The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions

4 authors, including:

Joel S. Brown
Moffitt Cancer Center
316 PUBLICATIONS **15,736** CITATIONS

SEE PROFILE

Mahesh Gurung
City Colleges of Chicago Harry S. Truman College
9 PUBLICATIONS **1,297** CITATIONS

SEE PROFILE

John William Laundre
Western Oregon University
108 PUBLICATIONS **3,927** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Landscape of Fear Conceptual Frame Work View project

Predation risk and community ecology View project

The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions

Joel S. Brown; John W. Laundre; Mahesh Gurung

Journal of Mammalogy, Vol. 80, No. 2. (May, 1999), pp. 385-399.

Stable URL:
http://links.jstor.org/sici?sici=0022-2372%28199905%2980%3A2%3C385%3ATEOFOF%3E2.0.CO%3B2-D

Journal of Mammalogy is currently published by American Society of Mammalogists.

THE ECOLOGY OF FEAR: OPTIMAL FORAGING, GAME THEORY, AND TROPHIC INTERACTIONS

Joel S. Brown, John W. Laundré, and Mahesh Gurung

Department of Biological Sciences, 845 West Taylor Street, University of Illinois at Chicago, Chicago, IL 60607
Present Address of JWL: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209

Mammalian predator-prey systems are behaviorally sophisticated games of stealth and fear. But, traditional mass-action models of predator prey dynamics treat individuals as behaviorally unresponsive "molecules" in Brownian motion. Foraging theory should provide the conceptual framework to envision the interaction. But, current models of predator feeding behavior generally envision a clever predator consuming large numbers of sessile and behaviorally inert prey (e.g., kangaroo rats, *Dipodomys*, collecting seeds from food patches). Here, we extend foraging theory to consider a predator-prey game of stealth and fear and then embed this game into the modeling of predator-prey population dynamics. The melding of the prey and predator's optimal behaviors with their population and community-level consequences constitutes the ecology of fear. The ecology of fear identifies the endpoints of a continuum of N-driven (population size) versus μ-driven (fear) systems. In N-driven systems, the major direct dynamical feedback involves predators killing prey, whereas μ-driven systems involve the indirect effects from changes in fear levels and prey catchability. In μ-driven systems, prey respond to predators by becoming more vigilant or by moving away from suspected predators. In this way, a predator (e.g., mountain lion, *Puma concolor*) depletes a food patch (e.g., local herd of mule deer, *Odocoileus hemionus*) by frightening prey rather than by actually killing prey. Behavior buffers the system: a reduction in predator numbers should rapidly engender less vigilant and more catchable prey. The ecology of fear explains why big fierce carnivores should be and can be rare. In carnivore systems, ignore the behavioral game at one's peril.

Key words: *Puma concolor*, mountain lion, *Odocoileus hemionus*, mule deer, predator-prey dynamics

There have been two complementary but somewhat divergent approaches to predator-prey interactions. Each approach focuses on different aspects of the interaction. The first (Taylor, 1984) focuses on predators killing prey; predators are lethal. The second (Lima and Dill, 1990) focuses on fierce predators scaring their prey; prey treat predation risk as an activity cost and respond accordingly. In fact, fierceness is not a property of the predator but rather a property of the prey. If prey exhibit conspicuous fear responses to their predator, the predator is deemed fierce.

The first approach has given rise to models of predator-prey population dynamics (Hassell, 1978; Murdoch and Oaten, 1975; Rosenzweig and MacArthur, 1963). In such models, predators influence population size of the prey and may influence number and stability properties of equilibrium points. Rarely, however, do these models consider the prey's behavioral response to the predator's presence. Ignorance of behavioral responses may result in large deviations between the model's predictions and empirical outcomes. These deviations may be particularly acute for large mammalian predator-prey systems where prey and predator respond to each other in behaviorally sophis-

ticated ways. In fact, for the prey, these non-lethal effects of predators may be more important than the direct mortality inflicted by predators (e.g., Indian crested porcupine, *Hystrix indica*—Brown and Alkon, 1990; cf. Brown, 1989; Kotler and Holt, 1989; Schmitz et al., 1997; Werner, 1992).

The second approach for investigating the non-lethal effects of predators draws heavily on foraging theory (Emlen, 1966; MacArthur and Pianka, 1966). Several models predict how foraging animals should balance conflicting demands for food and safety (Abrams, 1991; Brown, 1988, 1992, 1999; Gilliam and Fraser, 1987; Houston et al., 1993). When foraging under predation risk, individuals sacrifice feeding rate for safety either by allocating time among safe and risky habitats (Sih, 1980), or by using vigilance while active within a habitat (Lima and Dill, 1990). These responses result in a number of important behavioral indirect effects. For instance, as a result of behavioral resource depression (Charnov et al., 1976; Kotler, 1992), presence of more predators makes it harder for each individual predator to capture prey because of increasing prey wariness. As a result of predator facilitation (Charnov et al., 1976; Kotler et al., 1992), presence of one predator using a particular hunting tactic actually may drive prey into the jaws of another using a different tactic. Systems of large mammals should provide particularly rich foraging games (e.g., Hugie and Dill, 1994; van Balaan and Sabelis, 1993) because the predator attempts to maximize its success rate on prey that actively avoid predation. However, foraging theory deals mostly with systems where the predator consumes huge numbers of behaviorally inert and sessile prey. At present, foraging theory applies least well to systems like large mammalian predator-prey systems where behaviors are probably most sophisticated and important.

