

## A predator–prey behavioural game: how does number of food patches influence foraging tactics?

Merav W. Katz<sup>1</sup>, Zvika Abramsky<sup>1</sup>, Burt P. Kotler<sup>2</sup>, Inbar Roth<sup>1</sup>,  
Ofir Altstein<sup>1</sup> and Michael L. Rosenzweig<sup>3</sup>

<sup>1</sup>Department of Life Sciences, Ben Gurion University, Beer Sheva, Israel, <sup>2</sup>Institute of Desert Research, Ben Gurion University, Sde Boqer, Israel and <sup>3</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA

---

### ABSTRACT

**Background:** When exposed in previous experiments to a behavioural game in a three-pool laboratory theatre, common goldfish, *Carassius auratus* (the prey), and little egrets, *Egretta garzetta* (the predator), demonstrated optimal adjustments in their foraging and anti-foraging behaviours when confronted with different numbers of fish.

**Question:** In a similar theatre with one, two or three pools and a fixed number of fish per pool, will predator and prey again solve the game and optimally adjust their foraging and anti-foraging behaviours?

**Methods:** Experiments were conducted in two identical, circular aviaries (diameter 7 m) consisting of three circular pools (diameter 1.52 m), each of which could be covered so as to remove it from an experiment. We conducted experiments with one, two or three uncovered pools. Each pool had two available fish habitats: protected from predation but without food for fish, and exposed but with food. There were 15 goldfish in each experimental pool. One egret foraged in each aviary (none in controls). The egret moved at will among the pools. During six-hour observation periods, we observed, minute-by-minute, the distribution of fish among their habitats and the movement of the egret among the pools. In addition to compiling summary statistics of the behaviours, we counted the number of successful predation events and analysed the results to test their optimality.

**Results:** As the number of pools changed, the egret changed its foraging behaviour, moving among the pools in a way that maximized its capture success. The time an egret spent hunting correlated with the number of pools available, thus it captured fish at a higher rate when more pools were available. Regardless of the number of pools, egrets captured the same number of goldfish per pool per day. The time that fish used the exposed habitat was negatively correlated with the time the egret foraged in a pool. However, even in one-pool trials, goldfish emerged from protected habitat occasionally, which sometimes led to their capture.

**Keywords:** predator–prey behavioural games, optimal foraging, food patches, risk of predation, fear management.

---

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

Consult the copyright statement on the inside front cover for non-commercial copying policies.

---

## INTRODUCTION

Previously (Katz *et al.*, 2010, 2013), we reported some of the results of our studies of behavioural games between two interacting vertebrate species in a laboratory setting. One species, the common goldfish, *Carassius auratus*, is prey for the other, the little egret, *Egretta garzetta*. In this study we change the values of laboratory variables to discover whether the behavioural responses of fish and bird make sense as the result of natural selection. If they do respond adaptively despite the artificial environment, then it is quite likely that, when faced with similar challenges in natural environments, their behaviours are also adaptive products of natural selection.

The artificial environment (which we will describe in more detail below) consists of three pools of water in an aviary. In our previous experiments, we varied the number of fish in each pool but kept all three pools available to the egret in the aviary. In one set of experiments, each of the pools had 15 fish (Katz *et al.*, 2010). In another, one pool had 10 fish, a second had 15 fish, and the third had 20 fish (Katz *et al.*, 2013). 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. Thus, whatever adaptability they possess in natural environments would seem to be sufficiently plastic to be transferred to the artificial circumstances.

But authors who have considered adaptations of predators have also recognized the probable importance of habitat patchiness (especially Lima, 2002). Predators ought to respond to the number of patches and their density because these variables affect the time predators spend travelling between patches. So, in the present work, we decided to investigate patchiness. With the number of fish set at 15 in each pool, we varied the number of pools (i.e. patches). We examined the behavioural responses of both the egret and the fish.

We varied patchiness quite simply (see details in Methods, below). In some trials, all three pools were available to fish and egret. In others, only two were available and in still others, only one. Let us consider the hypotheses that pertain to these three conditions.

## HYPOTHESES

Changing the number of pools means changing the number of fish in the aviary (45, 30 or 15). Thus:

H1: Other things being equal, in an environment with more fish, an egret should catch more of them. Reasoning: Capture rate is correlated with prey density (Lotka, 1925; Volterra, 1926; Rosenzweig and MacArthur, 1963).

H2: In an environment with more fish, the egret's giving-up density in a pool will increase. Reasoning: Giving-up density is achieved when the density in a patch falls to a low enough level that the egret's rate of fish capture equals the average rate in the entire aviary (Charnov 1976; Brown, 1988). The more fish in the environment, the greater that threshold.

Corollaries of H2:

C2a: In an environment with more fish, the egret should take fewer fish from each pool.

C2b: In an environment with more fish, the egret should spend less time foraging in each pool.

H3: The more time the egret spends foraging in a pool, the less time the fish will expose themselves to predation. Reasoning: Prey should trade off food for safety by temporarily shifting their activity to safer microhabitats (time allocation) when a predator is present (Dill, 1987). *Note:* Prey may use other behavioural responses as well, such as adjusting the proportion of time spent in vigilance (Lima and Dill, 1990; Luttbeg and Kerby, 2005; Preisser *et al.*, 2005), but this study does not examine them.

The above three qualitative hypotheses rely on optimal foraging theory, which makes quantitative predictions, too. We tested two:

H4: In the three-pool trials, the egret should cycle among the pools. That is, when leaving one pool, it should next visit the pool it has been away from longest. Reasoning: The pool it visited longest ago will have goldfish more willing to expose themselves to predation and therefore generate a superior capture rate for the egret.

