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Ecology of fear: Foraging games between predators and prey with pulsed resources

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We model the foraging game between a prey and predator when the prey experiences a temporally pulsed resource (e.g., seed-eating gerbils). Animals have the options of foraging or remaining inactive. Prey harvest resources and incur a mortality risk only while foraging. ESS levels of prey and predator activity have three distinct phases over the time course of a resource pulse. During the first phase, resources are sufficiently abundant to permit profitable foraging by all prey and predators. During the second phase, only a fraction of prey and predator are active. The fraction of active prey is sufficient to allow profitable foraging by the predators. Resource abundances and activity level of predators decline synchronously, balancing the prey's needs for food and safety. During the third phase, resources decline to where both prey and predator cease activity. These adaptive behaviors of prey and predator to resources and to each other promote the stability of the predator-prey dynamics.

Introduction

Predators have lethal effects: predators kill their prey (Taylor 1984). Predators have non-lethal effects: predators frighten their prey into forgoing feeding or other opportunities (Sih 1980, Lima 1998). The ecology of fear examines the ecological consequences of these non-lethal ef-

fects (Brown *et al*. 1999). Ecological effects include the distribution and abundance of prey and predator (Werner 1992, Schmitz *et al*. 1997), coexistence or lack thereof among different prey species (Kotler 1984, Brown 1989a, Holt & Lawton 1994), and the population dynamics and stability of the predator-prey interaction (Schwinning & Rosenzweig 1990, Abrams & Matsuda 1993). Behaviorally flexible predator and prey engage in a foraging game (Sih 1984, 1998). Prey balance conflicting demands for food and safety so as to maximize fitness (= per capita growth rate). Predators capitalize on the prey's needs and try to outwit the prey's anti-predator behaviors.

The foraging game between predator and prey has been examined in the context of spatial variability in risk and feeding opportunities (van Balaan & Sabelis 1993). In some cases, strong behavioral top-down effects occur as predators distribute themselves so as to equalize fitness opportunities among habitats or patches. In such cases, the abundance of prey among habitats equalizes the product of prey density and prey catchability (this assumes that the predators do not interact directly with each other and that predators' foraging costs are the same across habitats). But, to be an ESS, the prey must also experience equal fitness opportunities among habitats. This introduces a bottom-up effect analogous to the paradox of enrichment (Rosenzweig 1971). More productive patches will harbor more predators (Holt & Lawton 1994, Hugie & Dill 1994, Grand & Dill 1999). The landscape of fear (sensu John Laundre) among habitats determines the distribution and abundance of prey, while the landscape of resource productivity for the prey determines the distribution and abundance of predators.

The behavioral game between predator and prey can also strongly influence the stability of predator-prey interactions as first suggested by Rosenzweig and MacArthur (1963). Effects can be stabilizing or destablilizing (Abrams & Matsuda 1993, Fryxell & Lundberg 1994, 1998). Also, such effects can occur when 'behaviors' represent irreversible life-history decisions (Kokko & Ruxton 2000 and references therein). Context dependencies suggest that rapid and perfect anti-predator responses on the part of the prey may destabilize the interaction (van Balaan & Sabelis 1993, 1999). Slower and less perfect responses by the prey to the predator may stabilize the interaction by introducing a positive slope to the predator's isocline (predators negatively affect themselves via the fear response of the predator, Brown *et al*. 1999).

Here, we model the foraging game between a prey species and its predator when the prey's resource renews in temporal pulses. This creates a continuum of temporal habitats represented by resource depletion and time since the last pulse. A variety of systems may exhibit the donor-controlled temporal pulsing of resource availability. Annual or seasonal changes in plant productivity or animal breeding create pulses of resources. Examples include seasonal flowering to a nectarivore, granivore or frugivore, and warm or wet season production of invertebrates to insectivores. Pulses of resources may also occur on a daily basis. Nectar resources may be highest in the morning following a night of production (Schaffer *et al*. 1979, Pimm & Pimm 1982). The emergence of insects from eggs or larval stages may be time-dependent and create resource pulses for their consumers (e.g. temperature and humidity influence the size of the insect pulse available to bats prior to a night's feeding). Plant productivity and/or diel shifts in the behavior of prey species create daily or nightly pulses in resource abundances (Tessier & Leibold 1997).

The gerbils (*Gerbillus andersoni allenbyi* and *G. pyramidum*) and barn owls (*Tyto alba*) of sand-dune habitats in the Negev Desert, Israel provide such a system. On most afternoons, winds redistribute sand in a manner that buries and unburies seeds (G. Ben-Natan, unpubl. data). In general, this creates a pulse of fresh foraging opportunities for the seed-eating, nocturnal gerbils. Initially, available seed resources and gerbil activity are high. As the night progresses, both seed availability (Kotler *et al*. 1994) and gerbil activity decline (Kotler *et al*. 1993). Presumably, the owls adjust their activity patterns accordingly.

How should prey and predator distribute their temporal activity in response to a pulsed resource? We build from one scenario to a second. In the first, we consider only the prey

species and its resource. The resource occurs as a temporal pulse, and the prey can choose at any given time between foraging or remaining inactive. In the model, resource pulses occur frequently enough, from the prey's perspective, that relatively few prey risk starvation over the interval. In the second, we introduce a predator who can also choose at any given time whether to forage for prey or to remain inactive. When prey are inactive, we assume that they are unavailable to their predators. For both scenarios, we are interested in:

1. modeling the optimal foraging behavior of the prey and predator. For the last scenario, this includes finding the ESS distribution of prey and predator activity with time.
2. predicting the roles of resource productivity and predation risk in influencing temporal activity patterns of prey and predator. How do feeding opportunities for predators vary with time, and how do feeding and risk vary with time for prey?
3. predicting the effects of the prey's and predator's ESS behaviors on population sizes, dynamics, and stability. How does pulse size create bottom-up effects, and how does the predator's tactics create top-down effects?

Prey foraging behavior in response to a pulsed resource

In what follows, Table 1 provides a complete list and description of the models' parameters and variables.

Consider a spatially-homogeneous environment that every T time units receives a pulse of resources that renews resource availability, R, to a size R_0 (Brown 1989b). This resource can be harvested by a consumer species. The consumer species can either spend its time foraging or resting within its burrow. Let N be the population size of consumers. While foraging, let the feeding rate of a consumer, f, be an increasing function of resource abundance. Holling's (1965) disc equation provides a suitable example:

$$f = aR/(1 + ahR) \quad (1)$$

where a is the consumer's encounter probability on the resource and h is the consumer's handling time on a resource item. While foraging, we assume that the forager expends energy at rate c

Table 1. A list with definitions of the important parameters, variables, and functions. Subscripts of "n" and "p" refer to prey and predator, respectively.

