Evolutionary Ecology Research, 2018, **19**: 455–468

Influence of prey-food abundance on predator–prey foraging games: a test with little egrets and goldfish

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

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

ABSTRACT

Background: A predator–prey relationship abounds with variables that might affect the behaviour of either species as it responds to the challenges of the predation game. In a series of experiments, we have studied the behavioural responses of goldfish (prey) and little egrets (predator) when brought together in a large laboratory apparatus – an aviary with three pools of water. To obtain a baseline, we measured their behaviour in an aviary without manipulating any variable (Katz *et al.*, 2010). Because the results of that study suggested that both fish and egrets follow the rules of optimal foraging, we undertook a series of experiments in which we manipulated the number of food patches (Katz *et al.*, 2014a), the number of fish per pool (Katz *et al.*, 2014b; Vijayan *et al.*, 2018a), and the size of goldfish refuges (Vijayan *et al.*, 2018b). In each case, the results supported the hypothesis of optimal behaviour. Mitchell (2018, this issue) makes four predictions about the behaviours of both species as the abundance of fish resources changes in a system such as the aviary. Specifically: (1) Prey should respond very weakly, if at all, to variation in the food ration among patches. (2) The predator should allocate more time to patches with a higher prey-food ration. (3) When moving to another patch, the predator should choose the patch with the higher prey-food ration more often than it would at random. (4) The predator will kill more prey in patches receiving a larger ration of prey-food.

Aims: Explore the effect of varying the abundance of fish-food on the behaviours of goldfish and little egrets in the aviary. Determine whether variation in their behaviours agrees with the predictions of Mitchell's theoretical model.

Methods: We used little egrets (the predators) and goldfish (the prey). We conducted experiments in two identical aviaries (7 m diameter). Each aviary contained three separate patches, i.e. three pools (1.52 m diameter, 0.60 m deep, ~1000 litres), each open to foraging by a single egret in the aviary. A fixed cover (22.75 cm radius) at the centre of each pool provided a refuge for the goldfish. Each pool had 15 fish. We manipulated intraspecific competition by offering three different amounts of goldfish food in an aviary each day: full (1.13 g per day), half (0.56 g

---

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

per day), and quarter (0.28 g per day) rations. We then observed and recorded the behaviours of both players for 6 hours.

Results: Patch-to-patch variation in the food ration had no effect on fish activity. But the egret allocated more time to foraging in the patch where the prey-food ration was highest (1.13 g). When moving to another patch, the egret moved to the patches containing high food rations (1.13 and 0.56 g) rather than the patch with the lowest food ration (0.28 g). And the predator caught significantly fewer goldfish in these poorest patches. Thus all four predictions were validated.

Keywords: food abundance, goldfish, intraspecific competition, little egret, optimal foraging, predator–prey behavioural games.

INTRODUCTION

Predator–prey interactions involve behaviours that cannot be understood fully by modelling or studying them in one species isolated from the other. Recognizing this fact 16 years ago, Lima (2002) encouraged behavioural ecologists to consider more closely the role of the predator's responses when researching anti-predator behaviour, i.e. to remove predators from their 'black box'. We need to realize that predator–prey interactions are responses and counter-responses that must be studied together (Brown *et al.*, 1999). Evolutionary game theory is an appropriate tool for such study (McGill and Brown, 2007).

Game theory has been applied to various predator–prey scenarios:

- Simultaneous habitat choice by predators and prey (Hugie and Dill, 1994; Alonzo *et al.*, 2003; Sih, 2005; Mitchell and Angilletta, 2009; Luttbeg *et al.*, 2009; Fraker and Luttbeg, 2012; Gvoždík *et al.*, 2013).
- The 'waiting game' (Hugie, 2003), which models how long it takes the prey to emerge from a refuge, and how long the predator should wait at a refuge for prey to emerge
- The 'shell game' (Mitchell and Lima, 2002; Mitchell, 2009), in which prey randomize their location, thus becoming less predictable to the predator.

In any case, predator and prey movements on a landscape generate an evolutionary game. A predator allocates hunting time among different landscape patches containing various numbers of prey as well as varying food resources for the prey. Meanwhile, prey allocate time between habitats that differ in exposure to predation risk and to their own foraging opportunities. The evolutionary game arises from the fact that the fitness associated with the strategy of each individual predator or prey depends on the strategies employed by the other individuals (Sih, 1984; Hugie and Dill, 1994; Alonzo *et al.*, 2003; Luttbeg *et al.*, 2009; Mitchell and Angilletta, 2009; Gvoždík *et al.*, 2013; Garay *et al.*, 2015).

Models of predator–prey spatial games predict different behaviours from models in which the behaviour of one of the players is fixed (non-responsive). For example, if predator behaviour is fixed, prey should simply avoid areas of greater predation risk or require a foraging premium to feed in those habitats (Gilliam and Fraser, 1987; Brown and Kotler, 2004). But when both predator and prey are free to choose their habitats, predictions from game theory can be surprising.

