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A predator–prey foraging game: how does prey density influence tactics?

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ABSTRACT

Background: Classical foraging theory studies the adaptation of a forager to a passive resource. But some resources are prey – sentient animals likely capable of responding to the predation challenge posed by their predator/forager. Such a combination of species constitutes an adaptive foraging game. We have been studying one between goldfish (the prey) and little egrets (the forager) in an experimental theatre that allows us to control and alter the environmental variables that should matter to both species.

Species: Common goldfish (*Carassius auratus*), a carp, and the little egret (*Egretta garzetta*), a heron.

Question: In what ways do egrets and goldfish adjust to a difference in goldfish abundance? Do such adjustments conform to foraging theory?

Experimental theatres: Two aviaries, each containing three pools for fish. Each pool had two habitats, one in which fish were safe from the egret but had no food, the other risky but with food.

Methods: There were two treatments: 15 fish per pool and 25 fish per pool, each with one egret allowed to forage freely among the pools. Control treatments had no egret. Digital cameras recorded fish and egret behaviour continuously during 6-hour experimental days. Each 6-hour period began with either 45 or 75 fish (i.e. 15 or 25 fish in each pool). During each experimental minute we recorded the egret's location, the number of fish alive in each pool, how many fish in each pool were outside the safer habitat, and all fish captures. We also measured the mean foraging time of an egret in a pool throughout an experimental day and how long it took an egret to return to a specific pool after leaving it (return time). Finally, we determined the amount of leftover fish food after each day.

Results: Fish and egrets adjusted their behaviours to variation in fish density. And the adjustments make sense as anti-predatory or as foraging improvement tactics. Fish faced with high risk of predation greatly reduced their exposure to the riskier habitat, and did so even more in the extremely risky 15-fish pools compared with the 25-fish pools. They did so although they suffered lower per-capita food consumption in proportion to their avoidance of the riskier habitat. The egrets responded to the greater fish density by foraging longer in a pool: 35%

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longer in the 25-fish pools than in the 15-fish pools. Thus the egrets behaved opposite to the prediction of the marginal value theorem. However, in so doing, egrets did optimize the rate at which they captured fish.

Keywords: predator–prey foraging game, prey density, anti-predatory behaviour, marginal value theorem, optimal foraging.

INTRODUCTION

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. It assumes that both predator and prey individuals forage in an adaptive way 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).

One major behavioural adaptation that reduces the risk of being preyed upon is aggregation behaviour. A variety of studies have demonstrated that the probability of a given individual being eaten declines as the size of the group increases (e.g. Pitcher and Parrish, 1993; Van Buskirk *et al.*, 2011). Schooling behaviour of fish is an example of group living that increases safety of individual members and reduces a fish's probability of being eaten. When an increased density of fish changes the per-capita predation risk, fish in larger groups should behave differently to fish in smaller groups. As a result, predators may take into account both marginal-value considerations for patches of different fish abundance, and the effect of fish group size on their anti-predatory and foraging behaviour.

Charnov (1976) proposed the marginal value theorem (MVT) to predict the optimal foraging time in a depletable food patch embedded in an environment with similar food patches. The forager is assumed to have evolved to optimize a cost–benefit ratio: searching for and manipulating food is costly, while consuming food is a benefit. According to this model, the decisions taken by animals are based on the perceived quality of the environment. Charnov (1976) developed the model for a forager that eats a food resource, such as seeds, and that cannot respond behaviourally to the approaching predator. However, in many situations predators hunt for a prey that can respond behaviourally to risk of predation by time allocation, vigilance, or both (e.g. Hugie and Dill, 1994; Brown *et al.*, 1999; Kotler *et al.*, 2002, 2004; Hammond *et al.*, 2007). Such a situation is a game and the optimal behaviours of the predator and the prey might depend on each other. Rules other than MVT might govern foraging time in a patch.