Term	Definition
R, N, P	Density of resources, prey and predators
R_0	Initial density of resources
a_n, a_p	Encounter probabilities of prey and predator on their respective foods
h_n, h_p	Handling times of prey and predator on their respective foods
c, k	Foraging costs of prey and predator
c_0, k_0	Resting costs of prey and predator
f_n, f_p	Feeding rates of prey and predator
e_n, e_p	Energy state of prey and predator
μ	Risk of predation to a prey while it is actively foraging
γ	Risk of injury to a predator while it is actively foraging
$q(t)$, $p(t)$	Probability that a prey and predator are actively foraging at time t
F_n, F_p	Survivor's fitness of prey and predator
s_n, s_p	Survival probability of prey and predator
R'	Threshold abundance of resources above which all of the prey will forage even if all of the predators are also foraging — above R´: $q(t) = p(t) = 1$
R''	Threshold abundance of resources below which no prey forage even when there no are predators foraging — below R'': $q(t) = p(t) = 0$
qN'	Threshold abundance of prey at which the predators are indifferent between foraging or resting
θ_n, θ_p	The sum of foraging costs for the prey and predator

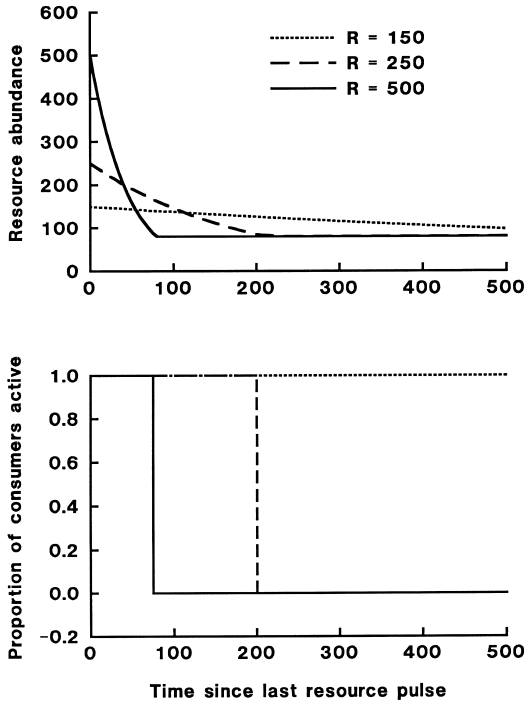


Fig. 1. The depletion of resources (Resource abundance vs. Time since last resource pulse) and the activity level of consumers (Proportion of consumers active vs. Time since last resource pulse) following a resource pulse. The figures consider initial resource pulses of $R_0 = 150$, $R_0 = 250$, and $R_0 = 500$ (dotted line, dashed line and sold line, respectively). Increasing the size of the resource pulse results in a higher equilibrium abundance of consumers. Resources decline smoothly until the consumers reach their threshold of profitability, at which point the consumers switch from all being active to all being inactive. As pulse size increases, this switch from activity to inactivity occurs earlier. For these illustrations: $c = 0.02$, $c_0 = 0.004$, $a = 0.0002$, $h = 0.5$, $T = 500$.

and while resting at rate c_0. Foraging is assumed to be more costly than resting: $c > c_0$ (both costs are in units of resources). The resting cost c_0 is the fixed cost of existence (also the maintenance cost in Mitchell and Porter (2001)), and the difference $c - c_0$ is the variable cost of foraging (Brown 1989b).

If the fitness of the consumer increases with net energy profit, then a consumer should remain active whenever foraging provides more gains than resting: $f - c > c_0$. Substituting Eq. 1 for f shows when foraging is more profitable than resting:

$$R > \frac{c - c_0}{a\left[1 - h\left(c - c_0\right)\right]} = R'' \qquad (2)$$

where h must be less then $1/(c - c_0)$ for the resource to be worth harvesting at all, and R'' defines the threshold of profitability.

The optimal foraging strategy of each consumer is simply to forage whenever resource abundance lies above the threshold of profitability ($R \geq R''$) and to remain inactive as soon as $R < R''$. If we let $q(t)$ be the probability that an individual consumer is active at time t (where t is time since the last pulse of resources), then $q^*(t) = 1$ when $R(t) \geq R'$, and $q^*(t) = 0$ when $R(t) < R''$ where the asterisk (*) indicates optimal value.

We can now model the temporal dynamics of resource availability, $R(t)$, and consumer foraging activity, $q^*(t)$, over the time course following a resource pulse. Resources decline with time:

$$\frac{\partial R}{\partial t} = -fNq(t) \qquad (3)$$

Using Eq. 1 for f, it is possible to solve implicitly for resource abundances during the period when all consumers are active ($q(t) = 1$):

$$t = \frac{\ln\left[R_0 / R(t)\right]}{aN} + \frac{h\left[R_0 - R(t)\right]}{N} \qquad (4)$$

For the period when $R(t) \geq R''$, the numerical solution to Eq. 4 describes the decline in resource abundances with time since the last pulse (Fig. 1). As soon as $R(t)$ declines to R'', the consumers cease foraging ($q^*(t) = 0$), and the resource abundance remains at R'' until the next pulse. Let t'' be the time at which $R(t) = R''$. This is the time taken by the consumers to deplete resources to their threshold of profitability (it can be found by substituting R'' from Eq. 2 into Eq. 4 for R). The consumers activity level with time is a step function that begins at $q(t) = 1$ for $t < t''$ and drops to $q(t) = 0$ for $t > t''$ (Fig.

1). If resource abundance remains above R'' throughout the time period ($t'' > T$), then foragers remain active and resource abundance declines throughout the period. For a fixed population size of consumers (N held constant), increasing the size of the resource pulse causes an increase in the time required for the foragers to deplete resources to their threshold of profitability: t'' increases with R_0 for fixed N.