Our objectives are to: 1) develop a model for the foraging behavior of fierce carnivores and their prey, 2) consider conse-quences of this foraging game on population dynamics, and 3) consider how this changes conservation approaches and management techniques.

ECOLOGY OF FEAR

In a model based on the ecology of fear, the value of a food patch to the predator includes number and catchability of prey. Upon entering a food patch, quality of the patch declines as prey flee the patch and become more wary. The predator should leave a patch as soon as the expected rate of capturing prey drops to some threshold level.

Prey must select their optimal level of vigilance in response to their perceptions of a predator's whereabouts. In particular, prey must select a baseline level of apprehension that determines their level of vigilance in the absence of any tangible evidence of a predator's presence. If prey set their level of apprehension too high they miss valuable feeding opportunities. If they set it too low, they likely are to be killed by the predator. When embedded into a model of predator-prey dynamics, resulting behavioral responses can simultaneously increase resilience, stability, and persistence of the predator-prey interaction.

In their seminal work, Rosenzweig and MacArthur (1963) modeled and anticipated different consequences of N-driven (purely mass action) versus μ-driven predator-prey systems. Their more familiar mass-action (behaviorally unresponsive prey and predators) model gives rise to a "Catch-22". Highly efficient predators result in intrinsically unstable systems (non-equilibrium population fluctuations that may lead to the extinction of one or both species). Inefficient predators result in extrinsically unstable systems (environmental stochasticity may lead to predator extinction). Rosenzweig and MacArthur (1963) recognized that behaviorally responsive prey and predators may break the Catch-22 by creating a behavioral feedback that generates a decelerating predator isocline with a positive

slope. In what follows, we conjoin the foraging theory of MacArthur and Pianka (1966) with the predator-prey models of Rosenzweig and MacArthur (1963) to produce a foraging game of stealth and fear that may underlie all predator-prey systems of fierce carnivores.

THE CATCH-22 OF MASS-ACTION PREDATOR-PREY MODELS

Consider the pioneering model of Rosenzweig and MacArthur (1963) in which they show how predator-prey interactions produce oscillatory dynamics. These dynamics may dampen toward a stable equilibrium, expand toward a limit cycle, lead to the predator's extinction, or result in extinction of prey and predator. Such a model can have the following form:

$$\partial N/\partial t = N\{r[K/(N+\chi) - c] - PH(N)\} \quad (1)$$

$$\partial P/\partial t = P(r'H(N) - d), \quad (2)$$

where N and P are the population sizes of the prey and predators, r describes conversion of the prey's net resource harvest into offspring, K is a measure of the availability of the prey's resource, χ is a saturation constant determining the prey's maximum rate of resource harvest, and c is the forager's maintenance cost, H(N) is the predator's functional response (generally type II which means safety in numbers for the prey), r' describes the conversion of prey consumed into per capita growth of predators, and d is the predator's density-independent death rate. The term K can represent the prey's carrying capacity in the absence of predation when $c = K/(K+\chi)$.

The above model yields a humped shaped prey isocline for sufficiently large values of the saturation constant. The predator's isocline is a vertical line that is independent of P. For instance, a strongly humped-shaped prey isocline results if $r = a = 0.1$, $K = 100$, $\chi = 300$, $h = 5$, and $c = 0.25$; where a and h are the predator's encounter probability and handling time, respectively, on prey in a Holling's Type II functional response (Holling, 1965).

In the mass-action model of Rosenzweig and MacArthur (1963), the intraspecific competition among prey stabilizes predator-prey dynamics while the safety in numbers experienced by the prey as a result of the predator's Type II functional response destabilizes the dynamic. Which effect outweighs the other determines stability and gives the prey isocline its characteristic hump shape. Safety in numbers prevails at low N while intraspecific competition prevails at high N. As a consequence of this and subsequent models, conservation and management of predator-prey systems focus on prey population sizes, predator population sizes (or the ratio of N/P), and the predator's functional response.

The model, however, places predators in an ecological Catch-22. According to this model, predator-prey systems should be highly extinction-prone due to either intrinsic instabilities (expanding oscillations around an unstable equilibrium point) or environmental stochasticity. If the predator is very efficient at capturing prey, the equilibrium point is to the left of the peak in the prey's isocline and the system is intrinsically unstable. If the predator is inefficient, the system has a stable equilibrium to the right of the hump, but now the predator is susceptible to extinction from stochastic or catastrophic declines in the prey's environmental quality. An inefficient predator may not be able to persist long on a reduced prey population.

The above system is purely N-driven in that the per capita growth rate of the predator is determined solely by the number of behaviorally inert prey. However, for fierce carnivores, the system is also μ-driven in that the fear dynamics of the prey also will influence the likelihood of a predator capturing prey. Does behavioral flexibility (MacArthur and Rosenzweig, 1963) rescue the predator from its Catch-22?

PATCH USE MODEL OF FIERCE PREDATORS SEEKING WARY PREY

Sample system of mountain lions and mule deer.—While the theory we develop here should be general, we have the following system in mind as an example. Mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*) in the mountains of southern Idaho approximate closely a single-prey single-predator system (Altendorf, 1997; Hornocker, 1970). The mountain lions capture deer on the boundaries and interiors of forest patches, and the deer move from these forest patches to open shrub habitat as bedding and feeding areas, respectively. Mountain lions move frequently among forest patches in a manner reminiscent of patch-use models from foraging theory (Brown, 1988; Charnov, 1976). However, unlike existing models of patch use, a mountain lion rarely harvests more than one food item per patch. Patch depletion is not the result of prey removal by the predator, but the result of resource depression as the deer either become warier and harder to catch or the deer vacate the woods for another patch. The mountain lion-deer system is a game of stealth and fear (van Baalan and Sabelis, 1993).