We previously discovered a foraging game in an experimental setting [Fig. 1 (see also Katz *et al.*, 2014)] with goldfish (*Carassius auratus*) as prey and little egrets (*Egretta garzetta*) as predators (Katz *et al.*, 2010, 2013). Fish inhabited three-pool aviaries with either equal numbers of fish [15 fish per pool (Katz *et al.*, 2010)] or different numbers of fish [10, 15 or 20 fish per pool (Katz *et al.*, 2013)], and showed density-dependent anti-predatory behaviour in both situations. Meanwhile, egrets responded adaptively by adjusting their visitation rates to pools and the duration of each visit, resulting in maximization of their capture success.

In both studies (Katz *et al.*, 2010, 2013), egrets faced an environment (aviary) with a constant abundance of fish initially (i.e. the total number of fish was equal: 45 fish per aviary). In the

real world, however, egrets may experience patches with a variety of fish group sizes. Fish abundance in a patch will affect both the marginal-value considerations of the egret and the anti-predatory behaviour of the fish. Will egrets change their tactics in response to fish behaviours that depend on fish density? How will fish respond behaviourally to their own density and to the changing tactics of the egret? Will the average number of fish captured per patch in a sparse environment be different to that in an environment of abundance?

We set up two experimental treatments in which an egret faced a spatially homogeneous environment in which each of the three pools contained either 15 or 25 fish. So the total number of fish per aviary was different: 45 fish and 75 fish, respectively. In all treatments, fish food was distributed only in the riskier of the two habitats within each pool.

Since there is never more than a single foraging egret at a time, fish in 75-fish treatments should experience a smaller per-capita predation risk than those in 45-fish treatments. The decreased risk should lead fish in a 75-fish treatment to spend more time in the riskier microhabitat, eat more food, yet suffer a reduced predation rate compared with fish in the 45-fish treatment. The reader will see that fish did behave that way.

At the same time, egrets should respond to the changing fish behaviour by adjusting their return time to, and foraging time in, each patch. According to classical MVT, when all patches have the same resource abundance, foragers exploiting an environment with patches of greater abundance should remain in each patch for less time than they should in an environment with patches of lesser abundance (Brewer, 1994). But classical MVT does not take into account prey behavioural responses to forager behaviour. Because, in our case, both prey and forager can adjust their behaviours to the circumstances of the game, we suspected that classical MVT might fail to predict the difference in egret foraging times between the 75-fish treatments and the 45-fish treatments. The reader will see that this is indeed the case. Opposite to the prediction of classical MVT, egret foragers exploiting an environment with patches of greater abundance remained in each patch for more time than in an environment with patches of lesser abundance. Yet, in doing so, the forager achieved the essence of MVT, adopting behaviour that maximized its average rate of fish capture and optimizing its success.

MATERIALS AND METHODS

Study species

The predator/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, amphibian, crustacean, and insect prey. Without alternative food, each little egret must eat 15–20 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 37805). After participating in the experiment, they were returned and released at the location of capture.

The prey was 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 uses 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 5 to 7 cm (5 to 7 g). Such individuals are easily captured and handled by egrets.

The system

We conducted the experiment in two specially designed aviaries (7 m diameter each) at the Ben-Gurion University Bergman Campus, in Beer Sheva, Israel. Each of the aviaries contained three equally spaced pools (patches), each with a diameter of 1.52 m and a depth of 60 cm (Fig. 1a). A plastic wire mesh placed horizontally in each pool created a false bottom that restricted fish to the top 15 cm of water. In each experimental treatment, the three pools were all stocked with either 15 or 25 goldfish.

Each pool was divided into two distinct microhabitats for the fish:

- a safe microhabitat – a circular opaque cover over the centre part of the pool with a radius of 23.75 cm, under which the fish could shelter; and
- a risky microhabitat – the rest of the pool, where the fish were exposed to risk of predation (Fig. 1b).

The space under cover is sufficient for more than 100 fish (Z. Abramsky, personal observation). Therefore, intra-specific competition for space under cover is not likely at either fish density. In our experiments, goldfish schooled naturally, seeking cover and re-emerging largely as a coordinated group (Pitcher and Magurran, 1983; Magurran, 1984).

In each pool, floating fish food (mean pellet size: 2.2 mm, extruded feed for cold water ornamental fish, Raanan Fish Feed, Ltd.; nutritional value: 4400 kcal/kg; 47% protein; 6% fat; 9.5% moisture; 8.5% ash; 2% calcium; 1.3% phosphorus) equivalent to 1% of the fish biomass and equal to their daily requirements was dispensed from a feeder into the open microhabitat at a constant rate over the course of each experimental day. To isolate the risk of predation from other factors (such as intra-specific scramble competition), we adjusted the amount of food to the density of the fish by keeping the per-capita amount of food constant. The floating food granules stayed in the open part of the pool (i.e. the risky microhabitat) and could not penetrate beneath the cover due to a polystyrene layer floating under the cover and touching the water surface. The polystyrene layer does not allow the granules to float under it so the fish had to leave the safety of the cover in order to eat. This design forced the goldfish to trade-off food against safety (e.g. Lima and Dill, 1990, Lima, 1998).

The experiment

There were two treatments: one egret in an aviary with 15 fish per pool, and one egret in an aviary with 25 fish per pool. Control treatments involved 15 or 25 fish per pool without an egret. We conducted the experiments from December 2010 to June 2011. During the winter, we heated the water to 20°C to maintain goldfish activity. Egrets were given five acclimation days. Fish were given one day of acclimation.

We used eight different egrets in the course of the experiments. All egrets participated in both treatments. This protocol controlled for idiosyncrasies among egrets and allowed us to test whether they differed in their behaviour towards the different densities of fish.

(a)

(b)

Fig. 1. (a) 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. Note the egret in the pool on the right. (b) An experimental pool as viewed from above by its digital camera. The safe microhabitat is beneath the circular cover at the centre of the pool (radius 23.75 cm). Note the school of goldfish swimming to the left of the cover in the exposed/risky habitat.

Egrets were captured in the wild and were kept at least 6 weeks in an occupation cage before participating in the experiments. We trusted that this period would allow them to 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 order, we assigned each egret to one or the other aviary during the entire set of the two experimental treatments.

Each density treatment consisted of two 6-hour experimental days. At the end of the first day, we counted the fish in each pool. We replaced missing fish with naïve fish, and put the egret in a holding cage for the night. At the end of the second day, we replaced all fish with naïve ones.

At the end of each day, we counted the number of leftover food particles floating in the water. From these data, we measured the percentage of food consumed by the fish.

We found no significant differences between the tactics of the egrets, as reflected by their foraging time in the pools in the first and the second days of the 15-fish and 25-fish treatments (Wilcoxon signed test: $P = 0.12$ and $P = 0.46$, respectively). Additionally, to test the strength of the argument for treating each day as an independent trial, we averaged the results of the two consecutive days to test its effect on the experimental results. We performed all of the statistical analyses again when $n = 8$ (the total number of egrets in the experiment) and obtained exactly the same significant results. Therefore, we present all results and statistical analyses for $n = 16$, which combines the results from the separate days.

In each aviary, we placed four high-resolution cameras, one above each pool and one that viewed 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 of every minute of the 360-minute daily experiment. We analysed these data using MATLAB and SPSS. In particular, we recorded where the egret was (one observation per minute), and any fish captured during that minute. We also counted (one observation per minute) how many fish in each pool were outside the sheltered habitat. From these data we calculated the mean percentage of fish that were outside cover as well as their total time outside cover in each experimental day of the two experimental treatments and in the controls (without an egret). For each day, we also defined and calculated re-emergence time as the mean time between the states of 'all-fish-under-cover' and 'one-fish-emerging-outside-cover'.

We counted the number of uncaptured fish at the end of each experimental day. Then, by following the egret behaviour continuously on the recorded videos, we discovered when each fish was captured. Thus we measured the number of fish alive during each minute of an experiment. We also measured the mean foraging time of an egret in a pool throughout an experimental day, and the egret's mean return time. Return time is simply how long it took an egret to return to a specific pool after leaving it.

We used the data of all three pools in an aviary to calculate all variables. Since many of our results are not distributed normally, we analysed them using non-parametric tests. (In most of the figures, however, we present the trends in the data by showing the means and standard errors.)

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 No. IL-49-10-2010). A licence 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 following all required regulations.

RESULTS

In the controls (with no egret), fish behaviour did not depend on fish density. At 15 fish per pool, the percentage of time fish swam outside of cover was 64.78% (±0.26). At 25 fish per pool, it was 64.64% (±0.36). These values are not significantly different (Wilcoxon signed rank test, $P = 0.954$). Also not significantly different were the total times outside of cover during a 6-hour experimental day (15 fish: 311.21 ± 8.1 min; 25 fish: 319.42 ± 5.5 min; Wilcoxon signed rank test, $P = 0.843$).

In the experimental treatments – with an egret present – the fish drastically and significantly reduced their activity compared with controls. In the high-density treatment, only 8.05% (±0.18) of fish activity occurred outside cover; in the low-density treatment, only 2.78% (±0.12) did. These two percentages differed significantly (Wilcoxon signed rank test, $P < 0.001$, $n = 16$), showing that at reduced fish density, fish responded by reducing their exposure to the riskier habitat.

Results were quite similar for the total amount of time fish spent outside cover. In the high-density treatment, fish spent 47.3 min (±9.0) there, whereas in the low-density treatment they spent 16.4 min (±5.0) there. This difference was significant (Wilcoxon signed rank test, $P < 0.001$, $n = 16$).

In the absence of an egret, fish at both low and high densities consumed all the food. However, with the egret present, fish in the 25-fish pools ate a significantly higher proportion of the food (0.91 ± 0.01) than fish in the 15-fish pools (0.82 ± 0.02), even though the amount of food supplied per capita was identical (Wilcoxon signed rank test, $P < 0.001$, $n = 16$).

Individual fish would occasionally peep out from under cover even when the egret was foraging in the same pool. The mean number of goldfish emerging from cover per minute during an egret's visit in the pool was significantly higher in the 25-fish pools than in the 15-fish pools (ANCOVA: $F_{1,28} = 12.4$, $P = 0.001$; Fig. 2). Peeping gave the egret a chance to capture the peeper, thus the egret had more hunting opportunities in the 25-fish pools.

Even though more fish in the high-density treatment were exposed to predation and ate more food, the proportion of captured fish during a 6-hour experimental day in the high-density treatment was significantly lower (0.18 ± 0.17 fish) than in the low-density treatment (0.27 ± 0.23 fish) (Wilcoxon signed rank test, $P = 0.001$, $n = 16$).

The fish emerged from cover relatively often when the egret took a long time to return to a pool but, on average, much less often when the egret tended to return in less than 40 minutes or so (Fig. 3a and 3b). This relationship was significant in both treatments (15 or 25 fish per pool). There is some statistical indication that fish at the lower density (Fig. 3a) were more cautious: for a given egret return time, fish living in a 15-fish pool tended to wait

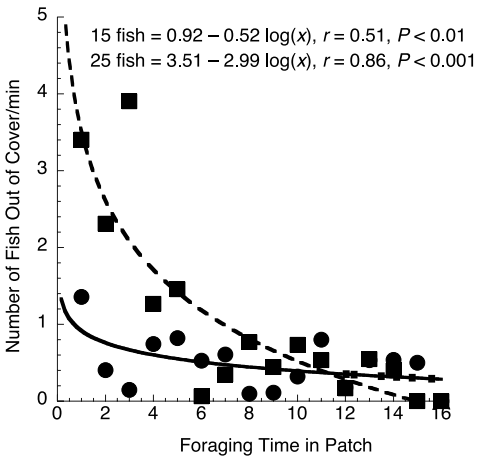

Fig. 2. Compared with the 15-fish pools, fish continued to expose themselves in 25-fish pools for more time after an egret entered. The extra exposure time was predicted by optimal foraging and led to the egret capturing more fish in the 25-fish pools. Data: Mean number of fish emerging outside cover per minute during an egret's visit in a pool (●: 15 fish; ■: 25 fish) (ANCOVA, $F_{1,28} = 12.4$, $P = 0.001$).

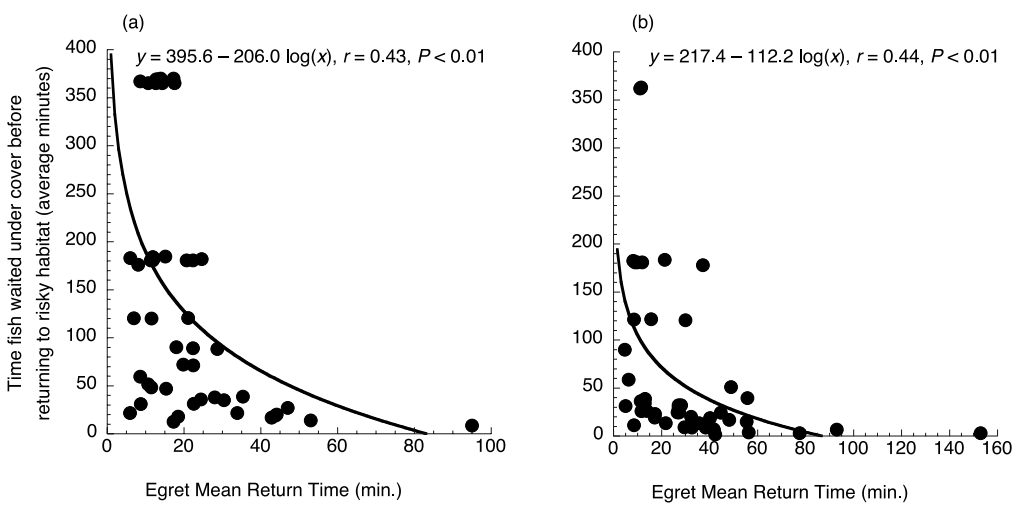

Fig. 3. The fish behaved as if they were aware of the mean visitation rate of the egret in their aviary during a single day. Fish waited longer to enter the open microhabitat when the egret returned quickly. For a given egret return time, fish living in (a) a 15-fish pool waited significantly longer than fish in (b) a 25-fish pool (ANCOVA, $F_{1,96} = 5.29$, $P = 0.024$).

significantly longer to emerge than they did if they were in a 25-fish pool (ANCOVA: $F_{1,96} = 5.29$, $P = 0.024$).

In the high-density treatment, the egrets' average foraging time in a pool per visit was significantly longer (10.93 ± 1.21 min) than in the low-density treatment (7.8 ± 0.70 min) (Wilcoxon signed rank test, $P = 0.027$, $n = 16$). Additionally, since the egrets spent more foraging time per pool in the high-density pools, their mean return time to a given high-density pool had to be greater than their return time to a given low-density pool. Indeed,

egrets in the high-density treatment returned significantly later (30.24 ± 3.88 min) than in the low-density treatment (21.35 ± 2.29 min) (Wilcoxon signed rank test, $P = 0.003$).

During the entire course of the experiments, the egrets captured similar numbers of fish in the low-density and high-density treatments (190 fish in the 15-fish treatment, and 219 fish in the 25-fish treatment). Each egret also captured a similar mean number of fish during each 6-hour experimental day (3.96 ± 0.35 fish in the 15-fish treatment and 4.56 ± 0.43 fish in the 25-fish treatment) (Wilcoxon signed rank test, $P = 0.11$). Additionally, the egrets spent the same amount of total foraging time per experimental day in the 15- and 25-fish treatments (333.36 ± 22.47 min and 335.55 ± 34.71 min, respectively) (Wilcoxon signed rank test, $P = 0.83$).

Using an MVT-like analysis in which we treated average return time as a form of travel time, we predicted the optimal foraging time per pool (Fig. 4). The predicted foraging times in the 15- and 25-fish treatments (8.5 min and 11.5 min, respectively) match those we actually measured (7.8 min and 10.9 min, respectively) (one-sample *t*-tests: $P = 0.992$ and $P = 0.852$ for the 15- and 25-fish treatment, respectively).

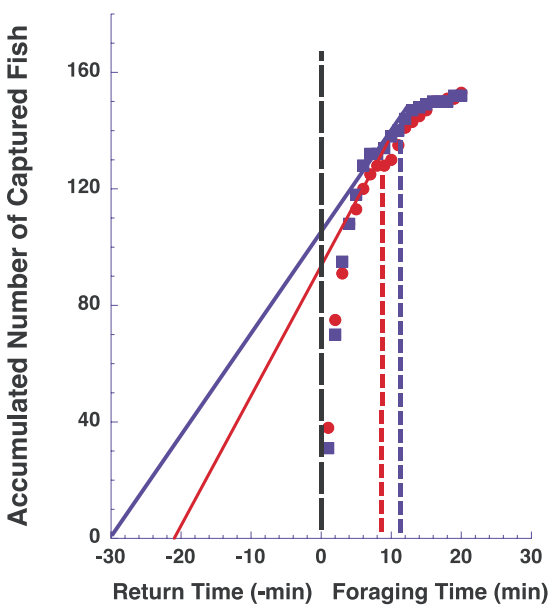

Fig. 4. Determining optimal egret foraging time in a pool. We calculated the optima for the two experimental treatments (15-fish and 25-fish pools). First, we fit equations to the data (symbols) to obtain the accumulation curves: 15-fish pools: $y = 16.624 + 27.639 \log x$; 25-fish pools: $y = 16.289 + 28.837 \log x$ (equations were estimated for one pool). Then, using the observed egret return times (21.35 min in a 15-fish pool; 30.24 min in a 25-fish pool), we solved for the straight line that touches one of the accumulation curves at a single point. (To make the analysis easier to read, we transposed the x-axis so that the zero value begins the foraging activity and the return times appear on the left as negative numbers.) The projection of that point onto the x-axis is the optimal egret foraging time in a pool. The two optima are quite similar to the mean foraging times (i.e. 15 fish: 8.5 min vs. 7.8 min; 25 fish: 11.5 min vs. 10.9 min). Thus the egrets did conform to Charnov-like optimal foraging rules, although not the rules of the marginal value theorem. Each point in the figure represents the accumulated total number of fish captured per foraging minute for all eight egrets together in all the pools and days.

DISCUSSION

We introduced two real species into a set of artificial habitats. Our underlying question was whether these species are able to respond adaptively to each other, and to the situations in which we placed them. Additionally, we tested experimentally if alternative Charnov-like optimal foraging rules could predict the patch-time residency of a forager facing a prey that can respond behaviourally to risk of predation. It was possible that both forager and prey would have random or otherwise inappropriate behaviours. However, our results show that the individuals of both species do have the capacity to respond adaptively to each other, and optimize their foraging behaviour.

Fish

The fish responded in accordance with the principles of optimality. The strongest contrast was between fish behaviour when the egret was not present versus when it was. The obvious qualitative prediction is that fish should forage freely when there is absolutely no risk of being eaten. Indeed, that is what they do. On average, 57% of fish were swimming outside the experimental cover in the control experiments (without any egrets). With an egret present, however, this percentage was much lower: 8% in 25-fish pools and 2.8% in 15-fish pools. Evidently, the fish do sense the danger.

Our results also support the prediction that fish facing high per-capita rates of predation should adjust their individual exposure to predation risk. Pools with 15 fish risked a higher predation rate than those with 25 fish. So each fish in 15-fish pools should spend more time in the safer microhabitat and feed less. Indeed, the total time fish spent outside cover was 47.3 min in the 25-fish pools, significantly more than the 16.4 min they spent outside cover in the 15-fish pools. In addition, the 8% of the time they spent outside cover in 25-fish pools was significantly greater than the 2.8% in 15-fish pools. In contrast, without the egret to impose a risk of predation, fish spent the same amount of time feeding whether in a 15-fish pool (64.8 min) or a 25- fish pool (64.6 min).

Egrets

In the more abundant resource environment of the 25-fish pools, egrets foraged longer per foraging bout than in the 15-fish pools (10.9 min vs. 7.8 min, respectively). Their return times were also greater to the 25-fish pools than to the 15- fish pools (30.2 min vs. 21.4 min, respectively). We will show below that the combination of longer foraging times and longer return times in 25-fish pools resulted in maximal rates of foraging in this treatment, whereas the shorter times did the same in the 15-fish treatment.

Results showed that during each 6-hour experimental day, an egret captured a similar mean number of fish and spent the same amount of total foraging time per experimental day regardless of whether they were participating in the 15- or 25-fish treatment. Thus the egrets changed their foraging tactics between the two treatments, keeping constant their total foraging time, while adjusting their mean foraging time and average return time to the fish group size.

Our results show that the egrets do not conform to the expectation of the marginal value theorem (Charnov, 1976) of classical optimal foraging theory. According to MVT, in the case where two environments with the same patch structure have different average resource

densities (analogous to 15 and 25 fish), the forager should work in a patch until it has reduced the resource density to the point of yielding the average rate of resource return. That takes less time if the surrounding patches are richer (analogous to the 25-fish pools) (Brewer, 1994). So foragers exploiting an environment with patches of greater abundance should remain in each patch for less time than they should in an environment with patches of lesser abundance. But on average, in our experiments, an egret foraged longer in the richer patch. Thus their response to fish anti-predatory behaviour produced a different outcome than classical MVT would predict (see Introduction).

We explain this result by recalling that the system we studied differs from systems modelled with typical optimal foraging theory. In those systems, the resource cannot respond behaviourally. Thus, travel time is not influenced by the resource but by the spatial distribution of the patches. But in our experimental system the resource, by adjusting its anti-predator behaviour, may influence foraging decisions of the forager such as when to return to a patch. Indeed, it seems that the egret responds to fish behaviour by selecting its travelling time. By treating the return time as a sort of travel time, we can solve for the optimal foraging time in a patch (Katz *et al.*, 2013, 2014). Using this method, we predicted how long an optimally foraging egret should stay in a pool during a foraging bout (Fig. 4) to maximize its rate of fish capture. The rate of capture is the number of captures divided by the time it took to make them. 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. Figure 4 shows, for each treatment, the accumulation curve for all fish captured by all egrets during both trial days as a function of the foraging time. 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 that yields the maximal rate. Indeed, the pattern of the foraging times' results predicted by Fig. 4 of the present work, and even their values, are very similar to those calculated from the data of the two experimental treatments.

Individual fish would occasionally peep out from under cover even when the egret was foraging in the same pool (see Katz *et al.*, 2014). They stick the tip of their head out from under the protective cover and then withdraw it very quickly. After the first few seconds of an egret's visit (during which time fish swam quickly to cover), we saw the fish continue to peep out at the fairly constant rate of approximately 0.48 ± 0.08 fish per minute. They were indeed risking their lives as the gamble often resulted in their being snapped up by the egret.

We believe that peeping behaviour allows a flow of up-to-date information, presumably about the presence of an egret and therefore about the risk of swimming away from cover entirely in order to feed. It seems that the fish cannot assess danger while they are hiding under cover. Yet, even in the case of peeping, fish adjusted the rate of performing the behaviour in accordance with the threat of being eaten: fewer fish peeped per unit time in 15-fish pools than in 25-fish pools (Fig. 2).

Our results demonstrate that goldfish and herons have a considerable amount of adaptive flexibility. A possible explanation for this flexibility is that natural selection has provided modalities to permit an organism to detect subtle gradients as a response to small changes in its behaviour, and follow those gradients in the direction of amelioration. A large body of classical experiments in animal behaviour shows that individuals can follow external

gradients (e.g. Hutchinson, 1961). Those flexible behaviours afford an inborn adaptability that should help organisms to withstand and even to benefit from the environmental variation and novelty they must face in nature.

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