The population size of consumers may also change. Assume that the population size of consumers changes following each resource pulse according to the following:

$$N(T) = N(0)G(e) \tag{5}$$

where G is the fitness of an individual (expressed as finite growth rate) as an increasing function of net energy profit over the time period. Assume that the population size increases ($G > 1$) when net profit is positive ($e > 0$) and N declines ($G < 1$) when net profit is negative ($e < 0$). Net energy profit in units of resources harvested and expended can be expressed as:

$$e = \frac{R_0 - R''}{N} - t''\left(c - c_0\right) - Tc_0 \tag{6}$$

where the first term on the RHS of Eq. 6 is the average amount of resources harvested by an individual (total resource harvest is divided equally among the N individuals), the second term gives the extra energy expended while foraging, and the third term gives energy expended for maintenance. The value for N^* can be found by setting Eq. 6 equal to zero, substituting the appropriate term for t'', and solving for N:

$$N^* = \frac{\left(R_0 - R''\right)}{Tc_0} - \frac{\left[(1/a)\ln\left(R_0/R''\right) + h\left(R_0 - R''\right)\right]\left(c - c_0\right)}{Tc_0} \tag{7}$$

Increasing the pulse size, R_0, increases the population size of consumers, decreases the time required for these consumers to deplete resources to R'', increases the proportion of resources harvested, and actually decreases the average amount of resources harvested by each consumer (Fig. 1).

We can use the following as a sample fitness function for modeling population dynamics:

$$G = (1 + be)^{\alpha} \tag{8}$$

where b scales the rate at which net energy profit can be converted into offspring, and α determines whether there are increasing ($\alpha > 1$), diminishing ($\alpha < 1$) or linear ($\alpha = 1$) returns to fitness from net profit. (We also require that $bc_0T < 1$, which insures that net energy never falls below –1 for a given foraging bout.) If Eqs. 5 and 8 are used as a difference equation model of population growth, then both the rate at which energy is converted into offspring and the initial pulse size can influence the stability of N^*. Increasing either b or R_0 can destabilize N^* and result in bifurcations into limit cycles and chaotic population dynamics.

Introducing a predator into the system

We introduce a predator species that, like the prey, can either forage or remain inactive. While foraging or resting, the predator expends energy at rate k or k_0, respectively. Furthermore, assume that the predator while foraging incurs some risk of fatal injury, γ. Such a risk of injury for a predator is probably realistic, and it insures that a predator in a high-energy state has more to lose from foraging than one in a low energy state (the asset protection principle of Clark 1994). Let $p(t)$ be the probability that a predator is actively foraging at time t. Requiring the predator to search for and handle prey yields the following feeding rate for the predator:

$$f_{\mathrm{p}}(t) = \frac{a_{\mathrm{p}}q(t)p(t)N}{1 + a_{\mathrm{p}}h_{\mathrm{p}}q(t)p(t)N} \tag{9}$$

where the subscript "p" indicates the feeding rate, encounter probability, and handling time of the predator on its prey.

Let P be the population size of predators where the change in predator population size with each period is given by:

$$P(T) = s_p F_p(e_p) P(0) \quad (10)$$

where s_p is the predator's probability of surviving the period to realize fitness, and F_p is its survivor's fitness (expected fitness given that the predator does not get injured while foraging). Survivor's fitness is an increasing function of net energy profit, e_p.

The predator's probability of avoiding fatal injury while foraging is given by:

$$s_p = \exp\left[-\gamma \int p(t)dt\right] \quad (11)$$

where γ is the risk of injury per unit time active. The integral, evaluated from $t = 0$ to $t = T$, simply evaluates the amount of time that a predator spends foraging during the period.

The predator's net energy profit during the period is given by:

$$e_p = \int p(t) f_p(t) dt - (k - k_0) \int p(t) dt - k_0 T \quad (12)$$

where the first integral evaluates cumulative harvest during the period, and the second integral gives total time spent foraging.

Let survivor's fitness be greater than 1 when net energy profit is greater than 0, and $G_p < 1$ when $e_p < 0$. As for the prey, a sample fitness function can take the form:

$$G_p(e_p) = (1 + b_p e_p)^{\beta} \quad (13)$$

where b_p scales the conversion of prey consumed into predator fitness, and β determines whether there are increasing ($\beta > 1$), diminishing ($\beta < 1$), or linear returns to fitness from net energy profit. (To insure that net energy profit never falls below –1, we require that $b_p k_0 T < 1$.)

With the introduction of predators, the prey now experience risk while foraging:

$$\mu(t) = \frac{a_p p(t) P}{1 + a_p h_p q(t) p(t) N} \quad (14)$$

where $\mu(t)$ is an active prey's probability of capture as influenced by the number of predators, their encounter probability with prey, and the number of other active prey. The activity level of other prey provides safety in numbers for the prey via the predator's decelerating, Type II functional response.

Using "n" to subscript functions relevant to the prey, we can write the following relationships for probability of surviving predation, s_n, net energy profit from foraging, e_n, and fitness:

$$s_n = \exp[-\int \mu(t) q(t) dt] \quad (15)$$

$$e_n = \int q(t) f_n(t) dt - (c - c_0) \int q(t) dt - c_0 T \quad (16)$$

$$N(T) = s_n F_n(e_n) N(0) \quad (17)$$

Characterizing the ESS activity levels of prey and predator

The above model represents a foraging game between and among predator and prey. An individual prey or predator must select its fitness maximizing activity schedule, $q^*(t)$ or $p^*(t)$, within the context of others' behaviors. Of direct relevance to a prey are the activity level of predators, $p(t)P$, and the availability of resources with time, $R(t)$. The availability of resources is directly a function of the average activity level of prey up to time t: $N\int q(t)dt$. Of direct relevance to the predators is the current activity level of the prey, $q(t)N$. The activity level of other predators is only relevant to an individual predator insofar as their activity influences the prey's activity levels.

To an individual prey, there are three effects of other prey increasing their activity levels. On the positive side, the prey experience safety in numbers for a given level of predator activity. On the negative side, the prey experience lower resource availability, and they may experience an increase in predator activity levels (short-term apparent competition, Holt & Kotler 1987). To the prey, there are two effects of the predators increasing their activity levels. On the negative side, the prey experience higher mortality. On the positive side, the prey may experience higher resource availabilities if prey reduce their activity levels in response.

In what follows, we assume that the predators do not substantially influence prey population size during a foraging bout of time T. Under this assumption, resource abundances do change significantly during a bout while meaningful

changes in prey and predator population sizes only occur between bouts.

Both prey and predator experience additional metabolic costs while foraging, experience risks of predation or injury, and have the choice of remaining inactive and avoiding risk and saving energy. With these hazards and opportunities, an individual (prey or predator) should forage only when its feeding rate is higher than the sum of its metabolic, predation, and missed opportunity costs of foraging (Brown 1988, 1992):

$$\text{Prey: } f_n \geq c + \mu F_n/(\partial F_n/\partial e_n) - c_0 \quad (18a)$$

$$\text{Predator: } f_p \geq k + \gamma F_p/(\partial F_p/\partial e_p) - k_0 \quad (18b)$$

The metabolic costs (1st terms on RHS) are straightforward. The predation cost includes the risk of death multiplied by the marginal rate of substitution of energy for predation risk. The marginal rate of substitution is the ratio of survivor's fitness and the marginal value of energy (Brown 1988, McNamara & Houston 1990). The missed opportunity is the return to the animal from remaining inactive, which is the negative of the metabolic cost of resting.

