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A spatial game between a predator and social prey in multiple patches*

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ABSTRACT

I build a theoretical model of an optimal predator and prey interaction. The predator allocates its hunting time among different landscape patches containing prey. Simultaneously, at a much smaller spatial scale, the prey allocate their time between different habitats within each patch. I obtain the Nash equilibrium strategy of each species. When applied to the experimental set-up of little egrets and goldfish in the system of Vijayan *et al.* (2018, this issue), the model makes four specific predictions available for testing.

Keywords: predator–prey behavioural games at two spatial scales, predation risk, foraging opportunity, optimal foraging of both species, predicted influences of food abundance.

INTRODUCTION

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, while prey allocate time between habitats which may differ in foraging opportunity and exposure to predation risk. The evolutionary game results because the fitness associated with the strategy of any individual predator or prey depends on the strategies employed by 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).

Behaviours predicted by game theory models can differ from those of non-game models. For example, when habitats differ in food and predation risk, prey may attempt to balance foraging return against predation risk. When predators do not play the game (respond to prey behaviour), prey can simply avoid habitats of higher predation risk or require a foraging premium to feed in those habitats (Gilliam and Fraser, 1987; Brown and Kotler, 2004). But in a game theory model the predators can move in response to prey foraging effort and thereby change the relative risk of different habitats, and this can lead to surprising predictions. For example, game theory predicts that when predator and prey can both move between

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habitats containing different amounts of prey food, the predator should concentrate more on the habitat rich in prey food while the prey distribute themselves equally between rich and poor habitats (Hugie and Dill, 1994; Sih, 1998). Sih (1998) called this pattern 'leapfrogging'. Some experiments confirm that predators bias their time towards patches rich in prey resource (Williams and Flaxman, 2012), while others suggest that predators manage prey risk differently (Fraker and Luttbeg, 2012). Other predator–prey games consider refuging by prey and the predator's response to the time the prey spends in refuge (Cressman and Garay, 2009). While other predator–prey game models differ in their specific assumptions, they yield predictions differing from non-game models, and careful empirical work supports many of the qualitative predictions (Hammond *et al.*, 2007; Fraker and Luttbeg, 2012).

Despite the success of game theory, certain realistic aspects of predator–prey spatial interactions have received little attention theoretically. First, current theory focuses on 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 many predators move at a larger spatial scale than their prey (Roth and Lima, 2007; Creel *et al.*, 2008; Goldberg *et al.*, 2014). In these cases, prey in spatially distinct patches may influence each other's fitness and behaviours through a 'predator pass-along effect', in which the anti-predator behaviour of prey in one patch can encourage a predator to shift its hunting effort to a different patch (Lima, 1990).

Another neglected feature of predator–prey spatial games is the formation and movement of groups of prey (Bertram, 1978; Cresswell and Quinn, 2011; Beauchamp, 2014; Heithaus and Dill, 2014). In some cases, groups may provide a foraging benefit (Creel and Winnie, 2005), but in many instances groups provide the anti-predator benefits of risk dilution and collective detection (Magurran and Seghers, 1991; Rosenzweig *et al.*, 1997; 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 decreases as prey group size increases (Bertram, 1978; Foster and Treherne, 1981; Turner and Pitcher, 1986). Collective detection occurs when a prey individual benefits from another group member detecting an approaching predator (Dehn, 1990; Roberts, 1996; Pays *et al.*, 2013). Risk dilution and collective detection likely influence the behaviours of both predator and prey (Jackson *et al.*, 2006).

Just as single prey respond individually to predation risk by allocating time between a refuge and open foraging habitat, so should groups of prey. But this raises the question of how prey decide – as a group – to allocate their time between a foraging area and a refuge; that is to say, how do prey in a group coordinate their movements to optimize individual fitness. The answer likely depends on group size and predation risk. For groups of prey in a landscape, the predation risk will depend on the behaviours of groups in other prey patches.

In this article, I model an experimental setup ready to test predictions. It contains a single predator that allocates its hunting effort between two or more patches containing prey. Prey are restricted to a single patch. But within that patch, prey can move between two habitats: open and refuge. The open habitat provides the prey access to food at the risk of predation. The refuge offers safety from predation but no food. Here, I analyse the case in which each patch holds a single individual prey, but similar results apply when the patch contains multiple prey individuals that coordinate their movements as a shoal between refuge and open foraging area.

MODEL

I assume that the fitness of the predator equals the sum of the rates at which it consumes prey from all patches. I assume also that the fitness of the prey is the probability of surviving predation over a period of time, T, multiplied by the survivor's fitness (Brown and Kotler, 2004). Prey fitness is an increasing function of a prey's energy state.