For simplicity, consider an environment in which prey occur as isolated individuals within patches of suitable habitat. (Allowing herds of prey would be of considerable interest, but it complicates the following model by introducing information transfer among prey of the herd). Let the feeding rate of prey be density-dependent and decline with prey number. Consider a predator that is obliged to move from patch to patch in hope of capturing a prey. The model considers how long a predator should remain in a prey patch before giving-up and moving onto the next patch, and how vigilant the prey should be when increased vigilance reduces both feeding rates and predation risk.

Prey Vigilance and Population Dynamics.—Based on equation 1, let a prey's per capita growth rate, G, be given by:

$$G = r[(1-\bar{u})K/(N+\chi) - c] - \bar{\mu}P, \quad (3)$$

where the first term represents fecundity as a result of resource harvest, $\bar{u}$ is the prey's average level of vigilance, and $\bar{\mu}$ is the prey's average mortality rate from predation. Fecundity can be thought of as scramble competition in which $f = K/(N+\chi)$ represents the forager's feeding rate while not vigilant, $(1-\bar{u})f$ is the forager's net feeding rate when vigilance is considered, and c is the forager's subsistence cost measured in the same units as the feeding rate. Vigilance can be thought of as the proportion of time that the prey spends scanning or looking for predators, $0 \le u \le 1$. The term r scales the conversion of net energy gain into fecundity. We have written the per capita growth rate of the prey as a fitness generating function, G, (Vincent and Brown, 1988), because ultimately fitness of an individual prey will be influenced by its own vigilance strategy, vigilance strategies of other prey, and patch-residence times of predators. This represents the foraging game between and among prey and predators.

Let the instantaneous risk of predation be influenced by the prey's encounter rate with a predator, m, the predator's lethality in the absence of vigilance, 1/k, the effectiveness of vigilance in reducing predator lethality, b, and the prey's level of vigilance, u:

$$\mu = m/(k+bu). \quad (4)$$

This model of vigilance follows that of Brown (1999). In this model, the prey uses vigilance to balance conflicting demands of food and safety (Fig. 1). Increasing vigilance will increase the prey's safety (reduce μ) but reduce its fecundity. Under equation 3 and these assumptions, the prey's optimal level of vigilance is given by:

$$u^* = SQR\{mr(N+\chi)/bR\} - k/b. \quad (5)$$

The prey's optimal level of vigilance increases with its encounter rate with predators, m, number of prey, N, the saturation constant, χ, the conversion efficiency of energy for offspring, r, and predator lethality,
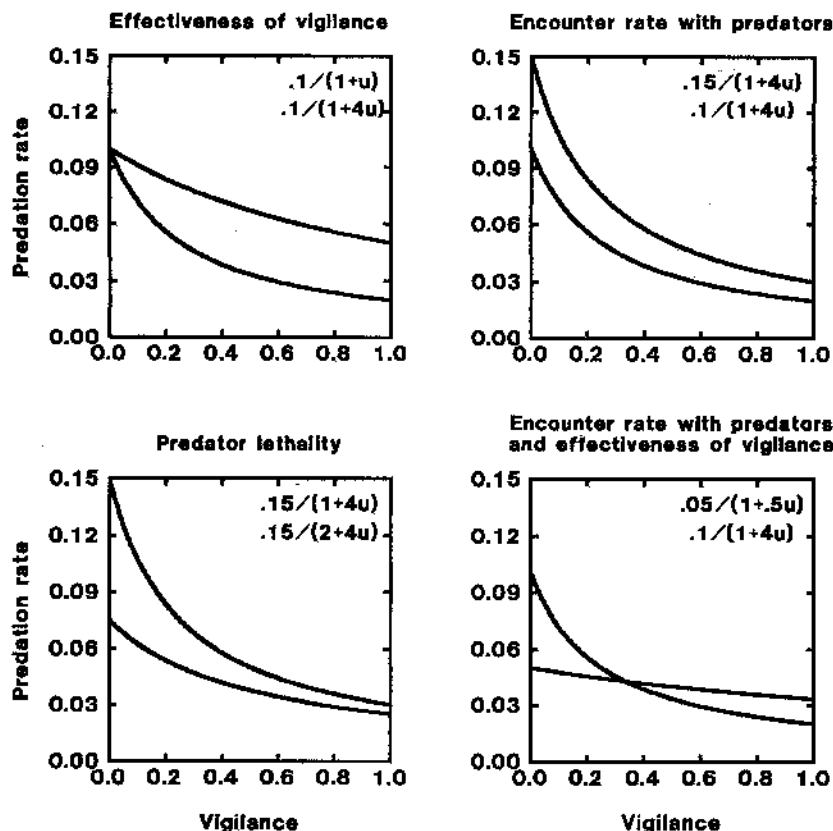
FIG. 1.—The effect of vigilance in reducing predation risk for various scenarios in which the encounter rate with predators, predator lethality, and effectiveness of vigilance vary.

$1/k$. Vigilance declines with resource abundance, K. The relationship between vigilance and effectiveness of vigilance is humped shaped. When vigilance is ineffective (b very small), vigilance is useless, and when vigilance is very effective (b very large), little vigilance is required. When equation 5 for vigilance yields a value >1, the forager should spend all of its time vigilant, $u^* = 1$. If equation 5 yields a value <0, the forager should spend no time vigilant, $u^* = 0$.