For example, when both predator and prey are free to move among habitats containing different amounts of prey resource, the prey may distribute themselves independently of their resources while the predators focus their efforts in habitats with more prey resources (Hugie and Dill, 1994; Sih, 1998). Careful empirical work supports many of the qualitative predictions of these and related models (Hammond *et al.*, 2007; Fraker and Luttbeg, 2012). Other predator–prey games consider the movement of prey into and out of refuges, and the predator's response to such refuge-seeking behaviour (Cressman and Garay, 2009).

Several realistic aspects of predator–prey spatial interactions have received little attention theoretically. First, many of the predator–prey spatial games discussed in the literature consider predators and prey that move at the same spatial scale (e.g. Hugie and Dill, 1994; Hammond *et al.*, 2007; Mitchell and Angilletta, 2009). But predators often move at a larger spatial scale than their prey (Roth and Lima, 2007; Creel *et al.*, 2008; Goldberg *et al.*, 2014). In such cases, prey in spatially distinct patches may influence each other's fitness through a 'predator pass-along effect', in which anti-predator behaviour of prey in one patch can encourage a predator to increase its hunting effort of prey in a different, spatially isolated patch (Lima and Dill, 1990). The predator–prey shell game (e.g. Mitchell, 2009) is one of the few models to consider this possibility. And although prey move at a smaller scale than predators, their movements may include refuges, which would in turn influence predator behaviours (Cressman and Garay, 2009).

Another neglected feature of predator–prey spatial games is the role of foraging groups as anti-predator behaviour (Bertram, 1978; Cresswell and Quinn, 2011; Beauchamp, 2014; Heithaus and Dill, 2014). Grouping behaviour benefits prey through risk dilution and collective detection (Magurran and Seghers, 1991; Ale and Brown, 2007; Wood and Ackland, 2007; Beauchamp and Ruxton, 2008; Hirsch and Morrell, 2011; Sorato *et al.*, 2012; Pays *et al.*, 2013). Risk dilution occurs when the per capita chance of being killed in a predator attack becomes smaller as prey group size becomes larger (Bertram, 1978; Foster and Treherne, 1981; Turner and Pitcher, 1986; Rosenzweig *et al.*, 1997). Collective detection occurs when a prey individual benefits from another group member detecting an approaching predator (Dehn, 1990; Roberts, 1996; Pays *et al.*, 2013). The predators and prey should adjust their respective behaviours in light of the consequences of dilution and/or collective detection (Jackson *et al.*, 2006).

Mitchell (2018, this issue) models a spatial predator–prey game that considers many of the variables we mention above. In that model, predators move among distinct patches of equal prey density that have different levels of food resources for the prey. The prey, which usually move as a group outside the refuge, cannot move between the patches, but can move within a patch between two habitats, namely a protective refuge and an open, risky foraging habitat that contains food.

This study tests the four specific predictions of Mitchell's model:

1. Prey should respond very weakly, if at all, to variation in the food ration among patches.
2. The predator should allocate more time to patches with a higher prey-food ration.
3. When moving to another patch, the predator should choose the patch with the higher prey-food ration more often than it would at random.
4. The predator will kill more prey in patches receiving a larger ration of prey-food.

All our experiments took place in two large aviaries, each housing three pools containing goldfish. The goldfish were subject to predation from little egrets. Fish could choose between a food-rich, but risky habitat and a poor, but safe one, and egrets could move among the three pools to hunt fish. The fish could retreat to the refuge in response to the presence of the egret and then choose when to emerge from cover to resume feeding following the departure of the egret from the pool. The egret could decide when to depart from a pool and hunt in a different one, and then when to return to the first pool.

In previous studies, we measured the behaviours of fish and egret in an aviary without manipulating any variable (Katz *et al.*, 2010). Then we undertook a series of experiments in which we manipulated the number of food patches (Katz *et al.*, 2014a), the number of fish per pool (Katz *et al.*, 2014b; Vijayan *et al.*, 2018a), or the extent of goldfish refuges (Vijayan *et al.*, 2018b). 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 behavioural foraging game. The egret responded adaptively by adjusting its visitation rates to pools and the foraging time within pools according to the behaviour of the fish, resulting in maximization of its capture success. Meanwhile, as egret behaviour varied, fish adjusted their behaviour by trading food versus safety. Thus, whatever adaptive responses the two species possess in natural environments would seem to be sufficiently plastic to transfer to the artificial conditions.