Let p be the proportion of time that a prey spends foraging in the open habitat, q the proportion of time that the predator spends in that prey's patch, and μ the rate of predation when the prey is in the open habitat and the predator is in the patch. Assuming, for simplicity, that predation is the only source of mortality, the probability that the prey survives a period of length T is,

$$S(p, q, \mu) = e^{-pq\mu T} \tag{1}$$

The survivor's fitness is the fitness of a prey that is not killed by a predator within the time period T. I assume that the survivor's fitness equals the prey's energy state raised to the power z ($0 < z \leq 1$):

$$F(X) = vX^2 \tag{2}$$

A prey begins with initial energy state, X_0, and it pays a constant metabolic cost of C_m per unit time for the entire period of length T. It can add to its energy state by foraging in the open habitat where it harvests energy at the rate f. I assume that f is proportional to the food available to prey in the open. Its energy state at time T is then,

$$X(p) = \max(0, X_0 + (pf - C_m)T) \tag{3}$$

I define a prey fitness-generating function (Vincent and Brown, 2005) using equations (1–3) with q_{res} denoting the resident predator strategy,

$$G(p, q_{res}, \mu) = S(p, q_{res}, \mu)F(X(p)) \tag{4}$$

The resident predator strategy, q_{res}, is used by virtually all predators, which means that it is the predator strategy most prey will experience.

I define the fitness-generating function for the predator to be the predator's rate of prey capture from m patches ($m > 1$). To simplify the analysis, I ignore the effect of prey depletion (Jackson *et al.*, 2006). Let the subscript i index patches ($0 \leq p_i, q_i \leq 1$, $i = 1, \ldots, m$), $\vec{p}_{res} = [p_{1,res}, p_{2,res}, \ldots, p_{m,res}]$ represent the vector of prey allocation to the open habitat in each patch for the resident prey strategy, $\vec{q} = [q_1, q_2, \ldots, q_m]$ represent the vector of predator allocations to patches, and μ_i represent the predation rate in each patch. I assume here that the predation rate is the same across all patches. The predator's fitness-generating function is then,

$$H(\vec{q}, \vec{p}) = \sum_{i=1}^{m} p_{i,res}\, q_i \mu \tag{5a}$$

subject to

$$\sum_{i=1}^{m} q_i = 1 \tag{5b}$$

The Nash equilibrium strategy for the prey is the strategy that maximizes the prey fitness-generating function subject to the behaviour of the predator. Likewise, the Nash equilibrium strategy of the predator is that which maximizes the predator fitness function subject to the prey behaviour and the equality constraint (5b). I find the conditions that the predator behaviour must satisfy at the Nash equilibrium using the technique of Lagrange multipliers and conjoin the fitness function (5a) with the constraint function (5b) multiplied by the multiplier λ,

$$L(\vec{p}, \vec{q}, \lambda) = H(\vec{q}, \vec{p}) - \lambda \left(\sum_{i=1}^{m} q_i - 1 \right) \tag{6}$$

The first-order conditions for maximizing the predator's fitness-generating function are then,

$$\frac{\partial L}{\partial q_i} \geq 0 \quad \text{for all } i \text{ in } (1, \ldots, m) \tag{7}$$

Substituting equations (5) and (6) into equation (7) yields the following conditions:

$$p_{i,res}\, \mu_i = \lambda \quad \text{for } 0 < q_i < 1 \tag{8a}$$

$$p_{i,res}\, \mu_i > \lambda \quad \text{for } q_i = 1 \tag{8b}$$

$$p_{i,res}\, \mu_i < \lambda \quad \text{for } q_i = 0 \tag{8c}$$

$$\text{for all } i \text{ in } (1, \ldots, m)$$

The Lagrange multiplier, λ, on the right-hand side of the equality (or inequality) represents the marginal rate of return on foraging that the predator receives from any patch it exploits. This rate must be equal for all patches exploited – otherwise the predator would simply spend more time in whichever patch yielded a higher rate of return, and in response the prey receiving more (less) predator attention would reduce (increase) its time in the open. If equality (8a) is satisfied, then the predator should spend some portion – but not all – of its time in patch i. If inequality (8b) is satisfied, then the predator should spend all of its time in patch i. Conversely, if the maximum rate of return from a patch is less than λ, then inequality (8c) is satisfied and the predator should not use that patch.

Although equations (8a–c) are obtained by maximizing the predator's fitness, they specify the Nash behaviour of *prey* in terms of the predation rate and λ, i.e. they indicate what the fitness-maximizing prey must do when the predator uses its (as yet unspecified) Nash equilibrium behaviour. To find the predator behaviour, I first take the derivative of the fitness (4) of prey in each patch with respect to p_i and rearrange terms to obtain,

$$p_i^* = \frac{z}{\mu q_i} - \frac{1}{f_i} \left(\frac{X_0}{T} - C_m \right) \tag{9}$$

Note that I index the prey's harvest rate of food, f_i, to permit different food availability in different patches. I then solve for the Nash behaviour of the predator behaviour by substituting p_i^* from equation (9) into equation (8) and rearranging:

$$q_i^* = \frac{zT}{\lambda T + \frac{\mu}{f_i}(X_0 - C_m T)} \tag{10}$$

If I consider only the cases in which the predator hunts in multiple patches, I can rearrange equation (8a) to provide the Nash behaviour of the prey,

$$p_i^* = \frac{\lambda}{\mu} \tag{11}$$

Analysis of (10) and (11) predicts how behaviours of prey and predator should change with between-patch differences in food available to prey.