PREY WITH PERFECT INFORMATION

Imagine that prey know the exact whereabouts of the predators. The prey know when there is no predator present in their patch, and they know instantly when a predator has arrived at the patch. The prey respond to the two following encounter rates with predators: $m = M$ when a predator is in the patch and $m = 0$ when there is no predator in the prey's patch, where M represents the predator's encounter probability with prey when the predator is in the prey's patch.

Under this scenario, the prey's response to predation risk should be: $\hat{u}^* = u^*(M)$ when a predator is present in the patch and $u^* = 0$ when there is no predator present. The level of predation risk when a predator is in the patch is given by:

$$\mu' = M/(k+b\hat{u}^*), \qquad (6)$$

and the average level of risk experienced by an individual prey, μ is:

$$\bar{\mu} = p\mu', \qquad (7)$$

where p is the probability that a mountain lion is actually present in a particular prey patch.

When a predator enters a patch, the prey instantly takes on the optimal level of vigilance, and this level will not change during the predator's tenure in the patch. In this case, the predator should stay in the patch until the prey has been captured (with some small probability that the predator is entirely unsuccessful and must move on prematurely). The predator's average time to prey capture is $\theta = 1/\mu'$ and this becomes analogous to handling time in a typical foraging model. The predator's functional response is analogous to the traditional models of patch use under sessile and unresponsive prey:

$$H = aN\mu'/(\mu'+aN), \qquad (8)$$

where a is the predator's encounter rate with patches of prey.

The probability that there is a predator within the prey's patch is given by:

$$p = aP/(\mu'+aN), \qquad (9)$$

The model of predator-prey population dynamics can be formulated by substituting $\bar{u} = p\hat{u}^*$, and equation 7 for μ into equation 3 for the prey, and substituting equation 8 for H into equation 2 for the predator. The prey's zero-growth isocline can be solved numerically by fixing a value for N (which then determines $\hat{u}^*$) and finding the value of P such that the prey's G-function, equation 3, equals zero growth. The predator's isocline remains vertical, and it can be found numerically by determining the value(s) of N such that the predator has zero growth rate (Fig. 2). There will be a particular $\hat{u}^*$ associated with each N. And, increasing the number of prey increases the prey's optimal level of vigilance because of the individual's reduced feeding rate.

Despite the μ-dynamics, the model has properties that closely approximate the mass-action model (Rosenzweig and Mac-Arthur, 1963). For a large range of parameter values the prey's isocline is hump-
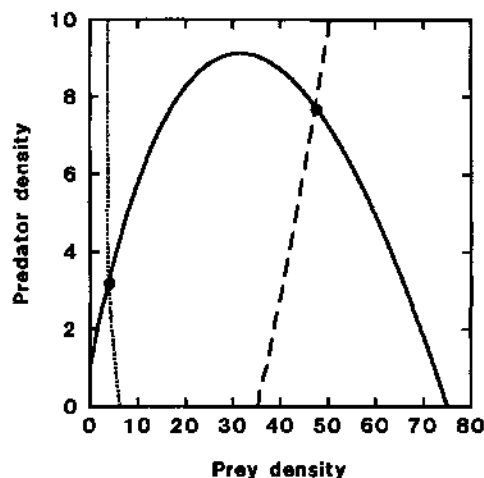

FIG. 2.—Predator-prey isoclines for a system where prey are prescient in that they know when a predator is present or absent from their patch. The solid hump-shaped isocline is for prey. Above and below this isocline the prey have a negative and positive growth rate, respectively. The dotted line to the left of the hump is the first predator isocline. To the right and left of this isocline, predators have a negative and positive growth rate, respectively. The dashed line is the predator's second isocline. To the right and left of this isocline, predators have a positive and negative growth rate, respectively. Neither interior equilibrium point is stable (solid dots). If the population trajectory crosses the second predator isocline (from left to right), the dynamics result in the extinction of the predator. Dynamics in the neighborhood of the first predator isocline can result in either a stable limit cycle, extinction of both predator and prey, or extinction of the predator (depending on parameter values). For these isoclines parameters have been set to: $r = c = 0.2$, $K = 100$, $\chi = 25$, $k = 1$, $M = 1$, $b = 100$, $d = 0.0011$.

shaped and the predator's isocline is vertical (Fig. 2). The predator actually may have two isoclines. As the prey population size increases the predator's fitness at first increases then decreases. At low N, having more prey to capture is more important than each prey's catchability. At high N, the catchability of prey is more important than the number of prey. Figure 3 shows the increase in the prey's ESS level of vigilance
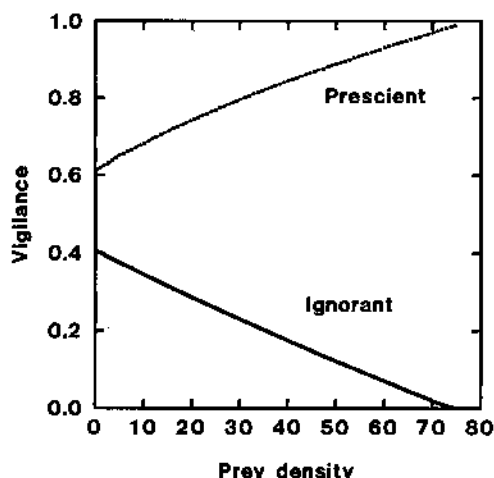
FIG. 3.—The ESS value for prey vigilance as one moves along the prey's isocline from low to high values of prey density. The dotted line corresponds to the example in Fig. 2 of a predator with prefect information (prescient). For prescient prey, the level of vigilance only applies to times when a predator is actually within the prey's patch. As prey density increases, the ESS level of vigilance increases because the prey's energy state and feeding rate are declining. The solid line corresponds to the prey's isocline in Fig. 4. These prey are ignorant of the actual whereabouts of the predators (the prey can estimate predator numbers). Ignorant prey have the same level of vigilance whether or not there is a predator within its patch. The ESS level of vigilance declines because of a dilution effect. Increasing the number of prey along the prey's isocline reduces the likelihood of a prey having a predator within its patch.