H5: The egret maximizes the rate at which it captures fish. We will explain the reasoning that allows us to test this hypothesis when we describe the analysis that finds the optimum time an egret should spend foraging in a pool. (See Optimal foraging analysis, below, and Fig. 8.)

## METHODS

### Study species

#### *Predator*

The little egret, *Egretta garzetta*, a small heron (Ardeidae), was the predator in our treatments. Adults are 55–65 cm long with a wing span of 88–106 cm. They weigh 350–550 g.

Little egrets are solitary, opportunistic hunters that take their prey (fish, amphibians, crustaceans, and insects) in shallow water, often through ambush while standing still. Without alternative food, each little egret needs to eat 15–20 goldfish a day to meet its energetic demands.

We caught the egrets individually using a butterfly net (36 cm steel hoop, 71 cm deep mesh bag) in the wild at Kibbutz Ma'agan Michael (Israel 37805) from covered, commercial, intensive fish ponds. We transferred each one from the net to its own 60 × 40 × 34 cm cardboard box, then transported it for 3 hours in an air-conditioned vehicle to our installation. All egrets survived the journey and we detected no adverse effects on their health. After the journey, egrets were given water and fed dead fish (common pandora, *Pagellus erythrinus*, and pilchard, *Sardina pilchardus*) *ad libitum*. Eight egrets participated in the experiments.

#### *Prey*

The common goldfish, *Carassius auratus*, a relatively small member of the family Cyprinidae, was the prey. It is a domesticated variety of a dark, greyish-brown carp native to eastern Asia. Introduced to Europe from its original source in China in the early sixteenth century, an olive green variety now inhabits most natural lakes, streams, and natural ponds there (Holopainen *et al.*, 1997). Except for their colour, common goldfish (*C. auratus*) closely resemble the wild ancestral form (Holopainen *et al.*, 1997).

A growing body of literature reports the use of goldfish as a model organism for research in behavioural ecology (e.g. Magurran and Pitcher, 1983; 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). In our treatments, goldfish schooled naturally, seeking cover and re-emerging largely as a coordinated group (Magurran and Pitcher, 1983; Magurran, 1984).

Almost all herons use similar foraging strategies to hunt fish. Thus herons such as egrets and *C. auratus auratus* have a long history of co-evolved behaviours. We used goldfish 5–7 cm long (weight 5–7 g) because these are easily captured and handled by egrets.

Goldfish, like other carp that evolved in muddy water, rarely respond to the approach of a potential predator from shore. In fact, they respond to an egret only when it approaches within  $15 \pm 1.0$  cm (Z. Abramsky, personal observation). Therefore, in our case, we could not study the role of vigilance as a strategy to reduce predation risk. Instead, we focused on the fishes' use of time allocation as they managed risk by hiding under the opaque cover when an egret was present or had recently visited.

Goldfish were supplied by a professional fish farmer (Kibbutz Ma'agan Michael, Israel 37805) and delivered to us by Jungle Fish (Bat Yam, Israel). Until they were needed, we stocked the goldfish in a separate pool away from the aviaries. Egrets consumed most fish during the experiments and the few that remained were fed to them afterwards.

### Ethical standards

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 number IL-49-10-2010). A licence to catch the egrets was obtained from the Israel Nature and National Parks Protection Authority (Authorization number 39323). The fish and the egrets were kept under strict veterinary supervision in accordance with all necessary regulations. The egrets and fish were kept up to 4 months, and participated in up to six experimental sessions. After the experiments, the egrets were certified for release by a veterinarian who ensured they were of normal weight, in good condition, and free of disease. Egrets were then returned to Ma'agan Michael and released where they had been caught.

### Experimental arenas

Two identical, specially designed circular (7 m diameter) aviaries constituted the experimental arenas (Fig. 1). We covered each one with welded wire mesh. We did not use artificial lighting and conducted all experiments only during daylight.

Each aviary contained three equally spaced pools of water (diameter 1.52 m; depth 60 cm). During the winter we heated the water above 20°C (with several thermostatically controlled heaters) so that goldfish would remain active. The inside bottom of all pools was of a pale colour. Because egrets do not hunt efficiently at depths below 15 cm, we limited fish to the upper 15 cm of the water column with a plastic, 1-cm mesh, horizontal net suspended at that depth.

Each pool could be covered to remove it from an experiment. We conducted experiments with one, two or three uncovered pools.



**Fig. 1.** An experimental arena (aviary) with three pools.

We divided each pool into two distinct microhabitats: safe and risky. The *safe* microhabitat had a circular opaque cover (radius 23.75 cm) at the centre of the pool. The cover provided a refuge for fish to swim under but the habitat offered no food. The *risky* microhabitat (i.e. the remainder of the pool) allowed fish to forage for food but exposed them to egret predation (Fig. 1). We created the risky microhabitat by dispensing extruded feed for cold water ornamental fish (Raanan Fish Feed Ltd.; nutritional value: 4400 kcal·kg<sup>-1</sup>, 47% protein, 6% fat, 9.5% moisture, 8.5% ash, 2% calcium, 1.3% phosphorus) into the uncovered part of each pool. We dispensed the food from an automatic feeder at a constant rate. The food particles (pellet size 2.2 mm) floated on the water's surface and could not penetrate underneath the opaque cover that sheltered the safe habitat.

Thus the fish were forced to trade off food and safety.