METHODS

Predator

We used the little egret, *Egretta garzetta* (Ardeidae), a small heron, as a predator/forager in our experimental aviaries. Little egrets generally hunt their prey by stalking them in shallow water or standing still in ambush. They hunt opportunistically and their prey consist of fish, amphibians, crustaceans, and insects. In our experiments (with no alternative food item), a little egret must consume 15–20 (about 100 g) goldfish per day to meet its daily energetic demands (Kushlan, 1978). Egrets were caught in the wild (Ma'agan Michael, Kibbutz Ma'agan Michael D.N. Menashe, Israel, 32°33′20″N, 34°54′51″E). The birds were kept for at least 6 weeks in a holding cage prior to the experiments. We intended the holding period as a time to allow egrets to become accustomed to captivity and perhaps even to forget their previous hunting experience. (Our earlier studies did suggest that this period would allow the egrets to forget previous hunting experience.) Nevertheless, after participating in the experiments, all egrets were returned and released at the location of capture.

Prey

We used the Comet goldfish, *Carassius auratus*, a relatively small cyprinid, as the prey. 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 their colour, comet goldfish are little changed from their ancestral form (Holopainen *et al.*, 1997). We used goldfish ranging in size from 6 to 7 cm (6 to 7 g). Such individuals are easily captured and handled by egrets.

The experimental system

We conducted the experiment in two specially designed aviaries (each 7 m in diameter; Fig. 1) at the Ben-Gurion University Bergmann Campus, in Beer Sheva, Israel (31°15′5.2″N, 34°47′59.2″E). Each of the two aviaries contained three pools (patches) equidistant from one another, each with a diameter of 1.52 m and 60 cm deep (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.

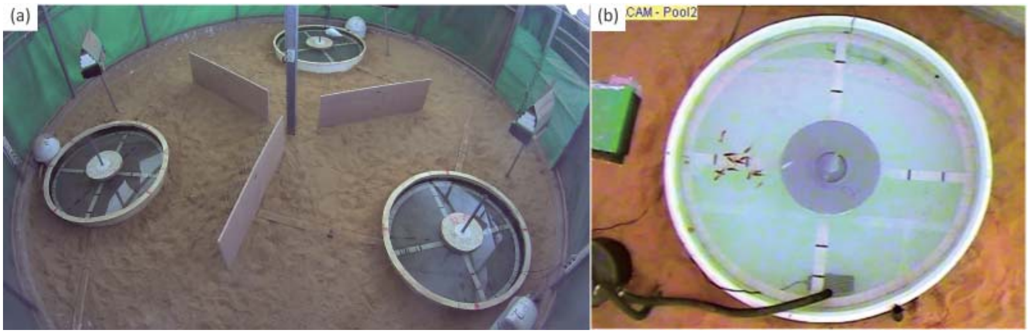

Fig. 1. (a) Panoramic view of the experimental aviary as viewed from one of the digital cameras, showing the three equally spaced pools, each 0.76 m in radius. Each pool has a protective central cover (radius 22.75 cm) that acts as a refuge. A timed food dispenser releases fish-food pellets during the 6 hours of an experimental trial. (b) An experimental pool as viewed from above. Note the school of goldfish swimming to the left of the cover in the exposed/risky habitat.

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

- a *safe microhabitat* – a circular (radius 22.75 cm), opaque cover over the central part of the pool under which the fish could seek shelter;
- an *open, risky microhabitat* – the rest of the pool, in open water, where the fish were exposed to predation (Fig. 1b).

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

Amounts of food for the prey

We offered one of three amounts of food to the goldfish in their pools. One pool received a full ration (1.13 g per day of fish-food, an amount that matched their basic daily energetic requirements). The other two pools received a half ration (0.56 g) and a quarter ration (0.28 g) respectively. The central cover that served as a refuge to the fish prevented the floating food particles from entering beneath it, forcing the fish to forage in the open risky areas and thus to trade off food and safety.

Experiment

We used both aviaries, each with 15 fish per pool and similar sized covers (radius 22.75 cm). We randomized the allocation of the amount of fish-food to a given pool. We placed one egret in each of the aviaries. The control treatment involved the same number of fish per pool but without an egret.

We conducted experiments in all four seasons from July 2015 to February 2017. During the winter, we heated the water to 20°C to maintain goldfish activity. Egrets were given 5 days to acclimate to an experimental aviary with three pools. Fish had one day of acclimation in their pool. We used 12 different egrets in the course of the experiments.

Since we used egrets captured from the wild and they were to be returned there, we wished to minimize handling them during their time in captivity. Therefore, we assigned each egret at random to one or the other aviary for all that egret's trials.

Each daily trial lasted 6 hours and each round consisted of 2 days without an egret (control) followed by 2 days with an egret (treatment). On days with egrets, we counted leftover fish-food particles at the end of each 6 hour session. From these data, we measured the number and percentage of food particles consumed by the fish. The fish consumed all the food on control days.

At the end of the first experimental day with an egret present, 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.