as one moves along the prey's isocline from low values of N to high values. The first predator isocline in Fig. 2, that intercepts the prey axis at low N, is the analog of the mass-action model. The equilibrium point is unstable (Fig. 2) because prey have a positive direct effect on themselves. The second predator isocline separates the state space into two regions. On the left side of the isocline the system dynamics become governed by the first predator isocline (leading to persistent oscillations, extinction of the predator, or extinction of both predator and prey). To the right of the second predator isocline, the system results in extinction of the predator and stable coexistence of prey at their carrying capacity. At the equilibrium point formed by the second predator isocline, the direct effect of the prey on the predator is actually negative, contributing strongly to an unstable equilibrium.

PREY THAT ARE IGNORANT OF PREDATOR WHEREABOUTS

Imagine prey that know numbers of predators and probability, p, that there is a predator within its patch. Otherwise, it has and gains no information on the actual whereabouts of the predators. Such a prey has the following estimate of its encounter rate with predators: $m = pM$. It should set its vigilance level to: $u^* = u^*(m)$.

The prey retain this level of vigilance regardless of whether there is a predator present within the patch or not. Obviously such a prey is over-vigilant when there is no predator in the patch and under-vigilant when there actually is a predator within the patch (Abrams, 1994; Sih, 1984). Like prey with perfect information, a predator pursues a prey with a constant level of vigilance. The predator's patch use strategy should be to remain in the patch until it has captured the prey: $\theta = 1/\mu(u^*)$. The appropriate terms for $\bar{\mu}$, μ', p, and H can be substituted into the prey and predator dynamics, and a numerical solution can be found for u^* and the prey's and predator's isoclines. The solution is more complicated to find because the optimal level of vigilance for an individual prey is influenced by size of the prey population size, the predator's population size, and the vigilance levels of other prey, all of which influence p (the likelihood of there being a predator within the patch). Values can be fixed for N and P and an iterative process can be used to find the ESS value for u^*.

The dynamics and isoclines of the model are now quite different from either the mass-action model (Rosenzweig and MacArthur, 1963) or the above model with pre-

scient prey. The model is now strongly μ-driven in the sense that the predator's functional response now is influenced directly by the changing fear levels of prey. When prey are prescient, the fear level encountered by predators is independent of the predator's population size. However, under ignorant but responsive prey, the prey's fear level increases directly with the number of predators and decreases with the number of prey. A prey becomes less catchable to an individual predator as there are more predators, and the prey becomes more catchable as the number of prey increases (Fig. 3). From the prey's perspective, increasing number of predators or decreasing number of prey increases the likelihood that individual prey will be pursued, which increases the prey's level of wariness.

As a consequence of the μ-dynamics, the predator's and prey's isocline change shape in ways that can increase both extrinsic and intrinsic stability of the population dynamics. The predator's isocline is decelerating with a positive slope (Fig. 4). The prey's fear response introduces a non-linear effect, in which presence of more predators makes it harder for each predator to capture prey. In this way, the predator can be very efficient at low population sizes of predators (increases resilience to environmental stochasticity and temporary catastrophes) but very inefficient at high population sizes of predators (increases stability of the equilibrium point and reduces amplitude of cyclic dynamics). As number of predators goes to zero, the prey's optimal level of vigilance also goes to zero. As the number of predators increases, prey should become increasingly vigilant and harder to capture.

The μ-dynamics shift the hump in the prey's isocline toward lower densities of prey (the isocline may lose its hump entirely). While the prey still experience safety in numbers as a consequence of a dilution effect (a predator can be pursuing and handling only one prey at a time), the effect is diminished by the prey's reduced vigilance in response to increased prey numbers. In
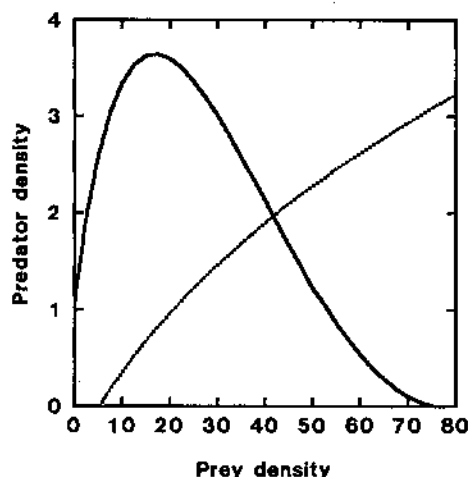

FIG. 4.—Predator-prey isoclines for a system where the prey are ignorant of the predators' whereabouts. The solid hump-shaped isocline is for the prey. Above and below this isocline, prey have a negative and positive growth rate, respectively. The positively sloped, decelerating dotted line is the predator's isocline. Increasing numbers of predators results in less catchable prey because prey increase their vigilance. To the left and right of this isocline, predators have a negative and positive growth rate, respectively. The interior equilibrium point is stable. For these isoclines parameters have been set to: r = c = 0.2, K = 100, χ = 25, k = 1, M = 1, b = 100, d = 0.05.

fact, as prey abundance goes to infinite the prey's optimal level of vigilance goes to zero, and predators are maximally efficient at capturing prey. Furthermore, increasing population sizes of prey reduces each prey's feeding rate and survivor's fitness. These changes further reduce the prey's level of vigilance. The effect by which more prey make it easier for predators to kill each prey, increases the range of prey population sizes that generates a stable equilibrium point.