### Experimental design

We conducted our experiments from May 2009 to October 2009 at the Bergman Campus of Ben-Gurion University of the Negev, Beer-Sheva, Israel. We set up four experimental treatments:

- One pool with 15 fish and an egret.
- Two pools with 15 fish in each pool, and an egret able to travel freely between the pools.
- Three pools, each with 15 fish, and an egret able to travel freely between the pools.
- Three pools, each with 15 fish, but with no egret. We used this treatment as a control.

Each treatment consisted of two consecutive experimental days. At the start of each treatment, we added 15 naïve goldfish to each pool and gave them one day to acclimate. Then we introduced an egret (except into controls) and allowed it 5 days to acclimate. Except during the actual trials, the egret lived in a specially designed cage in the aviary. After the 5 days of egret acclimation, we began the two-day data-gathering phase of the treatment by releasing the egret from its cage. We recorded data for 6 hours, after which we returned the egret to its cage and offered it extra food (up to a maximum of 90 g per day). The next morning we released the egret again and recorded another 6 hours of data.

We decided to minimize the amount of time we handled the egrets by assigning each egret randomly to one of the two aviaries and maintaining its assignment during the entire set of experimental treatments. Which egret would serve during a particular treatment was

determined by setting up a random order of egrets at the very beginning and cycling through that order as the treatments changed. Those egrets currently not participating in an experiment were housed together in a single holding pen.

At the end of the first day of data collection, we counted the goldfish and compensated for their losses by adding enough naïve goldfish to maintain their number at 15 in each pool. At the end of the second day, we replaced all fish with naïve ones. There was no significant difference between number of fish captured on the first and the second day of each treatment (Wilcoxon signed rank test =  $-1.12$ ;  $P = 0.26$ ). Therefore, we concluded that there was no time effect, and we thus treated each day as an independent result.

### Data collection

Four high-resolution cameras (one placed above each pool and one that viewed the entire aviary) recorded every six-hour trial. The cameras produced a permanent, continuous digital record of egret and fish behaviours for analysis and archiving.

For the fish, each minute we counted how many fish in each pool were swimming exposed in the risky habitat. By taking account of whether an egret was also present during a sampling minute, we also measured the separate percentages of fish in the risky habitat in the presence or absence of an egret. For the egrets, we counted where the egret was during each minute of the 360-minute long experimental day. We recorded all their hunting attempts and successes, before binning these into successive numbered minutes.

From these data we calculated total and mean egret foraging time and the mean time that an egret takes to return to a specific pool. We also measured the number and percentage of fish in the risky habitat, and the number of captured fish. We tagged the data as coming from particular experimental minutes (1–360) so that we could calculate accumulation curves and study how behaviours changed as a function of the time during the six-hour period.

We stored the data in Excel and analysed them using MATLAB and SPSS. Since many of our results are not normally distributed, we used non-parametric tests. However, in most of the figures, we present the trends in the data by showing means and standard errors.

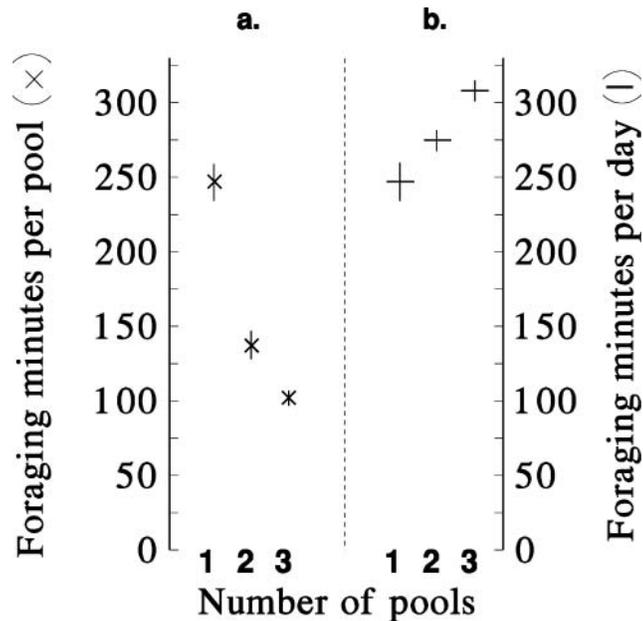
## RESULTS

### Egrets

Treatments had 15, 30 or 45 fish depending on whether one, two or three pools were used. Accordingly, the more pools available, the less time an egret spent in each pool during an entire six-hour trial: one pool =  $247.8 \pm 12.74$  min per pool; two pools =  $137.4 \pm 8.9$  min per pool; three pools =  $102.6 \pm 5.02$  min per pool. The trend is significant (Friedman's two-way ANOVA, d.f. = 16, 3;  $P < 0.001$ ) (Fig. 2a). Thus the more pools, the lower the density of egret foraging.

In addition, the more pools available, the more time an egret spent foraging during an entire six-hour trial (Friedman's two-way ANOVA, d.f. = 16, 3;  $P = 0.01$ ) (Fig. 2b). Total egret foraging time per treatment was as follows: one pool =  $247.9 \pm 12.7$  min; two pools =  $274.9 \pm 7.2$  min; three pools =  $307.9 \pm 7.3$  min.

With more pools in the treatment, the egret, having left a specific pool, took significantly longer to return to it (Friedman's two-way ANOVA, d.f. = 16, 3;  $P < 0.001$ ). Mean return



**Fig. 2.** The egret modified its foraging times as we changed the number of pools available. The more pools available, the less the total foraging time spent during each six-hour trial in each pool (a), but the more total foraging time spent in the set of three pools during the 6 hours (b). The values are means and the vertical line through each symbol is the standard error.

times to a pool (Fig. 3) increased from treatments with one pool ( $5.67 \pm 1.5$  min), to two pools ( $9.7 \pm 2.0$  min), to three pools ( $21.09 \pm 4.13$  min).