Behavioural recording

To observe the foraging behaviour of both players in the aviary, we used four high-definition CCTV cameras, one above each of the three pools and one that allowed a panoramic view of the whole aviary. The four cameras recorded all events in the experimental arenas, producing a permanent record of egret and fish behaviours for analysis and archiving.

We tabulated the behavioural data of egrets and fish on a minute-by-minute basis throughout the 6 hour sessions. In particular, we recorded the egret's location in the aviary (i.e. in one of three pools) at one-minute intervals. From these data we could ascertain the egret's foraging time in a pool (total and mean) and the average return time to a particular pool. Return time is simply how long it took an egret to return to a specific pool after leaving it. We also counted (one observation per minute) the number of fish in each pool that were outside the sheltered habitat (cover). We then calculated the mean number of fish that were outside cover as well as their mean and total time outside cover on each experimental day. We also studied egret hunting behaviour continuously on the recorded videos, and tabulated the exact time of fish depredation during the course of each experimental day. This allowed us to measure the number of fish alive during each minute of each of the two experimental days. We used the data for each of the three pools in an aviary, both separately and in combination, to calculate the behavioural variables.

Data analysis

We tabulated summaries of data variables using Python and performed statistical analyses using two different approaches to account for correlated error terms. For one approach, we used SPSS (v. 24, IBM SPSS) to perform a repeated-measures multivariate analysis of variance (ANOVA). For the second approach, we used the lme4 package (Bates *et al.*, 2015) in R (R Development Core Team, 2016) to conduct mixed model analyses that considered egrets and days nested within egrets as random effects. Both approaches yielded the same conclusions with respect to the rejection of null hypotheses with $\alpha = 0.05$. We report here the results of the multivariate ANOVA, and also the *P*-values generated by Pillai's trace statistic. When a null hypothesis was rejected, we conducted LSD pairwise comparisons to test for significant differences between behavioural variables in relation to levels of prey-food abundance.

Before performing the multivariate ANOVA, we checked for differences in egret behaviour between the first and second day. As in previous experiments, we found no significant differences between the tactics of the egrets on the first and the second day as reflected by their mean return time in the pools (Wilcoxon signed test: $P = 0.56$). We also did not find a significant difference between number of fish captured on the first and the second day of each experiment (paired t-test = 0.57, $df = 34$, $P = 0.13$). This result strongly suggests that since fish were schooling and always managing risk by shoaling, the naïve fish that were introduced after the first day followed the lead of the experienced fish. Therefore, we concluded that there was no day effect, and treated each day as an independent result. We present all results and statistical analyses for $n = 24$, which pools the results from 12 egrets, for each of the two experimental days.

Ethics

We followed protocols for animal maintenance, and conducted all experimental treatments 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). We obtained a license to catch the egrets from the wild from the Israel Nature and National Parks Protection Authority (Authorization No. 39323). We kept the fish and the egrets under strict veterinary supervision and followed all required regulations.

RESULTS

In the presence of an egret, the fish reduced their activity in the risky open water – both drastically and significantly (repeated-measures ANOVA, Pillai's statistic: $F = 121.2$, $df = 1,23$, $P < 0.001$). On average, fish were active for 228.4 ± 12.34 minutes (mean ± SE) on control days, but only 42.0 ± 7.3 minutes on experimental days with the egret present.

Prediction 1: When there is variation across patches in prey-food availability, prey should display a weak or no response to their food availability.

Indeed, fish activity in the three pools with different fish-food rations was not significantly different (Table 1).

Prediction 2: The predator should allocate more time to patches with the higher prey-food ration.

Table 1. Fish behavioural variables (mean ± SE)

	Food ration per day			P of repeated-measures ANOVA
	0.28 g	0.56 g	1.13 g	
Total time outside cover (minutes)	56.21 ± 15.67	45.79 ± 13.10	26.00 ± 7.74	0.24
Mean return time (minutes)	14.57 ± 5.05	20.96 ± 7.55	26.06 ± 6.72	0.47
Mean # of fish outside cover	6.19 ± 0.81	6.59 ± 0.64	6.58 ± 0.78	0.91
Mean foraging bout time outside cover (minutes)	2.5 ± 0.62	2.02 ± 0.38	1.60 ± 0.19	0.40
Mean % fish outside cover	9.78 ± 2.89	7.56 ± 2.17	4.76 ± 1.6	0.36

Note: The probability of the repeated-measures ANOVA was measured with Pillai's statistic ($df = 2,22$).