The following development will show how the ESS activity levels of prey and predator will pass through three phases as resources are depleted to R''. In the first phase, all of the prey and all of the predator individuals forage actively: $q^*(t) = 1$ and $p^*(t) = 1$. During this phase, both Eqs. 18a and 18b are satisfied as strict inequalities. During the second phase, only a fraction of prey and predator are actually active, $q^*(t) \in (0,1)$ and $p^*(t) \in (0,1)$, and Eqs. 18a and 18b are satisfied as strict equalities. In the third, resource levels have dropped to the prey's threshold level, R'' of Eq. 2. At this level, it is not profitable for the prey to remain active even in the absence of predation risk. Once this threshold has been reached, it is optimal for both prey and predator to remain inactive: $q^*(t) = p^*(t) = 0$.

The ESS activity level will always involve a subset of all three phases. Furthermore, within a foraging bout the three phases always occur in a strict ordering of (1) activity by all prey and predator individuals, (2) activity by a portion of prey and predator, and (3) complete inactivity of all prey and predator. If initial resource abundances are too low or predator numbers too high, then ESS activity levels at the start of a foraging bout may skip phase one and begin with phase 2 followed by phase 3 later in the bout. There is always a critical level of resources, R', such that the prey go from complete to only partial levels of activity. Hence, all prey and predators forage actively when $R(t) \geq R'$, a fraction of prey and predators forage when $R' > R(t) > R''$, and all prey and predators remain inactive as soon as $R'' \geq R(t)$.

The second and lower resource threshold of R'' is independent of the prey's survivor's fitness, the prey's population size, and the predator's population size. It only depends upon the prey's feeding rate and its metabolic costs of foraging and remaining dormant. However, the first resource threshold, R', that describes the shift from complete activity of prey and predator to partial activity is dependent on F_n, $\partial F_n/\partial e_n$, N, and P. The resource abundance, R', satisfies Eq. 18a with equality when $q(t) = p(t) = 1$. We can obtain an expression for the prey's first resource threshold, R', by substituting Eq. 1 for the prey's feeding rate and Eq. 14 for predation risk into 18a and solving for R:

$$R' = \frac{\theta_n}{a_n(1 - h_n\theta_n)} \quad (19)$$

where θ_n is the sum of foraging costs when all prey and predator individuals are active:

$$\theta_n = c + \frac{a_p P F_n}{(\partial F_n/\partial e_n)(1 + a_p h_p N)} - c_0 \quad (20)$$

Implicit in Eqs. 19 and 20 are the effects of the temporal depletion of resource abundances, $R(t)$, the level of prey activity, $q(t)$, and their subsequent effects on energy harvest, en, and the prey's survivor's fitness, Fn. Because the overall activity level required to harvest resource from R_0 to R'' is independent of P, N, and $q(t)$ (so long as there is enough time to deplete resources to R''), the number of predators does not influence net energy profit, survivor's fitness, nor the marginal value of energy.

We can now describe the factors influencing the prey's first resource-threshold, R'. Because of an increase in the foraging cost of predation, R' increases with the number of predators. In fact, as

the numbers of predators declines towards zero, the first threshold declines and converges with the second resource threshold: as $P \to 0$, $R' \to R''$. Because of safety in numbers, R' declines with the number of prey. The decline is further amplified by the reduction in survivor's fitness caused by the higher prey numbers: $\uparrow N \Rightarrow \downarrow F_n \Rightarrow \downarrow R'$. Despite the decline in R', the increased number of prey reduces the time required to reach R': t' declines with N. The initial resource abundance only has an indirect effect on the first resource threshold. Increasing R_0 raises survivor's fitness, F_n, which raises R'.

Above the first resource threshold, $R(t) > R'$, the activity of prey and predator is resource driven. The high availability of resources encourages foraging by all of the prey, and this high prey availability draws out all of the predators. However, once resource levels drop below R' the activity level of prey remains constant, and this level is predator driven. During phase 2 of resource depletion when $q^*(t) < 1$ and $p^*(t) < 1$, the activity level of prey insures that the predators have a feeding rate that just balances their foraging costs. Adjustments of $q(t)$ insure that Eq. 18b of the predators conforms to a strict equality. And, the activity level of the predators insures that the prey have a feeding rate that just balances their foraging costs. Adjustments of $p(t)$ insure that Eq. 18a of the prey conforms to a strict equality.

Just as the prey have threshold resource abundances (one each for the presence and absence of predators), the predator has a threshold abundance of active prey, qN', at which foraging and remaining inactive are equally profitable activities. Above qN', all predators should be active, and below qN', all predators should remain inactive. This threshold prey abundance can be found by substituting Eq. 9 for f_p into Eq. 18b and rearranging:

$$qN' = \frac{\theta_p}{a_p\left(1 - h_p\theta_p\right)} \tag{21}$$

where θ_p is the sum of foraging costs:

$$\theta_p = k + \frac{\gamma F_p}{\partial F_p / \partial e_p} - k_0 \tag{22}$$

Between the resource abundances R' and R'', the prey maintain a level of activity that satisfies Eq. 21. (If N' is too small for $q^* < 1$ then the predators are never active and the prey will forage as if there are no predators in the system.)

A declining activity level of predators between R' and R'' maintains the activity level of prey at q^*. At R', the ESS level of predator activity is $p^* = 1$. But once R drops below R' the prey will become inactive if all of the predators remain active. Hence, p^* drops below 1. The predator's ESS becomes the value of $p(t)$ that satisfies Eq. 18a as a strict equality. Between R' and R'' there is a monotonic relationship between $R(t)$ and $p^*(t)$. At the ESS levels of prey and predator activity, the predator's activity level tracks resource abundance while the prey's activity level remains constant. As $R(t)$ declines from R' to R'', the predator's activity level declines from $p^* = 1$ to $p^* = 0$ (Fig. 2).