Because equation (11) does not contain f_i, prey foraging time in patches is independent of differences in prey food availability between patches. If a prey in one patch were to spend more time foraging, it would attract all the predator's attention until that prey reduced its foraging activity to the same level as that of prey in other patches. The predator, on the other hand, should respond to prey food availability, as indicated by equation (10). But the specific response of the predator depends on the prey's initial energy state relative to its metabolic cost. To illustrate this dependence, I define the prey's 'reserve state' as the energy state that the prey would have at the end of the period of interest if it never fed during the period T. Whether the reserve state is positive or negative has a qualitative influence on the predator's behaviour. For example, if the prey's reserve state is positive, then both terms in the denominator of (10) are positive. This means that an increase in f_i results in an increase in q_i; that is to say, the predator should allocate more time to patches in which the prey food ration is greater. Although this prediction relies on the prey having the energy resources to survive a period T without foraging, the prey indeed forage (equation 11). This result for a positive reserve state is similar to the 'leapfrog' effect in the predator–prey double ideal free distribution (Sih, 2005). Conversely, if the prey's reserve state is negative (it would starve in the absence of foraging during time T), the predator should spend less time in patches with a higher prey food ration.

I can also predict the relationship between food availability in a patch and the chance the prey is killed by the predator. Because the foraging activity of prey is independent of its food availability, prey survival depends solely on the response of the predator. For example, if the prey's reserve state is positive, then the predator should spend more time in patches where there is more prey food and that, in turn, will result in more prey killed in those patches.

Finally, I use equation (10), which predicts the proportion of time that the predator should spend in each patch, to derive a prediction of the order in which it should visit different patches. To make this prediction, I assume that the predator's behaviour can be modelled as a continuous Markov process represented by a transition rate matrix, $\boldsymbol{A}$, in which the off-diagonal elements a_{ij} represent the transition rate from patch i to patch j for $i \neq j$, and the inverse of the diagonal elements, $a_{ii} = -\Sigma_{j \neq 1} a_{ij}$, are the average stay times per visit in patch i. The proportion of time that the predator spends in each patch equals the left null vector of the transition rate matrix, $\boldsymbol{A}$ (Durrett, 2012). This equality permitted me to address the transition rates of the predator between patches.

I describe the movement rule for the case in which there are three patches, because this represents the experimental set-up described in Vijayan *et al.* (2018, this issue).. First,

consider the case in which the predator spends equal amounts of time in all patches. In this case, the allocation of time to patches, and hence the left null vector, would be $[q_1, q_2, q_3] = [1/3, 1/3, 1/3]$, which means that the off-diagonal elements of $\boldsymbol{A}$ would all be equal. If all off-diagonal elements are equal, then the predator would show no bias when moving among patches.

What if the different patches contained different prey food rations resulting in the predator needing to spend different proportions of its time in different patches? In this case, the predator will achieve the optimal allocation if it biases its movement in favour of the patch with the higher desired allocation. More specifically, the vector of patch allocations will be the null vector of the transition rate matrix, $\boldsymbol{A}$, if the transition rate from patch i to j is proportional to the allocation of time to patch j. This means that the ratio of transition probabilities to two patches reflects the ratio of desired allocation to those patches. For example, consider a predator with an optimal temporal allocation of $[q_1, q_2, q_3] = [0.6, 0.3, 0.1]$. When this predator departs patch 1, its rate of transition to patch 2 will be three times higher than its transition to patch 3, or $a_{12}/a_{13} = q_2/q_3$. Equivalently, when the predator departs patch 1, it should be three times more likely to move to patch 2 than to patch 3. I can apply this rule to predict the relative probabilities of which patch the predator visits next after a patch departure.

SUMMARY OF PREDICTIONS

I used the model to predict how the behaviours of little egrets and goldfish in the experimental system of Vijayan *et al.* (2018, this issue) should respond to between-patch variation in prey food ration. Because previous observations on starved goldfish in this system indicated that the goldfish would not starve if they never ate during the experimental observations, I let the energy reserve of the goldfish take a positive value in the equations above. The model now makes the following predictions:

1. Prey should not respond to variation in 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.

These four predictions are, in fact, those tested in Vijayan *et al.* (2018, this issue).

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