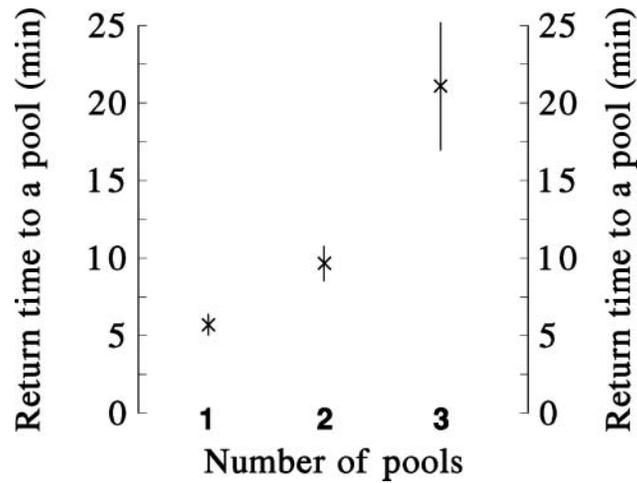
When we examined the length of foraging bouts (i.e. the times egrets spent in a pool before moving to another), the results were somewhat puzzling (Fig. 4). The mean times were as follows: one pool,  $12.6 \pm 0.9$  min; two pools,  $6.09 \pm 0.3$  min; three pools,  $9.07 \pm 1.03$  min. Those results were not uniform. The mean foraging bout time was significantly greater for the one-pool treatment versus either the two-pool or three-pool treatment (Wilcoxon signed test,  $P = 0.002$  and  $P = 0.011$ , respectively). But the difference between mean foraging bout times in treatments with two and three pools was not significantly different (Wilcoxon signed rank test,  $P = 0.23$ ).

Overall, an egret faced with an environment of more fishes and pools spends more time foraging, but less time in each pool. And it takes longer to return to a specific pool after leaving it.

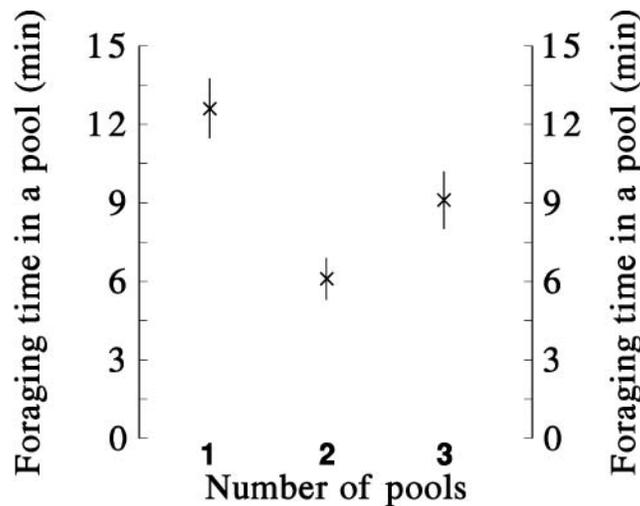
### Goldfish

In the absence of an egret (control treatment), an average of  $57.07 \pm 3.96\%$  of the goldfish swam in the risky habitat (outside the cover) at any given time in the treatment. When an egret was present, that percentage plummeted markedly and significantly regardless of the number of pools (Friedman's two-way ANOVA, d.f. = 16, 3;  $P < 0.001$ ).

The fishes' adjustment to the presence or absence of an egret was coarse scale but they also displayed a fine-scale quantitative adjustment. In the presence of an egret, the

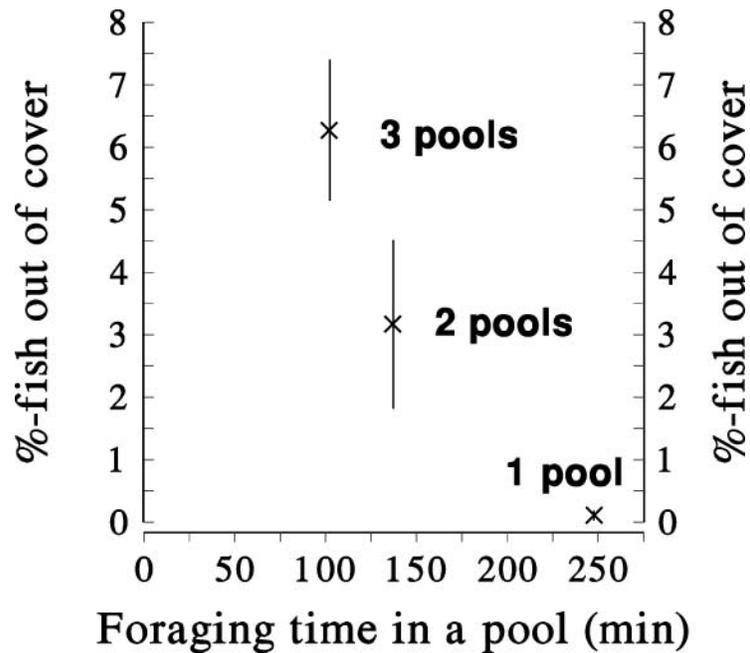


**Fig. 3.** The egret took significantly longer to return to a specific pool when a treatment had more pools. The values are means and the vertical line through each symbol is the standard error.