We can now use the threshold abundances of resources for prey and prey for predators to predict the three consecutive phases of the ESS. The first phase occurs if initial resource abundance is greater than the prey's first threshold: $R_0 > R'$. During this phase, the ESS has all prey and all predators actively foraging: $R(t) \geq R' \Rightarrow q^*(t) = p^*(t) = 1$ (Fig. 2). The second phase occurs when resource abundances lie between the prey's two thresholds: $R' > R(t) > R''$. During the second phase, the activity level of prey drops as a step function from $q^* = 1$ to a constant and intermediate value of $q^*(t) \in (0,1)$. This prey activity level remains constant throughout the phase. The continued decline in resource availability indirectly causes the decline in the predator's ESS from all individuals active to no activity: from $p^* = 1$ to $p^* = 0$ (Fig. 2). The third phase of ESS activity levels begins as soon as resource abundances reach the prey's second resource threshold. At this point, both prey and predators cease all activity, $q^*(t) = p^*(t) = 0$, and resource abundance ceases to decline further (Fig. 2). Subsets of these three phases will occur if initial resource abundance are too low to permit the first phase of complete prey and predator activity, or if initial resource abundances are so high that the prey never reduce resource levels to either those of R'' (omit phase 3) or even R' (omit phases 2 and 3).

Predator-prey dynamics with ESS foraging behaviors

The ESS for prey and predator foraging behaviors consider fixed values of prey and predator population sizes. Equations 10 and 17 describe the predator's and prey's population dynamics, respectively. For a given initial abundance of resource (fixed R_0), we can characterize and numerically solve for the predator and prey isoclines (Fig. 3) and simulate the population dynamics. For the predators to be present within the population two things must hold. First, initial resource abundance must be high enough to insure the first phase of ESS behaviors where all prey and predators forage actively: $R_0 > R'$. This is because the first phase of the ESS provides prey and predators with net profits above the subsistence levels given by Eqs. 18a and 18b. During the second phase, net profits are at a subsistence level. During the second and third phases of resource abundances, prey and predators are actually losing body condition at a rate equivalent to the metabolic cost of resting. Hence, profits during phase 1 are necessary to compensate for losses during phases two and three. As a second requirement, the prey's carrying capacity, in the absence of predators must be higher than the predator's threshold level of active prey: $K > qN'$. In what follows, we will consider scenarios that likely result in all three phases of resource depletion.

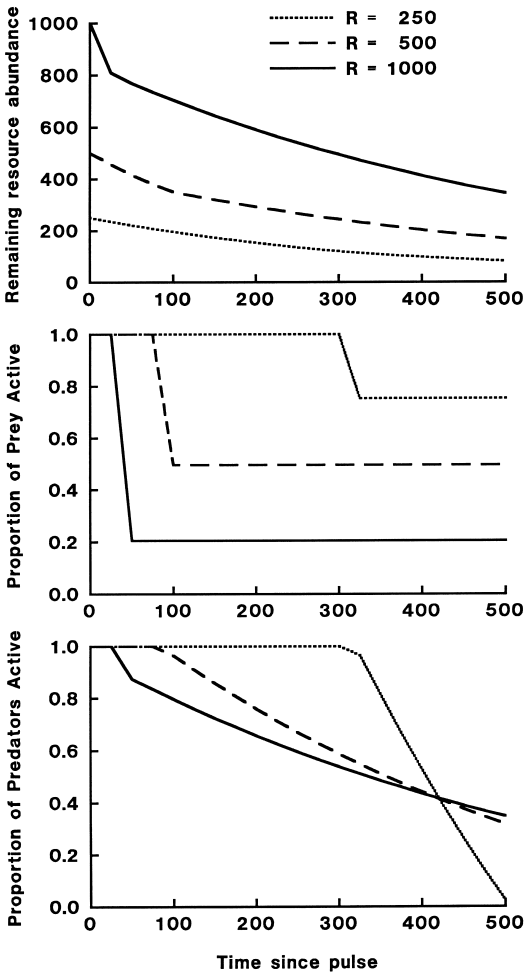


Fig. 2. The depletion of resources, the activity level of prey, and the activity level of predators following a resource pulse. The graphs consider three sizes of initial resource pulse: R_0 = 250 (dotted line), R_0 = 500 (dashed line) and R_0 = 1000 (solid line). Increasing the pulse size increases the equilibrium abundance of prey and predators. During the first phase of the foraging game, all prey and all predator individuals actively forage and resource abundances decline relatively rapidly. Increasing pulse size shortens the duration of this first phase. During the second phase, the proportion of actively foraging prey remains constant and below 1. This proportion declines with pulse size. During the second phase, the predator's activity level and resource abundance decline in synchrony. The decline in predator activity becomes more gradual as pulse size increases. For these illustrations: c = 0.02, c_0 = 0.004, a_n = 0.0002, h_n = 0.5, k = 0.01, k_0 = 0.001, a_p = 0.001, h_p = 2.5, $g = 2 \times 10^{-5}$, T = 500.

The prey's isocline

The prey's isocline considers all combinations of N and P such that the finite growth rate of the prey is 1: $s_n F_n = 1$. So long as the abundance of prey is below the predator's threshold value of qN', then the prey experience no risk of predation as the predators will remain dormant: $N'|_{p=0}$ indicating that qN' is calculated for a predator that spends no time active and experiences a net energy profit of $-k_0 T$. Below $N'|_{p=0}$, the prey can tolerate any number of predators. In the state space of P vs. N, the prey's isocline only begins at values of $N > N'|_{p=0}$ (Fig. 3). The prey's isocline rises asymptotically towards infinity as

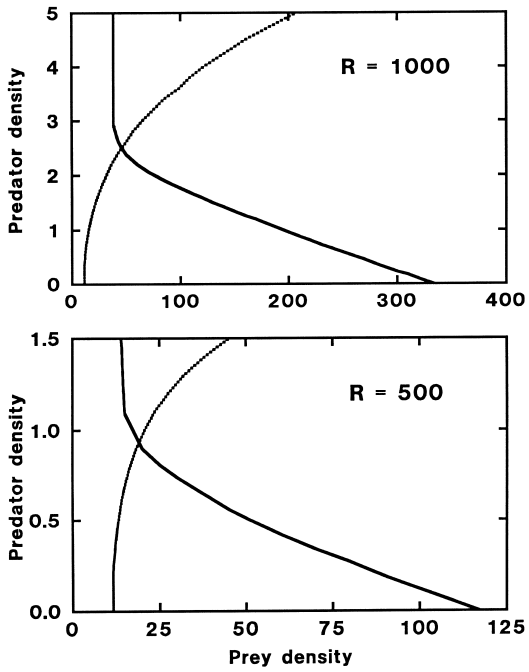


Fig. 3. Predator (dotted line) and prey (sold line) zero-growth isoclines for two different sizes of initial resource pulse (R_0 = 1000 and R_0 = 500). At low population sizes of prey, the prey's isocline becomes vertical at a behavioral refuge. This is the prey density at which it is no longer profitable for the predators to forage. The predator isocline begins vertical at the same prey density as the behavioral refuge, and then proceeds to increase as a decelerating curve. This shape is a result of the negative effect that the predators have on themselves via the fear responses of the prey. The prey suppress their activity in response to more predators. These illustrations use the same parameter values as those of Fig. 2.