Table 2. Egret behavioural variables and number of fish captured by an egret (mean ± SE)

	Food ration per day			P of repeated-measures ANOVA
	0.28 g	0.56 g	1.13 g	
Mean total time (minutes)	78.25 ± 14.47^{a}	54.20 ± 8.48^{a}	150.04 ± 20.55^{b}	0.02
Mean foraging bout time (minutes)	$10.03 \pm 1.42^{a,b}$	7.83 ± 1.31^{a}	14.71 ± 2.01^{b}	0.03
Mean return time (minutes)	$43.95 \pm 7.29^{a,b}$	52.93 ± 8.67^{a}	29.01 ± 3.94^{b}	0.04
Total # fish captured	45	85	71	

Note: The probability of the repeated-measures ANOVA was measured with Pillai's statistic ($df = 2{,}22$). Results of the LSD test are indicated by letters within cells of a row. The superscript letters (a, b) are different for treatment levels that resulted in significantly different responses. If two treatments share the same letter, they were not significantly different at $\alpha = 0.05$.

Indeed, the egrets devoted significantly more time to the pool with the highest ration and returned to it significantly faster (Table 2).

Prediction 3: When moving to the next patch, the predator should choose the patch with the higher prey-food ration more often than it would by random movement.

The results support the prediction. Even though there was an equal opportunity to move to any pool, the egrets made 120 moves to a pool with a higher food ration and only 75 to one with a lower ration. The difference is significant (Wilcoxon signed test, $P = 0.03$).

Prediction 4: Predators will kill more prey in patches with a higher prey-food ration.

The accumulated number of captured fish (Charnov, 1976 model) (Fig. 2 and Table 3) and total number of captured fish (Table 2) show that indeed more fish were captured in pools with the full and half rations than in pools with the quarter ration. In one case (a half-ration pool), the egret actually succeeded in capturing all 15 fish that were present in the pool.

DISCUSSION

Our experimental results support the predictions of the predator–prey spatial game modelled by Mitchell (2018, this issue). In this spatial game, a predator allocates its time between patches of prey while the prey allocates its time between a refuge and a risky, open foraging area within each patch. In other words, the predator moves at a larger spatial scale than do the prey. Although this is likely a common scenario in natural systems (e.g. Roth and Lima, 2007),

Table 3. Separate slopes ANCOVA of the foraging curves (fish captures) in Fig. 2

Effect	*df*	*SS*	*MS*	*F*	*P*
Intercept	1	888.589	888.589	83.1053	0.000000
Food Level × Log Foraging time	3	6075.904	2025.301	189.4163	<0.0001
Food Level	2	1.476	0.738	0.0690	0.933405
Error	45	481.155	10.692		
Total	50	9917.686			

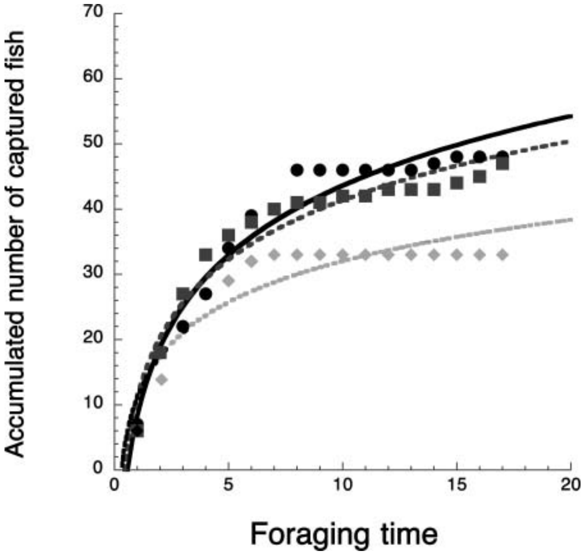

Fig. 2. Accumulated number of captured fish, in the three pools, as a function of foraging time in a patch for pools that have different fish-food rations. Regression equations: ■ + broken black line, 1.13 g per day → $y = 11.2 + 30.1 \log(x)$, $r = 0.97$, $P < 0.001$; ● + solid black line, 0.56 g per day → $y = 8.1 + 35.4 \log(x)$, $r = 0.98$, $P < 0.001$; ◆ + grey dashed line, 0.28 g per day → $y = 11.1 + 20.9 \log(x)$, $r = 0.92$, $P < 0.001$.

it has received less theoretical and empirical attention than games in which predator and prey move at similar spatial scales (e.g. Sih, 2005).

When we experimentally varied the ration of prey-food in different patches, the behaviours of predator and prey and the mortality of prey varied among patches as predicted by the game theory model. The observed patterns of behaviour and prey mortality would not have been predicted if prey and predators had been considered independently rather than responding to each other, and if the prey in different patches did not influence each other's behaviours.

A shared, responsive predator links the behaviours and fates of prey inhabiting different patches. The model predicted that prey inhabiting different patches – but sharing the same predator – would show no difference in feeding time, even if those patches differ in prey-food ration. If the predator did not respond to prey behaviours, then the prey in patches with more food should have spent more time feeding. How does a responsive predator equalize the foraging effort of prey in different patches?

