time and egret mean return time, the probabilities (Wilcoxon signed ranks test) were 0.79, 0.39, and 0.77, for the small, medium, and large covers respectively. Hence the egrets adjusted their return time to the pools so that they returned when the fish were starting to re-expose themselves to predation by leaving cover.

We obtain the same result when we compare the average fish refractory time in all pool types (28.23 ± 4.33 minutes) with mean egret return time to all pool types (28.23 ± 4.33 minutes) (Wilcoxon signed ranks test = 0.88). Also, mean foraging time spent in a pool by an egret matched its optimal foraging time (Table 1), which we estimated using our Charnov-like technique (Katz *et al.*, 2013).

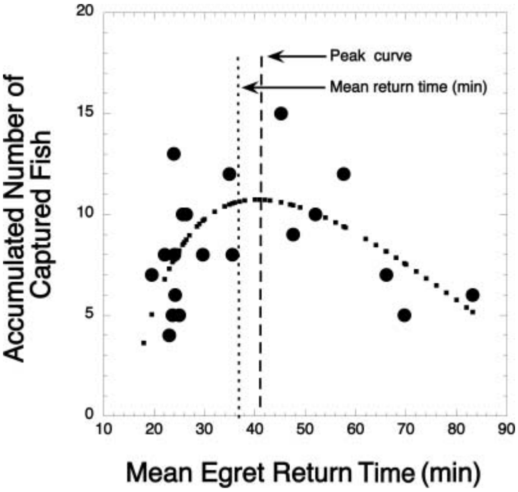

Fig. 4. The fish-captured curve, plotted on an arithmetic scale, peaks at an egret return time of 40.7 minutes, which is not significantly different from the observed time of 35.4 ± 3.76 minutes ($t = 1.02$, $df = 23$, $P = 0.32$). In the text, we point out two other close similarities between ideal and actual foraging properties of egrets and goldfish.

The two results reported in the previous paragraph suggest egrets in our experiments were capturing as many fish as possible. Figure 4 displays the evidence. The egrets that returned after about 40 minutes to the same pool fared the best.

- The curve of Fig. 4 fits the equation, $\text{FishCaptured} = -136.5 + 183.2 \times \log(\text{ReturnTime}) - 56.9 \times (\log(\text{ReturnTime})^2)$. It peaks at a mean egret return time of 40.7 minutes, which is not significantly different from the observed mean return time of 35.4 ± 3.76 minutes ($t = 1.47$, $df = 23$, $P = 0.16$).
- The observed mean egret return time of 35.4 ± 3.76 minutes is also not significantly different from the optimal fish refractory time of 35.15 ± 9.49 minutes ($t = 1.44$, $P = 0.16$).
- The estimated fish refractory time of 28.23 ± 4.33 minutes is also not significantly different from the estimated egret return time of 40.7 minutes ($t = 0.60$, $df = 12$, $P = 0.56$) at which egrets display their peak capture rate of fish.

These results strongly suggest that an egret's actual return times and foraging times lead to optimal exploitation of its resources.

Katz *et al.* (2010, 2013) experimented with this system when the covers were of equal size (similar to the medium-sized cover in the present study) and all three pools contained 15 fish. They found that the egret allocated similar foraging and return time to all pools, as in the present study. They also showed that the peak of the curve that described the relationship between number of fish captured and mean egret return time occurred at about 19 minutes, whereas in the present study, the highest capture rate occurred at a return time of 40.7 minutes – more than twice that in the earlier study.

The difference between the two studies was not just the size of the covers, but also the total fish captured per egret per day: the figures were 17.00 ± 1.47 fish in Katz and colleagues' (2010, 2013) study and 10.42 ± 1.09 fish in the present study. This difference is highly significant ($t = 3.59$, $df = 38$, $P = 0.001$). Apparently, the egrets solved the two experimental manipulations (covers of equal and different size) in a similar way and achieved what appears to be optimal success.

There was one more important difference between the two studies that might explain the different optimal return times observed. This difference suggests that egret behaviour appears to be triggered by the behaviour of the fish. In the work of Katz *et al.* (2010, 2013), the refractory time of the fish was 20.31 minutes, while in the present study it was 35.15 minutes. Thus, the optimal behaviour of the egret seems determined by the actual behaviour of the fish.

Our results provide compelling evidence that predator and prey play a foraging game as suggested by several theoretical models (Gilliam and Fraser, 1987; Brown, 1988; Abrams, 1991; Houston *et al.*, 1993; Brown *et al.*, 1999; Houston and McNamara, 1999). Moreover, they tell us that a game-theoretic perspective is useful for understanding predator–prey interactions and the ecological communities of which they are a part. In fact, our results are consistent with theories that predict how foragers should balance the conflicting demands of food and safety.

ACKNOWLEDGEMENTS

Israel Science Foundation grant #05/14 to Zvika Abramsky supported this research. We thank Avi Koplovich, Ofir Altstein, Jong Koo Lee, and Reut Vardi for their assistance with the experimental design and data collection in the aviary. We are grateful to Shiraz Cohen for her help in Python programming in extracting the behavioural data from Excel files. Yulia Dubinsky, Aviv Gruber, Anjala Pyakurel, Yulia Nekin, Marina Nochevny, Michal Elul, and Mor Peled helped with video data extraction. S.V. is grateful to the Azrieli Foundation for the award of an Azrieli Post-Doctoral Fellowship at Ben-Gurion University.

REFERENCES

Abrams, P.A. 1991. The effects of interacting species on predator–prey coevolution. *Theor. Popul. Biol.*, **39**: 241–262.

Abrams, P.A. 1993. Why predation rates should not be proportional to predator density. *Ecology*, **74**: 726–733.

Abramsky, Z., Rosenzweig, M.L. and Subach, A. 2002. The costs of apprehensive foraging. *Ecology*, **83**: 1330–1340.

Amano, M., Iigo, M. and Yamamori, K. 2005. Effects of feeding time on approaching behavior to food odor in goldfish. *Fish Sci.*, **71**: 183–186.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.*, **22**: 37–47.

Brown, J.S. 1992. Patch use under predation risk: I. Models and predictions. *Ann. Zool. Fenn.*, **29**: 301–309.

Brown, J.S. and Mitchell, W.A. 1989. Diet selection on depletable resources. *Oikos*, **54**: 33–43.

Brown, J.S., Laundre, J.W. and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.*, **80**: 385–399.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.*, **9**: 129–136.

Clark, C.W. 1994. Antipredator behavior and the asset-protection principle. *Behav. Ecol.*, **5**: 159–70.

Dunlop, R., Millsopp, S. and 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.

Fretwell, S.D. and Lucas, H.L. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.*, **19**: 16–36.

Gilliam, J.F. and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**: 1856–1862.

Hammond, J.I., Luttbeg, B. and Sih, A. 2007. Predator and prey space use: dragonflies and tadpoles in an interactive game. *Ecology*, **88**: 1525–1535.

Holopainen, I.J., Tonn, W.M. and Paszkowski, C.A. 1997. Tales of two fish: the dichotomous biology of crucian carp (*Carassius carassius* (L)) in northern Europe. *Ann. Zool. Fenn.*, **34**: 1–22.

Houston, A.I. and McNamara, J.M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.

Houston, A.I., McNamara, J.M. and Hutchinson, J.M.C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **341**: 375–397.

Hugie, D.M. and Dill, L.M. 1994. Fish and game: a game-theoretic approach to habitat selection by predators and prey. *J. Fish. Biol.*, **45**: 151–169.

Ingrum, J., Nordell, S.E. and Dole, J. 2010. Effects of habitat complexity and group size on perceived predation risk in goldfish (*Carassius auratus*). *Ethol. Ecol. Evol.*, **22**: 119–132.

Katz, M.W., Abramsky, Z., Kotler, B.P., Altshtein, O. and Rosenzweig, M.L. 2010. Playing the waiting game: predator and prey in a test environment. *Evol. Ecol. Res.*, **12**: 793–801.

Katz, M.W., Abramsky, Z., Kotler, B.P., Rosenzweig, M.L., Alteshtein, O. and 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, M.W., Abramsky, Z., Kotler, B.P., Roth, I., Altestein, O. and Rosenzweig, M.L. 2014a. A predator–prey behavioural game: how does number of food patches influence foraging tactics? *Evol. Ecol. Res.*, **16**: 19–35.

Katz, M.W., Abramsky, Z., Kotler, B.P., Roth, I., Livne, S., Altestein, O. and Rosenzweig, M.L. 2014b. A predator–prey foraging game: how does prey density influence tactics? *Evol. Ecol. Res.*, **16**: 323–335.

Katz, M.W., Abramsky, Z., Kotler, B.P., Rosenzweig, M.L., Altstein, O., Roth, I. and Klimovitsky, C. 2016. Comparing the non-lethal and lethal effects of predation risk on goldfish anti-predatory behavior. *Isr. J. Ecol. Evol.*, **62**: 121–127.

Kotler, B.P., Brown, J.S., Dall, S.R.X., Gresser, S., Ganey, D. and Bouskila, A. 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evol. Ecol. Res.*, **4**: 495–518.

Kotler, B.P., Brown, J.S. and Bouskila, A. 2004. Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. *Ecology*, **85**: 917–922.

Kotler, B.P., Brown, J.S., Mukherjee, S., Berger-Tal, O. and Bouskila, A. 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proc. R. Soc. Lond. B: Biol. Sci.*, **277**: 1469–1474.

Krivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. *Am. Nat.*, **149**: 164–178.

Krivan, V. 2007. The Lotka-Volterra predator–prey model with foraging predation risk trade-offs. *Am. Nat.*, **170**: 771–782.

Kushlan, J.A. 1978. Feeding ecology of wading birds. In *Wading Birds* (I.V. Sprunt, J.C. Ogden and S. Winckler, eds.), pp. 249–297. New York: National Audubon Society.

Lima, S.L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Stud. Behav.*, **27**: 215–290.

Lima, S.L. 2002. Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.*, **17**: 70–75.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.

Lima, S.L., Mitchell, W.A. and Roth, T.C. 2003. Predators feeding on behaviourally responsive prey: some implications for classical models of optimal diet choice. *Evol. Ecol. Res.*, **5**: 1083–1102.

Luttbeg, B. and Kerby, J.L. 2005. Are scared prey as good as dead? *Trends Ecol. Evol.*, **20**: 416–418.

MacArthur, R. and Pianka, E. 1966. On optimal use of a patchy environment. *Am. Nat.*, **100**: 603–609.

Magurran, A.E. 1984. Gregarious goldfish. *New Sci.*, **103**: 32–33.

Mitchell, W.A. 1990. An optimal-control theory of diet selection: the effects of resource depletion and exploitative competition. *Oikos*, **58**: 16–24.

Pitcher, T.J. and Magurran, A.E. 1983. Shoal size, patch profitability and information exchange in foraging goldfish. *Anim. Behav.*, **31**: 546–555.

Preisser, E.L., Bolnick, D.I. and Benard, M.F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**: 501–509.

Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology*, **62**: 327–335.

Rosenzweig, M.L. and Abramsky, Z. 1997. Two gerbils of the Negev: a long-term investigation of optimal habitat selection and its consequences. *Evol. Ecol.*, **11**: 733–756.

Schmitz, O.J. 2005. Behavior of predators and prey and links with population level processes. In *Ecology of Predator–Prey Interactions* (P. Barbosa and I. Castellanos, eds.), pp. 256–278. New York: Oxford University Press.

Sih, A. 1984. The behavioral response race between predator and prey. *Am. Nat.*, **123**: 143–150.

Sih, A. 1998. Game theory and predator–prey response races. In *Game Theory and the Study of Animal Behavior* (L.A. Dugatkin and H.K. Reeve, eds.), pp. 221–238. New York: Oxford University Press.

Sih, A. 2005. Predator–prey space use as an emergent outcome of a response race. In *Ecology of Predator–Prey Interactions* (P. Barbosa and I. Castellanos, eds.), pp. 240–255. New York: Oxford University Press.

Stenberg, M. and Persson, A. 2005. The effect of spatial food distribution and group size on foraging behavior in a benthic fish. *Behav. Process.*, **70**: 41–50.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Vargas, J.P., Lopez, J.C. and Thinus-Blanc, C. 2004. Encoding of geometric and featural spatial information by goldfish (*Carassius auratus*). *J. Comp. Psychol.*, **118**: 206–216.

Weir, L.K. and Grant, J.W.A. 2004. The causes of resource monopolization: interaction between resource dispersion and mode of competition. *Ethology*, **110**: 63–74.

Wolf, N. and Mangel, M. 2007. Strategy, compromise, and cheating in predator–prey games. *Evol. Ecol. Res.*, **9**: 1293–1304.

Yoshida, M., Nagamine, M. and Uematsu, K. 2005. Comparison of behavioral responses to a novel environment between three teleosts, bluegill *Lepomis macrochirus*, crucian carp *Carassius langsdorfii*, and goldfish *Carassius auratus. Fish Sci.*, **71**: 314–319.