N declines towards $N'|_{p=0}$. This threshold value of N in the prey's isocline is analogous to predator-prey models with absolute prey refuges (Rosenzweig & MacArthur 1963). In the present model, the prey refuge is behaviorally based. Below a certain number of prey, the prey experience complete safety as all predators should remain inactive.

In general, the prey's isocline will descend steeply from its asymptote of $N'|_{p=0}$ towards the prey's carrying capacity at the point where a population of prey can tolerate no predators and still maintain a constant population size (Fig. 3). In general, the isocline will not have a hump (a region where more prey can actually tolerate more predators). Besides N and P, much else changes along the isocline. As N increases along the isocline, the predator's density declines ($\downarrow P$), the prey's survivor's fitness declines ($\downarrow F_n$), the prey's survivorship increases ($\uparrow s_n$), the prey's first resource threshold declines substantially both from a decline in survivor's fitness and the decline in predator numbers ($\downarrow R'$), the time to reach the first threshold increases ($\uparrow t'$), the time to reach the second threshold declines ($\downarrow t''$), and each prey spends less time active ($\downarrow\int q(t)dt$). As the isocline approaches the prey's carrying capacity, the two threshold abundances of resources converge, $R' \rightarrow R''$, and the time to the first threshold converges on the time to the second threshold, t' and t'' converge. From the predator's perspective, movement along the prey's iscocline also has a variety of effects. As N increases along the prey's isocline, the predators spend a greater amount of time active ($\uparrow\int p(t)dt$), experience a higher average capture rate on prey while active ($\uparrow\int f_p(t)dt$), and hence experience a large increase in survivor's fitness and overall fitness.

In summary, the prey's isocline is a steeply declining function that indicates a generally strong negative direct effect of prey on themselves. This contrasts with the hump-shaped prey isocline typical of predator-prey systems where the predator has a Type II functional response. At low prey population sizes, safety in numbers often outweighs intra-specific competition to produce positive density-dependence among the prey. In the present model, however, the behavioral responses of the prey and predator alter the isocline's shape. Two processes in the foraging game work against the hump. First, the presence of additional prey reduces foraging opportunities and shortens the period over which prey can profitably remain active. Second, the presence of additional prey increases the duration over which it is profitable for the predators to remain active. More prey simultaneously shorten the period of useful activity, and on average, make that activity more risky by inviting increased predator activity.

The predator's isocline

The predator's isocline considers all combinations of N and P such that the predator's finite growth rate is 1: $s_pF_p = 1$. In mass action models of predator-prey interactions, the predator's isocline is typically vertical when the predators do not directly interact with each other (Rosenzweig & MacArthur 1963). And as noted by Rosenzweig & MacArthur (1963), adaptive fear responses by the prey may induce a positive slope to the predator's isocline (*see* Brown *et al*. 1999). The positive slope of the predator's isocline reflects the negative effects of the predators on themselves via their non-lethal effects on prey behaviors. In the present model, more predators make it harder for each individual predator to catch prey because the prey become less active and harder to catch.

The predator isocline begins vertical and then takes on a positive slope that becomes increasingly horizontal as the density of predators increases (Fig. 3). As one moves up along the predator's isocline, the prey and predator shift from being completely active (in this region, the predator isocline is and must be vertical) to decreasing levels of activity. Along the predator's isocline, the prey's fitness declines from a decrease in survival fitness and a decreased probability of surviving predation.

Factors influencing the equilibrium abundances of prey and predator

Resource productivity has effects on the community similar to Oksanen's theory of exploitation ecosystems (Oksanen *et al*. 1981). At low values of the resource pulse, R_0, there can be no prey or predators. As R_0 increases, there comes a point at which prey, but not predators, can occupy the system. In this region, the abundance of prey increases sharply with increased R_0. Eventually the pulse of resources becomes sufficiently large to support enough prey to support predators. Once predators can persist, further increases in productivity manifest as many more predators but few additional prey (paradox of enrichment, Rosenzweig 1971). But, the paradox of enrichment does not exist over a very large range of productivities. As productivity increases yet further, the abundance of predators increases at a roughly linear rate, and the abundance of prey begins to increase at an accelerating rate (Fig. 4).

The efficiency with which the prey can find their food and the efficiency with which the predators can find prey influences the relationship between resource productivity and the abundance of prey and predators. Increasing the efficiency of predators at finding prey (increased a_p) decreases the threshold level of productivity required for predators to persist in the system. However, it also greatly reduces the slope of the relationship between productivity and the abundance of prey and predators. So, with the exception of low resource productivities, efficient predators tend to result in a lower equilibrium population size of both prey and predators. In contrast, increasing the search efficiency of the prey (increasing a_n), always increases the equilibrium abundance of both prey and predators, independent of resource productivity (Fig. 4).

Discussion

When a resource occurs as a pulse, the activity of the foragers can deplete this resource and create temporal variability in resource abundances (Brown 1989b). In the absence of predation risk, the behavior of the foragers becomes a simple all or nothing rule. With resources sufficiently abundant, all foragers should feed. Once resources fall below a threshold of profitability, all foragers should cease feeding and conserve energy by becoming inactive until the next pulse of resources. When the predators are present, they can capitalize on the prey's behavior by directing activity towards the "pulse" of prey activity. As a foraging game, the prey should now adjust their activity patterns to the conflicting demands for food and safety.