**Fig. 4.** The length of a foraging bout (i.e. the time an egret spent foraging in a pool before moving to another) depended significantly on the treatment. But there was no simple pattern. Foraging bouts during the one-pool treatment lasted longer than during either of the other treatments, but the latter two did not differ significantly. The values are means and the vertical line through each symbol is the standard error.

percentage of fish in the risky habitat outside of cover depended inversely on the density of egret foraging activity (Fig. 5). In the three-pool treatment (with low density of egret foraging), an average of  $6.27 \pm 1.13\%$  of fish were seen in the risky habitat. In the two-pool treatment (medium density of egret foraging), the average declined to  $3.17 \pm 1.39\%$ . And in the one-pool treatment (high density of egret foraging), swimming in the risky habitat was almost non-existent (average  $0.11 \pm 0.08\%$ ).



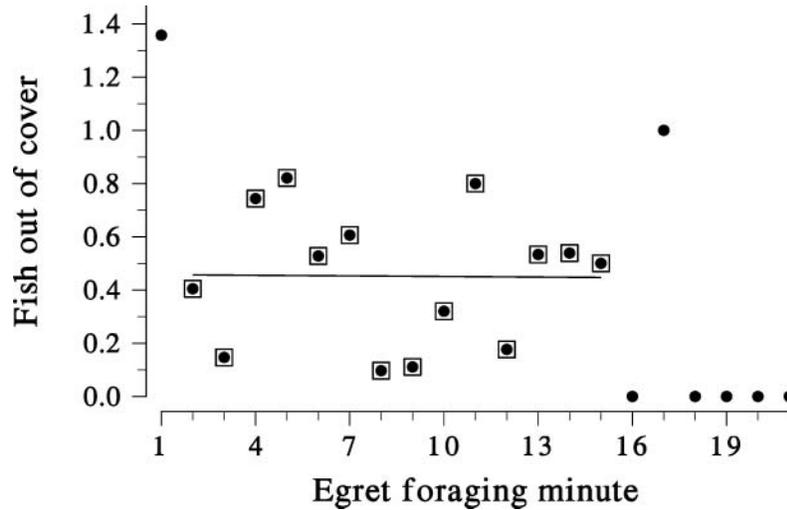
**Fig. 5.** The fish responded appropriately to the three treatments by varying the percentage of fish swimming in the risky habitat. They did so least in the one-pool treatment and most in the three-pool treatment. In the Discussion, we explain why this trend makes adaptive sense. The  $y$ -values are means and the vertical line through each symbol is the standard error.

Nevertheless, even in the presence of a foraging egret, goldfish still emerged from under the cover at a somewhat constant rate of approximately 0.46 fish per minute (Fig. 6). We term this behaviour ‘peeping’. Sometimes a peeping goldfish paid with its life.

### Capture rates

The average number of fish captured in a pool during a one-day (six-hour) experimental trial was similar in the three experimental designs (Friedman’s two-way ANOVA, d.f. = 16, 3;  $P = 0.78$ ) (one pool,  $5.25 \pm 0.97$  fish; two pools,  $5.47 \pm 0.41$  fish; three pools,  $5.5 \pm 0.28$  fish). However, during the first 4–5 min of foraging in a pool, the capture rates were not similar. To arrive at this result, we determined, for each treatment, the success rate at which the egrets caught goldfish each minute during a foraging bout (Fig. 7). We were then able to detect the difference between the one-pool treatment and the other two treatments. Early minutes in the one-pool treatment were significantly less productive for the egret, as can be seen by comparing two ANCOVAs as follows:

- The number of fish caught in a particular foraging minute differed significantly between the three treatments ( $F = 6.7$ ,  $P = 0.003$ ; Table 1).
- But the number caught was similar between the treatments with two and three pools ( $F = 0.6$ ,  $P = 0.45$ ; Table 2).



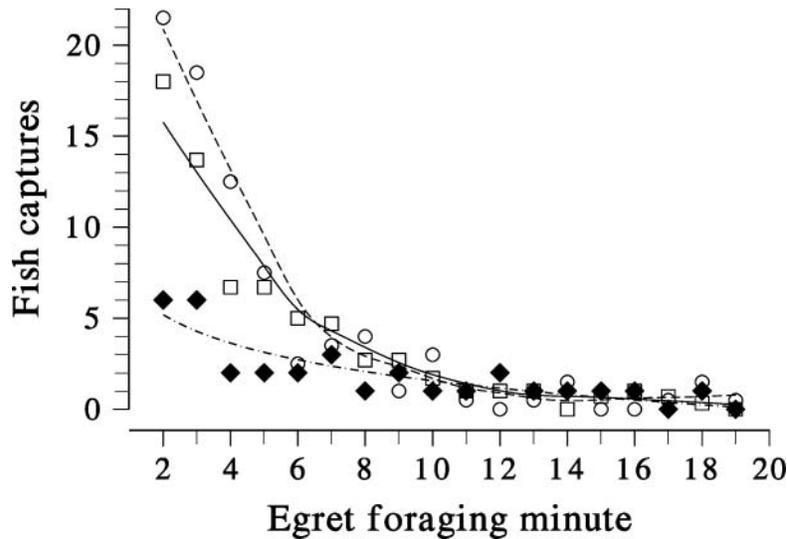
**Fig. 6.** Peeping behaviour in the three-pool treatment. The  $x$ -axis is the minute-by-minute time interval during an egret's foraging bout. During each of those one-minute intervals, a number of fish were outside cover at least a little bit, exposing themselves to predation risk. The mean of this number is the  $y$ -axis. During the first minute, when the egret first appears, the fish are caught off-guard and register a high number of exposed individuals. But they rapidly retreat to cover. From minute 2 through minute 14, the fish continue to explore the open and risky part of the pool at an average rate of about 0.46 fish per minute. These minutes (dots in boxes) are fit with a regression line in the figure. Its slope is zero. The regression ignores minute 1 (the time of fish adjustment) and those beyond minute 14 (for which data are too sparse for reliable statistics).

**Table 1.** Results of ANCOVA showing that the number of fish captured/foraging time in a pool was significantly different between the three experimental treatments (one, two, and three pools)

	SS	d.f.	MS	$F$	$P$
Intercept	1084.714	1	1084.714	115.1490	0.000000
Category	184.581	2	92.290	9.7972	0.000270
Time	608.008	1	608.008	64.5438	0.000000
Category $\times$ Time	125.623	2	62.811	6.6678	0.002784
Error	452.164	48	9.420		

**Table 2.** Results of ANCOVA showing that the number of fish captured/foraging time in a pool was not significantly different between the two- and three-pool experimental treatments

	SS	d.f.	MS	$F$	$P$
Intercept	1189.400	1	1189.400	87.97195	0.000000
Category	11.466	1	11.466	0.84807	0.363991
Time	696.579	1	696.579	51.52127	0.000000
Category $\times$ Time	8.070	1	8.069	0.59682	0.445463
Error	432.647	32	13.520		



**Fig. 7.** Number of fish captured in a given pool declines as a function of foraging minute. The  $x$ -axis of the figure identifies the particular foraging minute as in Fig. 6. The  $y$ -axis shows, minute-by-minute, the number of fish captured by all egrets during both days. Data were accumulated over the entire experiment. The numbers for the two- and three-pool treatments are similar, but those of the one-pool treatment are significantly less during the early minutes of a trial. ◆, one pool; ○, two pools; □, three pools. See text for statistics.

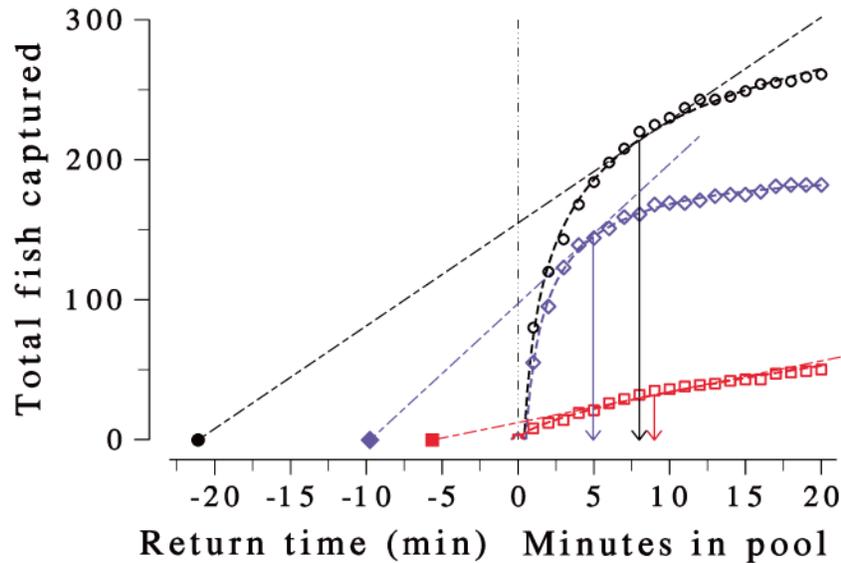
Inspection of Fig. 7 confirms the results of those ANCOVAs. Figure 7 shows that the fish quickly detected the egret and retreated to the safe habitat because the number of fish captured during successive minutes fell rapidly no matter which treatment the data relate to.

### Optimal foraging analysis

Combining the data of Figs. 3 and 7, we predicted how long an optimally foraging egret should stay in a pool during a foraging bout (Fig. 8) to maximize its rate of fish capture. Of course, the rate of capture is the number of captures divided by the time it took to make them. The latter has two parts: the travel time and the foraging bout time. First, the egret travels to a pool; then it forages in the pool; then it leaves. Finally, it returns, having spent time travelling time to get there (whether it is moonlighting in another pool or not). So the travel time is the time it takes to return to the pool.

As usual, one may depict the rate of capture as the slope of a straight line. In this case, the line connects the point  $(0, 0)$  to the point  $(x, y)$  where  $x$  is the sum of travel and foraging bout times, and  $y$  is the number of goldfish captured by all the egrets in an experiment. The egret should maximize this slope.

The egret can modify both of its behavioural variables: travel time and foraging bout time. That flexibility makes the egret's challenge quite different to that of a forager in a classical marginal-value-theorem analysis (Charnov, 1976), in which the travel time would be determined by the fixed distances between the pools. Indeed, our egrets did exhibit variable return times (Fig. 3).



**Fig. 8.** Determining the optimal length of an egret foraging bout. We calculate the optima for the three experimental treatments (one, two, and three pools) separately, since each has a different mean return time and a different accumulation curve. The lowest curve reports the one-pool results (red squares); the highest one reports the three-pool results (black circles); and the intermediate one reports the two-pool results (blue diamonds). The three optima are quite similar, at least qualitatively, to the mean foraging bouts reported in Fig. 4 (see text). To make the analysis easier to read, we transposed the  $x$ -axis so that the value zero begins the foraging activity and the return times (solid symbols) appear on the left as negative numbers.

From Fig. 7 we obtained, for each treatment, the accumulation curve for all fish captured by all egrets during both trial days as a function of the foraging time. Then we drew a tangent to this curve beginning not from zero, but from the empirical return time of an egret to a pool in this treatment. Thus we obtained the maximal rate of fish capture including both the egret's travel time and foraging bout time in a pool. The vertical line dropped from the tangent point touches the  $x$ -axis at the egret foraging bout time, which yields that maximal rate. The optimal foraging bout times were as follows: one pool, 9 min; two pools, 5 min; three pools, 8 min.

Note that if all three treatments had shared a return time, the results would have been different.

## DISCUSSION

We studied the behavioural responses of a predator (little egret) and its prey (common goldfish) in an experimental scenario that amounted to a behavioural game between egret and fish (e.g. Brown *et al.*, 1999; Lima, 2002; Sih, 2005; Wolf and Mangel, 2007). We furnished our contestants with two experimental arenas (i.e. aviaries; Fig. 1) containing one, two or three available fish pools (food patches). Each pool had an isolated population of 15 goldfish. All aviaries, except controls, had a single egret. For the fish, the game's goal was to stay alive; for the egret, it was to eat fish as rapidly as possible. We found that both species managed

their behaviours as if they were accommodating the rules of the game that we gave them to play.

Many prey species trade off food against safety by allocating the time they spend among microhabitats. When risk of predation is high, the prey should hide in protected areas and refuges, entering generally risky and productive habitats only when the risk is lower or 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). Consequently, we designed the pools in the aviaries to have two microhabitats, one safe from the egret but without food, the other nutrient-rich but risky if an egret were present. The fish had to allocate their time in the two habitats, trading off food in the risky habitat against the safety of the covered microhabitat that contained no food. Meanwhile, the goldfish's use of the tactic of vigilance is vanishingly small (Katz *et al.*, 2010).

While the fish managed their risk of predation, the egret could counter because it could move freely among pools inside the aviary and allocate its foraging time between the pools to manage fear in the fish and increase its capture success of fish. Lima (2002) hypothesized that a top predator may indeed have the spatial and temporal cognitive abilities to manage prey fear via its movement among patches in a way that maximizes its capture success.

Implicit in our experimental design was the question of whether an egret can maximize its capture success when faced with a prey species able to adjust its own behaviour to defend itself in a patchy environment. Meanwhile, can the prey (the fish) respond to the predator's behaviour and reduce its probability of being captured? Our results, along with those of Katz *et al.* (2010, 2013), suggest that these two species were playing the game and playing it well.

### Patterns in the goldfish results

The fish faced two related challenges in these experiments. They had to take to the safe habitat when the egret was foraging, and they had to stay in it for an appropriate time after it left. They appear to have done well with the first challenge and fairly well with the second.

Certainly, during experiments in which an egret participated, goldfish spent far less time in the exposed habitat than they did during controls. At any given moment, roughly ten times as many fish used the exposed waters during the controls as during the experimental trials when they might have encountered an egret. In addition, during experimental trials, the fish adjusted their exposure quantitatively. The egret spent more time foraging in each pool as the number of pools decreased (Fig. 2a) and the fish responded accordingly. The fewer the pools, the lower the percentage of fish using the risky habitat at any one time (Fig. 5). In the one-pool treatment, the egret foraged in the pool most of the time, and the fish responded by reducing their activity in the risky part of the pool almost to zero (Fig. 5).

Yet, the egret managed to capture just as many fish during the one-pool treatment as during the two- and three-pool treatments. This happened because in all treatments, even when the egret foraged in the pool, the fish continued to explore the open and risky part of the pool at an average rate of about 0.46 fish per minute (Fig. 6). We term this behaviour 'peeping'. We believe that the fish are breaking cover in order to explore the environment and assess the risk of predation. Otherwise, how could they know when it might be safe to return to the risky habitat?

### Patterns in the egret results

Our experiments varied the number of fish present in the aviary during a trial. Fifteen fish were present in each one-pool trial, 30 in each two-pool trial, and 45 in each three-pool trial. The egret responded accordingly (Fig. 2). Given higher numbers of fish, it paid the egret to spend more time foraging. Indeed, the more fish in a trial, the more time the egret spent foraging during it (Fig. 2b). But the egret spent less time in a pool if more pools were available in a trial (Fig. 2a).

Perhaps the latter result reflected a higher giving-up density (GUD) when more pools were present. But the GUD hypothesis was not supported. It predicted that the egret should leave a pool at a higher density of fish in a three-pool treatment versus a two-pool treatment. However, on average, the egrets left all pools with a similar number of fish (about ten fish per pool) no matter what the treatment.

The egret return times in these experiments were 5.67 min, 9.7 min, and 21.09 min for the one-, two-, and three-pool treatment respectively. It is becoming ever more difficult to interpret the return-time results as random, or capricious, or innate and irrelevant to the experimental conditions. There is variation in their values, but they fit reasonable patterns.

As expected, the number of fish caught by an egret in a treatment increases with the number of fish in the treatment. As the number of pools increased from one to three, the egrets became more efficient in capturing fish. The egrets, while foraging, captured fish at a higher rate in an environment with three pools (0.88 fish per pool per minute). With two pools, the rate was less (0.64 fish per pool per minute). With only one pool, it was only 0.34 fish per pool per minute.

In the one-pool treatment, the egret captured fish by taking advantage of their peeping behaviour. In a system where no alternative food patches are present and the cost of foraging is very low, an egret is obviously better off staying longer in the one pool trying to capture the occasional fish that exposes itself.