Consider first the optimal behaviour of a fish that must decide how to allocate its time between a safe refuge and a risky, open area that contains food. The optimal time balances the trade-off between the benefit of foraging and cost of predation (Gilliam and Fraser, 1987; Brown, 1999; Heithaus and Dill, 2014). If food abundance increases while predation risk remains constant, the optimal time in the open should increase. Conversely, if predation risk increases while food abundance remains constant, the optimal time in the open should decrease (Cerri and Fraser, 1983).

Now introduce two more features of the landscape on which the prey lives. One of these is the presence of other patches containing similar fish, making similar decisions. The second feature is a predator that can allocate its time among these different patches. An optimal predator will allocate its time across patches to maximize its overall foraging success. Because the time the egret spends in one patch necessarily subtracts from the time it spends in other patches, the predator will always allocate more time to the patch in which the expected rate of return is higher. If the predator's rate of return increases with the time the fish spend in the open, then the predator will increase its allocation to wherever the fish spend the most time in the open. This is simple optimal foraging by the predator. But as the predator spends more time in a patch, it elevates the predation risk therein with the effect that the fish will reduce their time in the open. So the predator allocates time to the patch until the fish reduce their activity to the activity level of fish in other patches. At this point, the egret experiences the same expected return across all patches. If the egret's expected rate of return increases monotonically with the time the fish spend in the open, then the egret in effect equalizes the time spent in the open by fish across all patches. This constitutes our Prediction 1 and it is consistent with the behaviour of the fish in our experiment. The fish in pools with low, medium, and high food rations spent approximately the same time in the open.

The rule by which the egret equalizes its expected return, and hence the time in the open by fish across all patches, holds even if fish in different patches experience different foraging benefits. If one patch provides more food to the fish in the open, the foraging benefit in the open is higher in that patch. But, if the fish inhabiting that patch increase their time in the open, they attract more attention from the predator, which elevates the predation risk in that patch. An optimally foraging egret would devote just enough extra time to the patch with the higher fish-food ration as will reduce the fish activity in that patch so that it equals the activity of fish in other patches. Consequently, the patch with a higher abundance of fish-food attracts more time from the egret, but not more foraging time from the fish eating the food. This is Prediction 2, and it is consistent with the behaviour of egrets in our experiments. While the egrets did not allocate different amounts of time between the patches with low and medium fish-food rations, they did spend significantly more time in the patch with the highest ration.

The movement of egrets was consistent with Prediction 3, which states that, when moving to another patch, a predator will be more likely to choose the patch with the higher prey-food ration. This prediction results from the behaviour of the prey. Consider the different ways that egrets could have allocated more time to patches containing more fish-food. One way would be to move randomly with no bias among patches, but then extend the foraging bout longer in patches with more fish-food. But this would not be a good strategy because previous and current results with this aviary system indicate that the egrets experience diminishing returns during a foraging bout (Fig. 2) (Katz *et al.*, 2010). One reason for the diminishing returns is that the egret consumes some fish during the bout and thereby reduces their abundance. But, a stronger driver of diminishing returns in this system is that fish become harder to catch during a foraging bout because they increase their use of the refuge (Katz *et al.*, 2010).

A better way for the egret to increase its use of a better patch is to increase the frequency with which it enters that patch. Specifically, the egret should show a probabilistic bias when moving among patches; it should tend to travel next to a patch with more fish-food. This is the strategy used by egrets in our experiment. We might expect that they would also spend some additional time in patches with more fish-food because the fish there are more motivated to feed in the open, but there was no clear relationship between the amount of fish-food and egret feeding-bout duration (Table 2). We note that the strategy of biasing movement to the patch with more fish-food requires that the egrets learn the relative payoffs between patches and incorporate that information into their movement decision. Apparently, they could do this.

Spatial variation in prey-food abundance drives spatial variation in mortality due to predation. Our fourth prediction was that there would be a positive association across patches between the fish-food ration and the number of fish killed by the egret. Indeed, the fish in patches with a larger ration suffered higher mortality, even though they spent no more time in the open than did fish with less food. This higher mortality most likely reflects the increased predation risk that attends the higher allocation by the predator to those patches with more fish-food.

Fish suffering higher mortality in patches with a larger ration do receive one benefit – higher foraging gains by virtue of having more food available in their patch. Another way to view this result is that the behaviour of fish in the patches with more food increases the survival of fish in patches with less food. This is a direct result of the fact that fish in disjunct patches are engaged in a predator–prey game with a common, responsive predator. The interdependence of behaviour and fitness of prey in disjunct patches is the converse of short-term apparent competition (Holt and Kotler, 1987; Brown and Mitchell, 1989) in which prey in the same patch negatively influence each other's fitness.