In this scenario, both prey and predators must decide between foraging or remaining inactive. When foraging, both prey and predators incur risks (mortality for prey and injury for predators), gain food, and expend energy at a

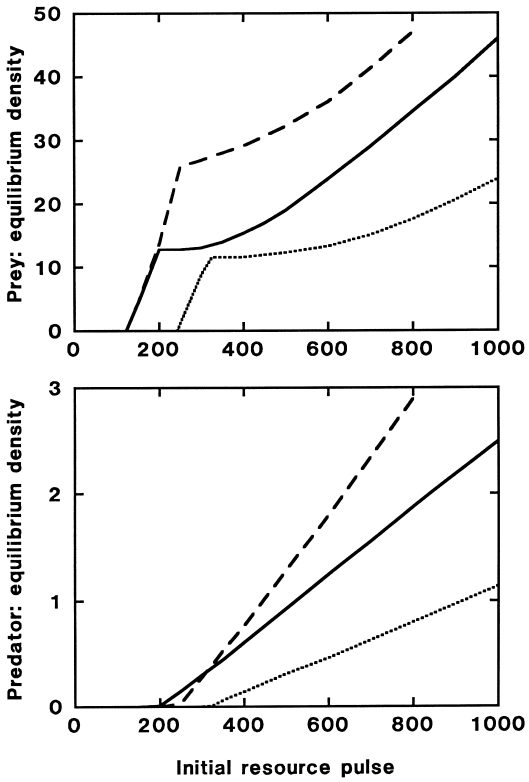


Fig. 4. The effect of the initial pulse size of resources on the equilibrium densities of prey and predators. The solid lines represent a baseline set of parameters as given in Fig. 2. A certain pulse size of resources is required to support any prey at all. Above this threshold, the abundance of prey increases almost linearly with pulse size. As the abundance of prey increases, there comes a point at which predators can now subsist in the community. At this point, the equilibrium abundance of prey increases much more slowly with pulse size, and the equilibrium abundance of predators begins to increase almost linearly. Even in the presence of predators, the prey's equilibrium population size increases with pulse size because of their fear response to the predators. As pulse size increases, each prey lowers its average level of activity, and hence is less valuable to the predator. The dashed line shows the effect reducing by a half the predator's encounter rate on prey. In general, a predator with a lower search efficiency will promote a higher equilibrium population size of both prey and predator. However, the pulse size at which the predator can persist in the community increases with a less efficient predator. The dotted line shows the effect of halving the search efficiency of the prey. Less efficient prey require a higher initial pulse size to persist in the community, and they support lower equilibrium population sizes of both predator and prey.

comparatively high rate. When inactive, prey and predators remain safe, acquire no food, and expend energy at a comparatively low rate. At any given time between resource pulses, prey and predator individuals must choose between activity and inactivity.

At the start of the pulse, the high abundance of resources encourages a high level of prey activity. This attracts predators. As the resource depletes, both prey and predator activity might be expected to decline. In fact, the ESS distribution of prey and predator behavior has up to three distinct, sequential phases. The first phase sees complete activity by all prey and predator individuals. This phase starts the sequence, providing the resource pulse is sufficiently large. The high resource abundance makes it profitable for all of the prey to forage even in the presence of all of the predators.

The second phase is "controlled" by the predators. Resources have been depleted to a level that can no longer support profitable foraging by the prey in the face of all predators. During this phase, the activity rhythms of prey and predators maintain an ideal free distribution between actively foraging and inactivity in one's roost or burrow. For the prey, this means that the value of foraging (which includes energetic and predation costs of foraging) equals the energetic cost of remaining dormant. For the predators, the value of hunting (which includes energetic and injury costs) just balances the energetic cost of inactivity. To achieve this, there must be a fixed proportion (between 0 and 1) of active prey that equals the predator's threshold of profitability. To insure this level of prey activity, the level of predator activity must track and decline with the declining abundance of resources. During this phase, prey activity levels remain constant. The predator's threshold of profitability indirectly dictates the ESS level of prey activity, and the level of resource dictates the level of predator activity required to maintain the prey's activity level.

The third phase follows if there is sufficient time between pulses. During phase 2, the level of predator activity converges on zero as the abundance of resources converges on the prey's threshold of profitability in the absence of predators. By the time this resource threshold is

reached, all prey and predators should have become inactive. Inactivity continues until the next resource pulse.

With a pulsed resource, the foraging game between predator and prey must, at equilibrium, have the first two phases of the sequence. During the second and third phases, the net profit to an individual (whether it is foraging or not) is equivalent to the negative of the resting metabolic rate. With a negative net energy gain, both populations' finite growth rates would be less than one, and prey and predator populations would decline. It is only during the first phase of the foraging sequence that both predator and prey experience positive net energy profits from foraging (after subtracting the metabolic and predation/injury costs of foraging). At equilibrium, the positive net energy profit during the first phase becomes exactly canceled by the negative net energy profits incurred during the second and third phases of the game. During the phases of the game, the prey and predator have shared experiences with respect to periods of positive and negative net energy profits.

Our results in time compare favorably with those in space (van Balaan & Sabelis 1999). Hugie and Dill (1994) considered how prey and predator should distribute themselves among habitats that vary in productivity. In the absence of predators, the ideal free distribution of prey among habitats conformed to resource matching. With predators, it was the predator's ideal free distribution that matched the prey's resource productivity. The number of prey among habitats conformed to what would equalize predator fitness, and the predators distributed themselves in a manner that generated equal prey fitnesses among the habitats. For the prey to have equal fitness, the more productive habitat offered higher food and higher risk, and the less productive habitat offered less food and less predation risk. The ideal free distribution of prey and predators in space conformed exactly to the distribution of active predators and prey in time during the second phase of the foraging game on a temporally pulsed resource. The first and third phases of the foraging game do not have analogs in the spatial model of predator-prey distributions.

The foraging game between predator and prey when resources are pulsed has some properties in common with exploitation ecosystems (Hairston *et al*. 1960, Oksanen *et al*. 1981, Oksanen 1990), paradox of enrichment (Rosenzweig 1971), prey refugia (Gause 1934, Rosenzweig 1977), and even ratio-dependent predation models (Power 1992). In the present model, resource productivity is dictated by the size of the resource pulse. The equilibrium population sizes of predator and prey conform quite closely to those predicted by Oksanen *et al*. (1981) for exploitation ecosystems. When the resource pulse is very low, neither prey nor predator can persist, and the standing crop of resources at the end of each pulse remains the same as at the start. At higher resource pulses, there is an almost linear relationship between size of resource pulse and equilibrium prey population size.

At a sufficiently high resource pulse, predators can now invade the system. At the start of this region, the model conforms closely to the paradox of enrichment. In this range, as the pulse size increases, the equilibrium population size of prey remains essentially constant, while the predator population size increases almost linearly with pulse size (Rosenzweig 1971).

As pulse size continues to increase, the relationship between equilibrium prey population size and resource productivity increases in an accelerating fashion. This is because of the higher population size of predators. As predator numbers increase, they suppress prey activity, and hence, the predators require more prey to subsist. In this region, the model may approximate the properties of ratio-dependent models where predator success is assumed to be a function of the ratio of prey to predator (Power 1992).