When the fear response of prey increases and decreases with numbers of predators and prey, respectively, predators are freed from their Catch-22. They can be highly efficient predators at low population sizes but rapidly become inefficient predators as the

population size of predators increases. Fierce carnivores and their prey's response to them promote an equilibrium in which the prey appear to be near carrying capacity and the predators are rare. In such a system, predators do not seem to regulate prey abundances in the traditional sense of killing a large proportion of prey (N-driven). But, they do regulate their prey in the sense that prey forgo much of their own feeding opportunities in response to the threat of predation (μ-driven). Catchability of prey is as important to the predator as the actual number of prey.

In this model, prey respond actively to the densities of prey and predators. But, predators are still passive players in this predator-prey game because they have a predictable and simple behavioral solution. They should pursue a prey until it has been captured. Prey are playing a vigilance game among themselves. The optimal level of vigilance by an individual depends on the likelihood of being pursued by a predator, and this likelihood decreases with the vigilance level and densities of other prey. By default, a predator spends more time within a patch as the prey become more vigilant. The next scenario shows how giving prey imperfect information regarding predators' whereabouts retains properties of the present model while making predators active players in the predator-prey game.

PREY WITH IMPERFECT INFORMATION

Imagine prey that are uncertain as to the actual whereabouts of the predators but are able to make an estimate of its encounter rate with predators based on cues emitted by the predator when it occupies a prey's patch (such cues may be auditory, olfactory, or visual). Such a prey should have some background level of apprehension even in the absence of any nearby predators. This level of apprehension is determined by its baseline expectation of encountering a predator in the absence of any cues of predatory risk. Refer to this background level of apprehension as m'. When

a predator actually enters a patch, the forager acquires information regarding its possible presence and, on average, adjusts its apprehension higher the longer the predator remains in the patch. For example, following the arrival of a predator, the prey's expected level of apprehension may be approximated as a learning curve: $m(t) = m' + (M+m')(1-\exp(-\alpha t))$, where α is the rate at which a prey perceives the presence of a predator and t is the time since a predator has actually been in the patch (the prey never actually knows this). As t goes from zero to infinite the prey's expectation of encountering a predator rises from m' to M. The level of apprehension changes with the time prior to and after the arrival of the predator in the patch (Fig. 5). Under this model of imperfect information the prey's level of vigilance can be approximated as: $u*_{ab} = u(m')$ in the absence of a predator and $u*_{pr} = u(m(t))$ in the presence of a predator.

The challenge for the prey is to select the optimal level of background apprehension, m'. Increasing apprehension reduces feeding rates and reduces predation risk. If the level of apprehension is set too high, the forager misses out on valuable feeding during periods when there are no predators in the patch. If set too low, prey experiences unacceptably high predation risk in the presence of a predator. The background level of apprehension must strike a balance between feeding rate in the absence of predators and safety in the presence of a predator. The average risk of predation is given by:

$$\bar{\mu} = p \int [M/(k+bu*_{pr})]dt, \qquad (10)$$

where p is the probability that a predator is actually in the prey's patch, and the risk is integrated from 0 to t (the giving up time of the predator).

The forager's average level of vigilance over time is given by:

$$\bar{u} = (1-p)u*_{ab} + p\int u*_{pr}(t)dt. \qquad (11)$$

The values of $\bar{\mu}$ and $\bar{u}$ calculated from equations 10 and 11 can be substituted into

Time Before and After Predator
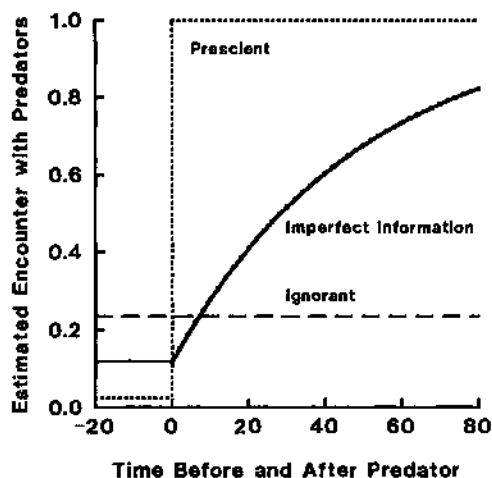
FIG. 5.—The prey's estimate of its encounter with predators as influenced by the arrival of a predator into its patch. The interval between [−20,0] represents the period prior to the predator's arrival (actual encounter rate with predators is zero). The prey's estimate of encountering a predator during this interval represents the prey's background level of apprehension. The interval between [0,80] represents time since the predator has been in the patch (actual encounter rate has been set to $M = 1$ for the period when a predator is actually in the patch). The prey's estimate of encountering a predator during this interval indicates how well the prey can respond to the actual presence of a predator. The prey with perfect information (prescient = dotted line) has no background level of apprehension and accurately assesses risk as soon as a predator enters its patch. The prey that are ignorant of the predators' whereabouts have the highest background level of apprehension (dashed line), and their perception of risk does not change with the arrival of a predator. The prey with imperfect information has a level of background apprehension that lies below that of the ignorant prey but above that of the prescient prey. While constantly underestimating risk when a predator is present in the patch, the prey with imperfect information, on average, increases its assessment of risk the longer a predator remains in its patch.