In the three-pool treatment, the egrets moved between the pools in a manner that makes adaptive sense. Upon leaving a pool, they usually chose, as the next pool to visit, the one they had not visited for the longest time (correct choice  $24.71 \pm 3.71$ ; incorrect choice  $16.8 \pm 2.37$ ; Wilcoxon signed rank test,  $P = 0.002$ ). (Trivially, the egrets always selected the other pool after leaving a pool in the two-pool treatment.)

We now consider the puzzling results of Fig. 4. The time an egret spends in a single foraging bout differs significantly between treatments. Recall that mean foraging time per bout in a pool was as follows: three pools, 9.07 min; two pools, 6.09 min; one pool, 12.6 min. These times do not seem to suggest any pattern, but there is one, as follows.

We have two sets of results for the times egrets spend in a pool during a single foraging bout. One set came from the data (Fig. 4), the other from the predictions of Fig. 8. Fortunately, the pattern of the predicted foraging bout times and even their values are very similar to those calculated from the data of the three treatments.

	Data (Fig. 4)	Predicted (Fig. 8)
1 pool	12.6	9
2 pools	6.1	5
3 pools	9.1	8

The results of Katz *et al.* (2013) also showed the agreement of predicted and observed egret foraging bout times. So the pattern of the data in Fig. 4 becomes evident: the egret in each treatment sets its foraging time per bout so as to achieve its maximum rate of capture.

One may argue that the egrets evolved in a situation in which several food patches were always available to them and therefore that our experiments amounted to a negligible challenge. But even so, one cannot dispute the success of the egrets in choosing their foraging tactics.

### General thoughts

We introduced two real species into a set of artificial habitats. So we cannot and do not use our results as descriptions of what goes on in nature. Instead, our underlying question is whether natural selection has equipped these species to respond adaptively to the strange situations into which we put them.

We had to consider the possibility that neither goldfish nor egrets could do that. It was possible that both would have evinced ritualized, random, hardwired or otherwise inappropriate behaviours. But instead, our results show that the individuals of both species do have the capacity to adapt to unfamiliar situations.

One can think of three alternatives to explain the adaptive flexibility of goldfish and egrets. Maybe, just like an evolutionary ecologist, they can do the mathematics. Or maybe they are loaded with pre-evolved libraries of rarely used tactics to meet almost-never-encountered situations. Or maybe natural selection has provided modalities to permit an organism to compare its actual perceptions of its internal states with its ideal perceptions of its internal states. That way an individual could detect subtle gradients as a response to small changes in its behaviour, and follow those gradients in the direction of improvement. We cannot prove it but we believe the third alternative is correct. Certainly, a host of classical experiments in animal behaviour demonstrate that individuals can follow external gradients.

We have learned also that goldfish (at least) combine their flexible tactics with innate behaviours, in their case, ‘peeping’, a behaviour that assures a flow of up-to-date information. We saw them risk their lives peeping to obtain this information. Except for the first few seconds of an egret’s visit (contained within minute one), the fish emerged from cover at a somewhat constant rate of approximately 0.46 fish per minute (at least until the fourteenth minute). Often the gamble resulted in their death. One might have expected the fish to adjust their rate of peeping in accordance with the probability that the egret still remained, in which case the peeping rate would have risen as egret foraging time increased. But if anything, the peeping rate fell to near zero after minute fourteen. Together, innate and flexible behaviours provide a grounded adaptiveness that should help organisms to withstand and even to take advantage of the inevitable environmental variation they must face.

Our results strongly support Lima’s (2002) suggestion that a vertebrate predator such as a little egret should have well-developed spatial and temporal memory and the ability to respond to the prey’s anti-predator behaviour by adjusting its foraging tactics. Here, when number of food patches allowed it, egrets responded to the anti-predator behaviour of goldfish by changing adaptively their re-visitation schedule to pools containing prey and the length of visits to each pool. The responses depended on the number of pools, and egrets responded in a manner that maximized their capture success. At the same time, goldfish responded to the visitation duration and frequency of the egrets by reducing their use of the

open and risky habitat and using it when the frequency of egret visitation was low. The results of this study and our previous two strongly suggest that both egrets and goldfish respond and counter-respond optimally to each other in a predator–prey foraging game.

### ACKNOWLEDGEMENT

This project was supported by ISF grant number 485/08 to Zvika Abramsky.

### REFERENCES

- 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., 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.
- Dill, L.M. 1987. Animal decision-making and its ecological consequences: the future of aquatic ecology and behavior. *Can. J. Zool.*, **65**: 803–811.
- 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.
- 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. *Zool. Fem.*, **34**: 1–22.
- 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, P.B., Rosenzweig, M.L., Altshtein, 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.
- 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.
- 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.
- Lotka, A.J. 1925. *Elements of Physical Biology*. Baltimore, MD: Williams & Wilkins.
- Luttbeg, B. and Kerby, J.L. 2005. Are scared prey as good as dead? *Trends Ecol. Evol.*, **20**: 416–418.
- Magurran, A.E. 1984. Gregarious goldfish. *New Sci.*, **103**: 32–33.
- Magurran, A.E. and Pitcher, T.J. 1983. Foraging, timidity and shoal size in minnows and goldfish. *Behav. Ecol. Sociobiol.*, **12**: 147–152.
- 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. and MacArthur, R.H. 1963. Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.*, **97**: 209–223.

- Sih, A. 2005. Ecology of predator–prey interactions. In *Predator–Prey Space Use as Emergent Outcome of a Response Race* (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 bentic fish. *Behav. Process.*, **70**: 41–50.
- 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.
- Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. Acad. Lincei Roma*, **2**: 31–113.
- 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.