The eventual increase in both prey and predator equilibrium populations sizes with resource productivity can be anticipated from the prey and predator isoclines (Fig. 3). The prey's isocline is everywhere negatively sloped. The behavioral responses of prey and predators to each other preclude the typical hump in the prey's isocline that emerges from a predator's Type II functional response (Rosenzweig & MacArthur 1963). Rather than gaining safety in numbers (e.g., Rosenzweig *et al*. 1997), increased prey numbers simply attract more predator activity in

a manner analogous to short-term apparent competition (Holt & Kotler 1987). However, the prey's isocline does exhibit a refuge (Rosenzweig 1977). There is a threshold abundance of prey below which it is not profitable for the predators to forage. Within this behavioral refuge, the prey can tolerate any numbers of predators since no predators should actively forage. Adding to the stability of the predator-prey system is the positive slope of the predator's isocline. The predators have a negative direct effect in themselves. More predators make it harder for each predator to capture prey as the prey become less active in response to increased numbers of predators (Rosenzweig & MacArthur 1963, Brown *et al.* 1999).

Starting with Sih's (1980) work on aquatic invertebrates, it has been well established that most foragers must balance food and safety (Lima 1998). The use of depletable food patches in space provide a titration of food and safety in which organisms deplete food more thoroughly in safe than risky microhabitats (Brown 1988, Hughes & Ward 1993, Kotler & Blaustein 1995). Interestingly, the second phase of the foraging game of predator and prey on a pulsed resource results in a natural titration of food and safety over time. During this phase, prey activity levels remain constant, resource abundance and predator activity decline, and the ratio of predation risk to net energy profit from foraging remains constant (analogous to the μ/f rule of Gilliam & Fraser 1987).

Furthermore, this titration of food and safety reflects strongly the foraging aptitudes of both the prey and predators. If the prey are particularly good at finding resources, then it takes a lower abundance of resources to encourage all prey to be active, and phase 1 of the game sequence will continue to a lower resource density. A drawn out phase 1 also indirectly benefits the predators. Hence, efficient prey transfer enhances the standing crop of both prey and predator. Efficient predators create a situation in which predators can and must be scarce. As efficient predators, they can subsist profitably on a lower abundance of prey. And, as efficient predators, they encourage the prey to switch from complete activity (phase 1) to partial activity (phase 2) at a higher abundance of resources. While efficient predators can invade systems with low productivities, they will stabilize at low population sizes even at high resource productivities.

Consequences of risk of predation and risk of injury

The prey's risk of predation and the predator's risk of injury have three consequences. First, risk of injury or risk of predation becomes a foraging cost that influences the prey's and predator's thresholds of profitability (Brown 1988, Nonacs & Dill 1990, Kotler & Blaustein 1995).

Second, energy gain and safety from predation or injury are complementary inputs into fitness. Energy becomes more valuable the higher an individual's survival prospects, and the value of survival increases with individual's energy state (Brown 1992). Because food and safety are complements, during phase two of the foraging game, individual predators and prey should use a mixed strategy rather than form a mixture of pure strategies in the population (Brown 1998). As a mixed strategy, each individual should exhibit some likelihood of activity expressed as $p^*(t)$ and $q^*(t)$. In contrast, a mixture of pure strategies would require having some fraction of individuals that always prefer to be inactive and some fraction $p^*(t)$ that always prefer to be active during phase 2.

Third, the correlation between food and safety during phase 2 of the foraging game allows animals in unusually high energy states to sacrifice energy state for safety (asset protection principle of Clark 1994), and animals in unusually poor energy states to sacrifice safety for food. The titration of food and safety during phase 2 provides the prey and predator the opportunity to tailor their behavior to their own specific needs and opportunities. For instance, a prey or predator individual with a lower than average survivor's fitness will have a lower cost of predation. It should thereafter spend more of phase 2 foraging. This will raise the individual's survivor's fitness back towards the population mean at the expense of heightened exposure to risk. The opposite applies to individuals with above average survivor's fitness. They have a higher cost of predation, should forage less than average during phase

2, and consequently will be safer while experiencing a decline in their survivor's fitness towards the mean. The temporal variability in food and safety encourages a compression of individuals' states towards the mean (*see* Lima 1988 for an example with birds).

Scope of foraging games between predator and prey

The foraging game described here may occur in systems where a prey experiences predation risk while exploiting a pulsed and depletable resource. The model applies best where pulses are frequent enough that prey population sizes change little within a single pulse. The pulsing may be periodic in the case of daily or seasonal flushes of productivity, or aperiodic as in the outbreak of some resource in conjunction with irregular suites of ideal environmental conditions. The prey and predator experiencing this pulse of resources must have some alternative activity in addition to harvesting the resource or hunting for the prey, respectively. This alternative activity can be one of inactivity, or it may involve migrating to another place or habitat that offers alternative but unconnected foraging possibilities.

Resources may renew or become available on a daily, monthly, aperiodic, or seasonal basis. Bats may respond to nightly pulses of insects, and their owl predators may respond accordingly. Nectarivores (birds and insects) often adjust their foraging to daily pulses in nectar availability (Schaffer *et al*. 1979). Do their predators respond to their changes in activity? Irregular fruit production in the tropics or more seasonally predictable fruiting by trees may attract the attention of frugivores and their predators alike. A resource patch for a consumer is generally likely to provide one for its predators (e.g., congregations of frogs around ponds capturing insects; or lions waiting in ambush of ungulates at water holes).

For the gerbil system, this model may provide a starting point for understanding their foraging behavior in time (B. Kotler, unpubl.). The gerbils should have higher foraging costs early in the night than later. Giving-up densities (GUDs, the food remaining following use by a forager) in food patches provide one means of measuring these changing costs. All else equal, GUDs should be higher in risky places and during risky times relative to safe places and times (Brown 1988, Kotler *et al*. 1991, Hughes & Ward 1993). In response to successive fresh resource patches, the GUDs of gerbils generally declined during the night (B. Kotler, unpubl.). Furthermore, steeper declines occurred during nights with no moon than nights with full moon. This accords with model expectations if moonlight increases the predator's encounter rates on gerbils. The model does not include other important features of the gerbils's ecology such as bush and open microhabitats, and the temporal partitioning of the two species, with *G. pyramidum* foraging earlier in the night and *G. a. allenbyi* later in the night.

Foraging games between predator and prey represent an expected consequence of behaviorally sophisticated predators seeking behaviorally responsive prey. These behavioral games influence the stability of predator-prey interactions (a highly stabilizing effect in the present game), blur the distinction between bottom-up and top-down ecological effects (in our donor controlled system, the predator still exerts a top-down effect during the second phase of the foraging game), and offer behavioral windows in which prey behavior can provide insights into predator populations and predator behaviors indicate characteristics of prey populations.

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