Vigilance is another anti-predator behaviour (Lima and Dill, 1990). If the optimal vigilance by prey varies with food abundance, then some of the predictions of the predator–prey spatial game could change. For example, if prey used less vigilance at higher food levels (Brown, 1999), then there may actually be a negative relationship between food abundance and time spent in the open by prey. If so, at high food levels, the prey would use less vigilance. Less vigilance would confer upon the predator a higher expected rate of capture where food levels were higher. The predator would spend even more time in patches with more prey food. The precise predictions would depend on the trade-offs between sheltering, vigilance, and foraging. Katz *et al.* (2010, 2013) concluded that vigilance plays a minor role in the anti-predator behaviour of the goldfish, perhaps because they evolved in muddy water. Our experiments strengthen that conclusion; if vigilance played any role, it was apparently too weak to change the basic prediction of the game that ignored the role of vigilance.

The predator–prey spatial game that we study here has obvious similarities to previously described predator–prey spatial games (e.g. Sih, 1984, 1998, 2005; Luttbeg and Sih, 2004; Hammond *et al.*, 2007; Mitchell and Angilletta, 2009; Gvoždík *et al.*, 2013). The novelty in our game is the relative scale at which predators and prey move. In our system, the predator moves at a larger spatial scale than the prey, whereas in the others, the predator and prey move at the same spatial scale. In both cases, the optimal predator equalizes its expected return from different patches. So, for either movement scale, the prey should distribute themselves independently of their food resource, and predators should spend more time in patches with more prey-food (Sih, 2005).

Nonetheless, predators that move at a larger scale than their prey connect the fate of the spatially disjunct prey. In effect, the prey in different patches – who may never encounter each other – play a game among themselves mediated through their shared predator. Consequently, the prey in different patches modify one another's behaviour and influence one another's fitness. This is due in part to what Lima (2002) described as the 'predator pass-along effect'. Any anti-predator behaviour such as refuge use or vigilance in one patch will depress the fitness of prey in other patches, because the prey in those other patches must then adjust their own behaviours (e.g. reduce foraging effort) in response to the increased predator attention directed towards their patch.

A predator pass-along effect may reduce the spatial variation in prey fitness across patches that differ in prey food abundance. In the absence of a shared, responsive predator, prey in patches with higher food abundance would spend more time feeding without increasing their predation risk (e.g. Mitchell and Brown, 1990). However, with a responsive predator, prey with more food cannot spend more time feeding, and will experience a higher predation risk when they do feed. That higher predation risk reduces some of the fitness advantage of inhabiting a patch with more food. Thus, across the landscape, the predator–prey game may reduce spatial variation in prey fitness.

Many predator–prey interactions involve predators that move at a larger spatial scale than their prey (e.g. Roth and Lima, 2007). Our results suggest that evolutionary game theory can provide a guide to understanding such interactions. Although our experiments took place within aviaries smaller than the foraging range of a typical egret, we believe that the behavioural decisions exhibited by the egrets in making their choices about time and space would be mimicked on the larger scales at which these and other predators feed in nature.

ACKNOWLEDGEMENTS

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

REFERENCES

Ale, S.B. and Brown, J.S. 2007. The contingencies of group size and vigilance. *Evol. Ecol. Res.*, **9**: 1263–1276.

Alonzo, S.H., Switzer, P.V. and Mangel, M. 2003. Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, **84**: 1598–1607.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software*, **67** (1): 1–48.

Beauchamp, G. 2014. *Social Predation: How Group Living Benefits Predators and Prey*. Boston, MA: Academic Press.

Beauchamp, G. and Ruxton, G.D. 2008. Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. *Anim. Behav.*, **75**: 1837–1842.

Bertram, B.C.R. 1978. Living in groups: predators and prey. In *Behavioural Ecology* (J.R. Krebs and N.B. Davies, eds.), pp. 64–96. Oxford: Blackwell Scientific.

Brown, J.S. 1999. Vigilance, patch use, and habitat selection: foraging under predation risk. *Evol. Ecol. Res.*, **1**: 49–71.

Brown, J.S. and Kotler, B.P. 2004. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.*, **7**: 999–1014.

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

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

Cerri, R.D. and Fraser, D.F. 1983. Predation risk in foraging minnows: balancing conflicting demands. *Am. Nat.*, **121**: 552–561.

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

Creel, S., Winnie, J.A., Christianson, D. and Liley, S. 2008. Time and space in general models of antipredator response: tests with wolves and elk. *Anim. Behav.*, **76**: 1139–1146.

Cressman, R. and Garay, J. 2009. A predator–prey refuge system: evolutionary stability in ecological systems. *Theor. Popul. Biol.*, **76**: 248–257.

Cresswell, W. and Quinn, J.L. 2011. Predicting the optimal prey group size from predator hunting behaviour. *J. Anim. Ecol.*, **80**: 310–319.

Dehn, M.M. 1990. Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.*, **26**: 337–342.

Foster, W.A. and Treherne, J.E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, **293**: 466–467.

Fraker, M.E. and Luttbeg, B. 2012. Predator–prey space use and the spatial distribution of predation events. *Behaviour*, **149**: 555–574.

Garay, J., Cressman, R., Xu, F., Varga, Z. and Cabello, T. 2015. Optimal forager against ideal free distributed prey. *Am. Nat.*, **186**: 111–122.

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

Goldberg, J.F., Hebblewhite, M. and Bardsley, J. 2014. Consequences of a refuge for the predator–prey dynamics of a wolf–elk system in Banff National Park, Alberta, Canada. *PLoS One*, **9**: e91417.

Gvoždík, L., Černická, E. and Van Damme, R. 2013. Predator–prey interactions shape thermal patch use in a newt larvae–dragonfly nymph model. *PloS One*, **8**: e65079.

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

Heithaus, M.R. and Dill, L.M. 2014. Food availability and tiger shark predation risk. *Ecology*, **83**: 480–491.

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

Holt, R.D. and Kotler, B.P. 1987. Short-term apparent competition. *Am. Nat.*, **130**: 412–430.

Hugie, D.M. 2003. The waiting game: a 'battle of waits' between predator and prey. *Behav. Ecol.*, **14**: 807–817.

Hugie, D.M. and Dill, L.M. 1994. Fish and game – a game theoretic approach to habitat selection by predators and prey. *J. Fish Biol.*, **45**: 151–159.

Hirsch, B.T. and Morrell, L.J. 2011. Measuring marginal predation in animal groups. *Behav. Ecol.*, **22**: 648–656.

Jackson, A.L., Beauchamp, G., Broom, M. and Ruxton, G.D. 2006. Evolution of anti-predator traits in response to a flexible targeting strategy by predators. *Proc. R. Soc. Lond. B: Biol. Sci.*, **273**: 1055–1062.

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

Katz, M.W., Abramsky, Z., Kotler, B.P., Rosenzweig, M.L., Alteshtein, O. and Vasserman, G. 2013. Optimal foraging of little egrets and their prey in a foraging game in a patchy environment. *Am. Nat.*, **181**: 381–395.

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

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

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

Lima, S.L. 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.

Luttbeg, B. and Sih, A. 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. *Isr. J. Zool.*, **50**: 233–254.

Luttbeg, B., Hammond, J.I. and Sih, A. 2009. Dragonfly larvae and tadpole frog space use games in varied light conditions. *Behav. Ecol.*, **20**: 13–21.

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

Magurran, A.E. and Seghers, B.H. 1991. Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. *Behaviour*, **118**: 214–234.

McGill, B.J. and Brown, J.S. 2007. Evolutionary game theory and adaptive dynamics of continuous traits. *Annu. Rev. Ecol. Evol. Syst.*, **38**: 403–435.

Mitchell, W.A. 2009. Multi-behavioral strategies in a predator–prey game: an evolutionary algorithm analysis. *Oikos*, **118**: 1073–1083.

Mitchell, W.A. 2018. A spatial game between a predator and social prey in multiple patches. *Evol. Ecol. Res.*, **19**: 469–476.

Mitchell, W.A. and Angilletta, M.J., Jr. 2009. Thermal games: frequency-dependent models of thermal adaptation. *Funct. Ecol.*, **23**: 510–520.

Mitchell, W.A. and Brown, J.S. 1990. Density-dependent harvest rates by optimal foragers. *Oikos*, **57**: 180–190.

Mitchell, W.A. and Lima, S.L. 2002. Predator–prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos*, **99**: 249–259.

Pays, O., Beauchamp, G., Carter, A.J. and Goldizen, A.W. 2013. Foraging in groups allows collective predator detection in a mammal species without alarm calls. *Behav. Ecol.*, **24**: 1229–1236.

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

R Development Core Team. 2016. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing [https://www.r-project.org/].

Roberts, G. 1996. Why individual vigilance declines as group size increases. *Anim. Behav.*, **51**: 1077–1086.

Rosenzweig, M.L., Abramsky, Z. and Subach, A. 1997. Safety in numbers; sophisticated vigilance by Allenby's gerbil. *Proc. Natl. Acad. Sci. USA*, **94**: 5713–5715.

Roth, T.C. and Lima, S.L. 2007. The predatory behavior of wintering Accipiter hawks: temporal patterns in activity of predators and prey. *Oecologia*, **152**: 169–178.

Sih, A. 1984. The behavioral response race between predator and prey. *Am. Nat.*, **124**: 143–159.

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

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

Sorato, E., Gullett, P.R., Griffith, S.C. and Russell, A.F. 2012. Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Anim. Behav.*, **84**: 823–834.

Turner, G.F. and Pitcher, T.J. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *Am. Nat.*, **128**: 228–240.

Wood, A.J. and Ackland, G.J. 2007. Evolving the selfish herd: emergence of distinct aggregating strategies in an individual-based model. *Proc. R. Soc. Lond. B: Biol. Sci.*, **274**: 1637–1642.