the prey's fitness generating function, equation 3. Given the probability that a predator is actually within the prey's patch, p, and given the predator's giving up time, t, it is possible to find the ESS value of m' (back-

ground level of apprehension) that maximizes the prey's finite rate of growth. The model possesses the two extremes of prey with perfect information ($\alpha \to \infty$) and completely ignorant prey ($\alpha \to 0$). When $\alpha \to \infty$, then the optimal value for $m' \to 0$. As $\alpha \to 0$, the optimal level for apprehension, $m' \to pM$.

The baseline level of apprehension has the following properties. Baseline apprehension increases with the predator's population size, the predator's encounter rate with prey, and the prey's energy state. Baseline apprehension decreases with the prey's population size, effectiveness of vigilance, the prey's detection rate of predators, the prey's intrinsic growth rate, and the predator's patch residence time.

We have characterized the vigilance behavior of the prey. When the prey have imperfect information, how long should a predator remain in a patch before moving to another?

PREDATOR'S RESPONSE TO PREY WITH IMPERFECT INFORMATION

In the examples with prescient and ignorant prey, the predator remained in a patch until it had captured the prey (except instances where events force the predator to leave a patch prematurely, such as the prey abandons the patch before the predator captures it). Now, consider a predator that is aware of the prey's level of apprehension. Such a predator may still elect to remain in a patch until the prey has been captured. But, the predator's expected harvest rate within the patch, $\mu(t)$, declines with time spent in the patch. The longer the predator pursues the prey the less catchable it becomes. There may come a point, t^*, at which the prey is no longer worth pursuing and the predator is better off abandoning the prey and seeking another. The predator's optimal stay time within the patch before abandoning the hunt, t^*, satisfies a marginal value theorem (Charnov, 1976). The predator should abandon the hunt on a given prey at the point where its expected capture

rate, $\mu(t)$, drops to its average capture rate from seeking and pursuing a new prey. The optimal giving-up time, t^*, satisfies:

$$\mu(t^*) = H(t^*), \qquad (12)$$

where the predator's average harvest rate is given by the probability of making a kill within a given patch divided by the time required to find the patch, $T = 1/aN$, and dispatch the prey:

$$H(t) = [1-\exp(-\int\mu(t)dt)]/[T+t^*], (13)$$

where the integral is evaluated from $t = 0$ to $t = t^*$.

For any given N, P, t, and prey background level of apprehension, m', it is possible to find a given predator's optimal value for t^*. All else being equal, increasing N increases a predator's harvest rate without altering the likelihood of capturing a prey within its patch. Hence, t^* should decline. Increasing P has the opposite effect by increasing the predator's travel time among patches, reducing its H and, hence, increasing t^*. Increasing the t of all the other predators decreases a predator's T, increases its H, and, hence, reduces t^*. Increasing m' decreases H and decreases the quality of a given patch. The net effect of increasing m' is to increase t^*.

The probability of capturing a prey declines with time spent by the predator in the patch (Fig. 6). The predator should remain in the patch until this line intersects the horizontal line showing the predator's average capture rate across all patches of prey. For instance, the predator's patch-residency time (similar to a giving-up time) should be longer in a poor environment than in a rich environment.

To a fierce predator, the number (N) and catchability (μ) of prey determines patch quality. Increasing patch quality increases the amount of time that a predator should hunt within a patch before giving up if it has not yet captured any prey. Increasing patch quality also increases the probability that a predator will have captured a prey before it gives up on the patch. All else
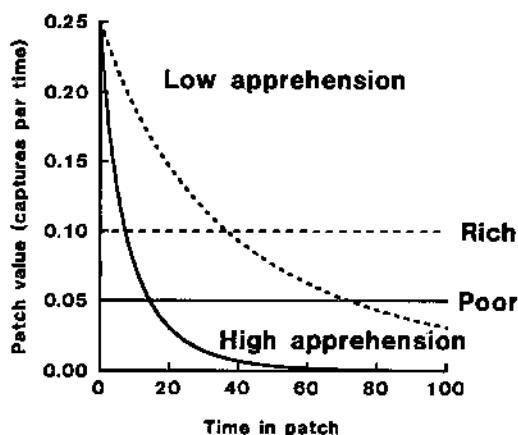

FIG. 6.—The decline in patch quality experienced by a predator hunting a prey with imperfect information. To the predator, the prey is most catchable at the moment the predator arrives in the patch. Subsequently, the prey becomes less catchable, and eventually the likelihood of making a successful capture declines to the threshold level. At this threshold, the predator has as good a chance of capturing a prey by traveling to and hunting a less wary prey in a different patch. An unsuccessful predator should leave the patch when its expectation of making a successful capture no longer exceeds the threshold. Relative to one in a poor environment, a predator in a rich environment should have higher threshold and spend less time in each unsuccessful patch. Relative to prey with a high baseline level of apprehension, a predator should spend more time in a patch when prey have a low baseline level of apprehension.

being equal, increasing the background apprehension level of the prey or increasing the energy state of the prey will reduce patch quality. All else being equal, increasing the number of prey, increasing the marginal value of energy to the prey, and increasing the prey's feeding rate will increase patch quality.

The ESS values for the prey's baseline level of apprehension and the predator's giving-up time must be found iteratively. The resulting isoclines for the predator-prey system generally resemble those for a prey that is ignorant of the predator's whereabouts, except the case where the prey is

quickly able to detect a predator within its patch (α very large).

DISCUSSION

We make the distinction between population size driven (N-driven) and fear driven (μ-driven) predator-prey interactions. In N-driven systems, the killing of prey by the predators is the principle impact of predators on prey's fitness and population dynamics. In μ-driven systems, predators have their largest impact via their effects on the feeding behaviors and feeding rates of prey. In response to predators, prey sacrifice other components of fitness by spending time vigilant or by foregoing opportunities in risky habitats (Kotler and Holt, 1989). Predator-prey systems with fierce carnivores provide ideal candidates for μ-driven interactions.

Fierceness is not a property of predators but indicates the ability of prey to recognize and respond to risk of predation. By taking appropriate behavioral responses, a prey may be able to significantly reduce the actual mortality risk of the predator. Brown and Alkon (1990) found that predation risk strongly influenced habitat selection and patch use by Indian crested porcupines in the Negev Desert of Israel. As a consequence, porcupines have an actual risk of predation that approaches nil. Schaller (1972) concluded that lions (*Panthera leo*) on the Serengeti did not regulate populations of wildebeest (*Connochaetes taurinus*) or zebras (*Equus burchelli*). This conclusion was based on the observation that lions kill only a small fraction of their prey populations. By scaring their prey, lions probably strongly influence their prey's fitness. Risk of predation causes wildebeest and zebras to be more vigilant and shift activity towards safer habitats (Illius and Fitzgibbon, 1994; Mills and Schenk, 1992). Similar responses of prey to predation risk have been documented in guinea pigs (*Cavia aperea*—Cassini, 1991) and redshanks (*Tringa totanus*—Cresswell, 1994). Frightened herbivores are unlikely to overgraze

their forage in the manner of unwary sheep and livestock (e.g., pikas, *Ochotona princeps*—Huntly, 1987). Frightened prey have high giving-up densities as they sacrifice food for safety (Brown, 1988; Brown and Morgan 1995; Kotler et al., 1991, 1994). In fact, it is the ability of the prey to purchase safety with reduced feeding rates that creates a μ-driven system. The system moves from N-driven towards μ-driven, as the prey become more effective at reducing predation risk via reduced feeding rates.

Adding fear responses of prey to models of predator-prey population dynamics have revealed diverse consequences. Adding behaviors can be destabilizing or stabilizing (Abrams, 1994; Fryxell and Lundberg, 1994,1998; Schwinning and Rosenzweig, 1990; van Balaan and Sabelis, 1993). Antipredator and predator behaviors can promote diversity or inhibit diversity of prey species that can coexist (Abrams and Matsuda, 1993; Holt, 1977; Holt and Lawton, 1994). Here, we considered the outcome of three different scenarios that differed in prey knowledge of the predators' whereabouts. We considered a system in which the prey are patchily distributed and the predator is obliged to move from patch to patch in hopes of encountering prey. When the prey had perfect knowledge of the predator's whereabouts, the optimal behavior of the prey destabilized the interaction. Increasing number of prey actually reduced the predator's efficiency at capturing prey (Fig. 2 and 3). When prey had information on number of predators but no information on their whereabouts, their fear responses were strongly stabilizing. Increasing number of prey or decreasing number of predators strongly increased efficiency with which a predator could catch prey (Fig. 3 and 4).

When prey have imperfect information on predator's whereabouts, they select a baseline level of apprehension. The baseline level of apprehension responds to number of prey, state of the prey, prey's feeding rate, and numbers and characteristics of the

predator. The prey's level of apprehension also determines catchability of prey and quality of a prey patch to the predator. This determines optimal giving-up time of a predator in a prey patch. Such a predator-prey system may generate a very robust and resilient persistence of prey and predator. As the predator becomes rare or the prey become exceedingly abundant, prey should lose their apprehension and be sheep-like in their wariness. Under these circumstances a predator should be very efficient, should have an easy time killing prey, and should have high fitness. A low number of predators then can be sustained by a relatively low population of prey. As predators become more abundant, prey should become increasingly difficult to catch. Under these circumstances, a predator should be inefficient and should require a large population size of prey for subsistence. In our model of imperfect information, big fierce carnivores must be rare. Otherwise they would find their prey uncatchable from fright. And, in our model, big fierce carnivores can be rare and persist because of the increasing catchability of prey as predators decline in number.

Mountain lions and mule deer may illustrate how N-driven and μ-driven systems might differ. Imagine an area with ca. 25 mountain lions and ca. 5,000 mule deer (e.g., Altendorf, 1997; J.W. Laundré et al., in litt.). Consider a situation in which the deer are unusually rare as a consequence of a harsh winter or drought. Imagine that five mountain lions (ca. 20%) have died of starvation or have been shot by people protecting their livestock. Under an N-driven system, the remaining mountain lions are no better off than before the five starved. They do not experience a higher density of deer (even if they can expand into the vacated territories) and only after a lengthy time lag will the reduced population of mountain lions result in a higher deer density. This is the typical time-lag in the collapse and recovery of prey populations that can cause limit cycles in predator-prey pop-

ulation dynamics (Hassell, 1978). Under an N-driven system, the remaining 20 mountain lions might be subject to extinction in the absence of a rapidly recovering deer population.

Now consider the mountain lions as a μ-driven system. