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Playing the waiting game: predator and prey in a test environment

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ABSTRACT

Background: Optimal behaviour of a predator depends on what its prey are doing and vice versa. Yet empirical tests of optimal foraging generally take place with only one of the two species free to adjust its behaviour.

Question: Do predators and prey follow predictions of optimality when they are interacting and each is free to adjust its behaviour?

Organisms: Commercially purchased common goldfish (*Carassius auratus*) and wild-caught little egrets (*Egretta garzetta*).

Experimental arenas: Covered circular enclosures (radius 3.5 m), each with three artificial pools (radius 0.76 m). Each pool had a habitat where the goldfish could hide, and an open habitat where they could collect their food but were exposed to predation.

Methods: An egret was allowed to forage in an arena each of whose pools contained 15 goldfish (replaced daily according to the number consumed). We measured the time goldfish spent in the open and under cover; the time it took for them to emerge from cover after an egret visit (i.e. the refractory time, rf); the number of fish eaten; and the time an egret took to return to a pool after leaving it (i.e. the return time, rt).

Predictions: *Qualitative*: during an egret's visit to a pool, fish should spend a greater proportion of time hiding and thus become less and less vulnerable to predation. *Quantitative*: An egret will maximize its chance to encounter exposed fish by adopting a return time equal to fish refractory time ($rt = rf$). An egret should maximize its catch of fish if $rt = rf$.

Results: In the presence of an egret, goldfish significantly reduced the time they spent in the open (2.09% vs. 65.4%). The average goldfish refractory time was 20.31 min. The average little egret return time was 21.09 min. These values are not significantly different. Egrets catch the most fish if $rt = 18.6$ min (not significantly different from that observed).

Keywords: anti-predatory behaviour, foraging games, optimal foraging behaviour, predator–prey interaction.

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INTRODUCTION

Lima (2002) points out that theoretical and experimental studies of predator–prey interactions typically hold one side fixed so as to focus on the behaviour of the other. But in nature, both predator and prey are free to exercise patch or habitat choice and respond behaviourally to each other. The fact that the two species must adjust their behaviours to each other changes the usual single-species foraging problem into a two-species foraging game. Many studies have viewed the predator–prey interactions as such a game in which the decisions of each player are affected by the decisions of the other players (Sih, 1984, 1998, 2005; Hugie and Dill, 1994; Brown *et al.*, 1999; Kotler *et al.*, 2002, 2004, 2010; Hammond *et al.*, 2007; Berger-Tal and Kotler, 2010).

In this paper, we explore – theoretically and experimentally – some behavioural adaptations of a predator, the little egret, to the anti-predator behavioural adaptations of a prey, common goldfish. We designed a two-habitat study so that the goldfish faced a trade-off of food versus safety (Sih, 1980; Brown, 1988; Vander Wall, 1990; Abrams, 1991; Luttbeg and Kerby, 2005). But the fish also faced another behavioural problem. After hiding from an egret in the safe habitat, how long should they wait before re-exposing themselves in the habitat with food? Their waiting behaviour produces reciprocal questions for the egret: How long should it hunt in a single habitat patch and how long should it wait until it returns? It is a 'battle of waits' (Hugie, 2003) with potentially wide-ranging significance (Morris, 2004).

We were able to predict some answers to these questions. Some of the predictions are qualitative and two are quantitative. Although we delay explaining the predictions until after describing the experimental arena and our methods, we are happy to report that the fish and egrets conformed to them all. You will also see that given the prey behaviour, the predator's adjusted behaviour did maximize the number of fish it caught.

MATERIALS AND METHODS

Prey

We used the common goldfish, *Carassius auratus auratus*, a relatively small member of the family Cyprinidae. Common goldfish are a colourful, domesticated variety of a dark, greyish brown carp native to eastern Asia. They differ from their ancestors only in colour (Holopainen, 1997). We used common goldfish 5–7 cm in length (5–7 g). Such individuals are easily captured and handled by the egret.

During winter, when water temperature drops considerably, goldfish become sluggish, stop eating, and often stay on the bottom of their pool. If the water is heated (>17°C) goldfish remain active. Thus, to perform our experiments during the winter, we kept the wintertime water temperature above 20°C using several heaters controlled by a thermostat.

In our experiments, goldfish schooled, both seeking cover and re-emerging virtually as a single organism.

Predator

The predator was the little egret, *Egretta garzetta*, a small heron of the family Ardeidae. Little egrets have all-white plumage, long black legs, yellow feet, and a slim black bill. Adults are 55–65 cm long with a wingspan of 88–106 cm. They weigh 350–550 g. Little egrets take their prey in shallow water, often standing still in ambush. They hunt alone rather than in groups and eat a variety of small animals, including fish, amphibians, crustaceans, and insects. Without alternative food, each little egret must eat 15–20 goldfish per day to meet its energetic demands.

The system

We conducted the experiments from October 2009 to May 2010 at the Bergman Campus of Ben-Gurion University of the Negev, Beer Sheva, Israel. We built and used a specially designed aviary as the experimental theatre (Fig. 1). The aviary contained three equally spaced pools each with a diameter of 1.52 m and a depth of 60 cm. However, because egrets cannot hunt at depths below 15 cm, we forced goldfish to use only the upper 15 cm of the water column by installing a plastic, 1-cm mesh at that depth.

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

1. A safe microhabitat – a circular cover was placed over the centre of the pool with a diameter of 47.5 cm; egrets could not hunt fish that swam under the cover.
2. A risky microhabitat – the rest of the pool area, where the fish could feed but were exposed to predation by egrets.

In each pool, over the course of each 6-h experimental day, floating fish food (in an amount equivalent to 1% of the fish biomass) was dispensed from a feeder at a constant rate. The food remained in the open part of the pool and could not enter the water beneath the cover. Hence the fish had to leave the safety of the cover to feed. This design forced the fish to trade-off food and safety.

Fig. 1. Panoramic view of the experimental arena. There are three equally spaced pools, each 0.76 m in radius. In the centre of each is a disk (radius 23.75 cm), which fish can hide under. Each pool has its own pump (not seen), feeder, and filter. To prevent egrets from seeing more than one pool at a time, we installed opaque partitions. We put vertical wooden skewers on all partitions and feeders to prevent the birds from perching atop them.

Experimental procedures and methods

When we began an experiment, each egret was given 5 days of acclimation. Before each of the three treatments (see below), fish were given 1 day of acclimation. The order of the treatments was randomized. Each treatment consisted of two experimental days. At the end of the first experimental day, we counted the goldfish in each pool. We replaced missing goldfish with randomly selected new goldfish and put the egret into a specially designed cage. At the end of the second experimental day, we replaced all fish with naïve ones.

We tested a total of eight egrets. Every event in the experimental arena was recorded by four high-resolution internet cameras. Three cameras were hung above the centre of each pool, which allowed us to observe and record the density and the distribution of the fish throughout the experiment. The fourth camera was placed below the roof of the theatre, which allowed us to follow and record egret behaviour at all times. The cameras produced a permanent record of egret and fish behaviour for analysis and archiving. The data were quantified in Excel and analysed using MATLAB and SPSS.

The three treatments

1. *Basic*: One egret per arena and 15 fish per pool.
2. *Fish control*: Fifteen fish per pool, no egret. This treatment measured the baseline behaviour of the fish.
3. *Refractory time* (*rf*): We put 15 fish into a single experimental pool. We introduced an egret and allowed it to forage. After it left the pool, we removed it from the arena. Then we recorded the time it took the fish to return to baseline activity. We repeated this procedure, performing up to five trials in one day. (*Note*: We pooled trials because *rf* was independent of trial number.)

PREDICTIONS

All predictions depend on the basic assumption of optimal foraging theory, i.e. individuals should exhibit foraging behaviour that maximizes their fitness (Emlen, 1966; MacArthur and Pianka, 1966; Stephens and Krebs, 1986). In the context of our experiments, a pool is like a patch in foraging theory. As soon as goldfish perceive that an egret is present, the safe habitat increases in value to goldfish relative to the exposed habitat and they should tend to abandon the latter for the former. Therefore, the patch value to the egret will decline from the time it enters the food patch. The situation very much resembles a classic case of patch resource depletion (Charnov, 1976; Brown *et al.*, 1999). At some point in time the patch will retain so small a value to the egret – relative to the other two patches – that the egret will abandon it for one of those other two. That reasoning yields the following two qualitative predictions and the first of the two quantitative ones.

Qualitative

Let t_v be the time since the start of an egret's visit to a pool. At each successive interval of t_v, fish should spend a greater proportion of time hiding.

And thus, at each successive interval of t_v, fish should suffer reduced rates of loss to predation.

Quantitative

An egret should catch the most fish when it adopts the optimal foraging behaviour because the rate of fish capture is the sole measure of an egret's fitness while it forages in the experiment; it has no competing demands on its time and is free of any threat from any of its own predators.

An egret's optimal foraging behaviour is to set its own return time to the prey's refractory time, i.e. $rt = rf$. We deduce this prediction as follows.

Deduction: rf = rt

Assume the egret does nothing but forage during a 6-h session and needs to maximize its feeding rate (captures/time).

Let the feeding time (fd) be the time an egret spends in a pool before moving on. If an egret had an fd in pool i less than the fd in either of the other pools, its terminal, marginal rate of fish capture in i would exceed those of the other two pools. Thus the bird would do better if instead of leaving one pool early, it stayed the same amount of time in each of the three pools. This is simply an ideal free distribution of its fd-values (Fretwell, 1972).

Because fish perceive the egret and take precautions, the rate of fish capture ought to decline from the first minute of a visit to the last. What is an egret's optimum strategy? To time its visits so that it arrives at each pool just after the fish have emerged from cover. If it returns sooner, it will disturb hidden fish and delay their emergence from cover. If it returns later, it will have wasted the interval between the fish's emergence and its own revisit.

The ideal sequence is clear. Feed in one pool for time fd. Move to a second and feed fd minutes, then to the third for fd minutes. Then return to the first. The return time, rt, will be $2fd$ minutes, which will equal the goldfish refractory time, rt.

RESULTS

We designed our experimental arenas to give goldfish an opportunity to protect themselves from egret predation, and they did. In the presence of the egret, goldfish spent only 2.09% (S.E. = 0.86%) of their time in the open habitat. Without the egret, they spent 65.4% (S.E. = 2.15%) of their time in the open habitat. The difference is significant (Friedman test, $P = 0.005$).

The actual times spent by each species during a single feeding bout reflected their adaptive responses to each other's presence or absence. When no egret was present, foraging bouts of the school of goldfish (mean ± S.E.) lasted an average of 102.95 ± 18.96 min. In the presence of an egret, each foraging bout lasted only 1.73 ± 0.30 min. The difference is significant (Freidman test, $P = 0.005$, $n = 16$). The mean length of visit (± S.E.) of an egret to a pool was significantly higher when fish were present (9.07 ± 1.78 min) than when fish were absent (3.48 ± 0.41 min) (Freidman test, $P = 0.003$, $n = 16$).

Fish become less and less vulnerable to predation during an egret's visit to a pool. This is reflected by the decline in the rate at which an egret captures fish during a visit to a pool (Fig. 2). The rate is the total number of fish captured during successive 1-min intervals divided by the number of times that interval occurred in our data. The rate of fish capture declined sharply from 0.47 fish caught by egrets during the first minute of a visit to none caught during the seventeenth. The linear regression: $rate = 0.4 - 0.017 \times minute$ ($R^2 = 0.64$; $P_{(\mathrm{slope})} = 2 \times 10^{-5}$). Having shown the significance of the decline, we can seek a better fit to

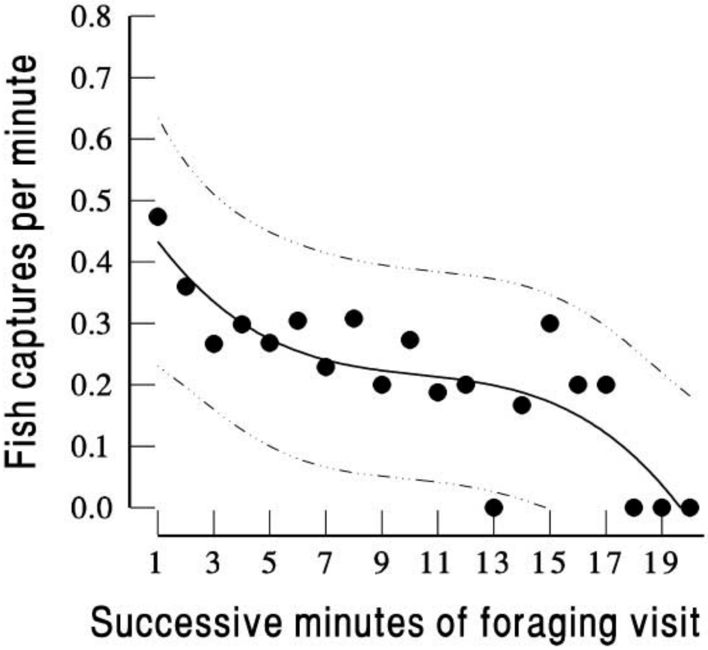

Fig. 2. Rate at which an egret captured fish during successive minutes of a foraging visit to an experimental pool. The egrets visited as individuals. Fish were more exposed to predation early in a visit because the egret allowed them at least some time to recover from the previous visit. Third-order polynomial regression with 95% confidence band.

the data with a polynomial regression. This is displayed in Fig. 2 together with a 95% confidence band.

An egret's optimum strategy is to time its visits to a pool so that it arrives just after the fish have emerged from cover. So we measured *rf* and *rt*. The average goldfish refractory time was 20.31 min (S.E. = 3.33 min). The average little egret return time was 21.09 min (S.E. = 3.73 min). As predicted, these values are not significantly different (Mann-Whitney *U*-test, $P = 0.37$).

Implicit in our reasoning is that egrets should be catching the most fish when they adopt the optimal foraging behaviour. They do. Binomial regression (Fig. 3) estimated the maximum catch (~21.2 fish per day) at a return time of 18.6 min (not significantly different from the observed *rt* of 21.09 min; one-sample *t*-test, $P = 0.61$).

DISCUSSION

We set common goldfish (the prey) and little egrets (their predators) to interact in a laboratory arena of three artificial pools with two habitats, one safe and with no food, the other risky but with the food goldfish require. Both predator and prey responded behaviourally to the predation interaction as they should have done (Sih, 1984, 2005; Lima, 2002; Schmitz, 2005). In the absence of an egret, fish fed in safe habitat 65.4% of the time; under threat of predation, fish reduced this to 2.09%. Fish waited an average of 21 min before re-exposing themselves. Most astonishingly, the egrets adjusted their foraging schedules

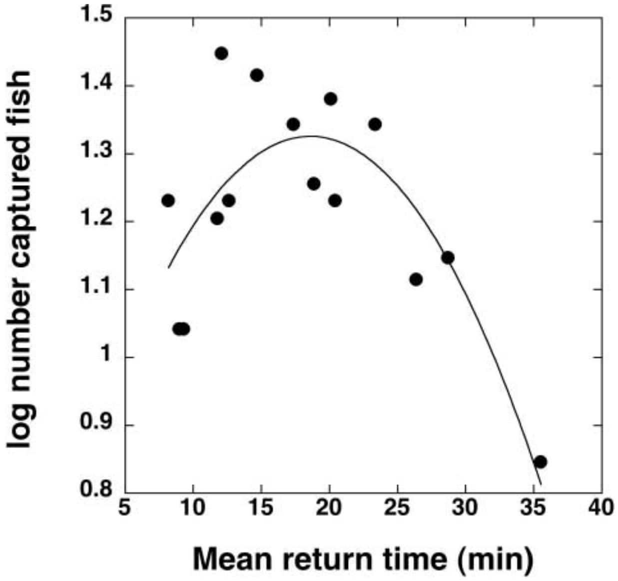

Fig. 3. How long little egrets remain away from a test pool with goldfish affects the amount of fish they catch when they do return. We tested eight egret individuals on two consecutive days. The fitted curve was generated with a binomial regression: $y = 0.72 + 0.0645rt - 0.0017rt^2$ ($R^2 = 0.65$; $P = 0.002$). Egret mean return time (21.09 min) is not significantly different ($P = 0.61$) from the time required to optimize their catch (18.6 min).

according to our prediction. Egrets timed their return visits to a pool to match the waiting time of the fish. Because they did, they maximized the rate at which they captured the wary 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 in understanding predator–prey interactions and the ecological communities in which they occur. In fact, our results are consistent with theories that predict how foragers should balance the conflicting demands of food and safety.

In the present study, the egrets had a return time of 21.09 min (S.E. = 3.73 min), and we have attached considerable significance to that result. But perhaps it has nothing to do with adjustment to the conditions of our experiment? Perhaps the return time of the little egrets is innate and agrees with our prediction merely by coincidence?

We can dismiss this possibility by looking at the preliminary results of an ongoing, more comprehensive one in which egrets are exposed to a variety of conditions. Those tests show that egrets exhibit a wide variety of return times. In particular:

- with 15 fish in one pool and none in the other two, $rt = 5.64$ min;
- with 15 fish in each of two pools and none in the third, $rt = 10.18$ min;
- with 10, 15, and 20 fish in each of the three pools respectively, $rt = 12.10$ min.

Common goldfish (*Carassius auratus*) and little egrets (*Egretta garzetta*) are virtual evolutionary strangers. Moreover, we caused them to interact in the alien environment of an experimental arena. It would be nonsense to conclude that they evolved their behavioural responses to each other in this habitat. The fact that they each responded so appropriately must reflect a more general set of adaptations to the predation and foraging challenges that each faces in more natural circumstances.

To avoid a mass extinction, species will have to be able to adjust to very novel anthropogenic habitats (Rosenzweig, 2003). Our results suggest that the adaptations and behavioural flexibility that they already possess may give some of them that capacity. Thus conservationists should be somewhat comforted by the successful behavioural adjustments of these species.

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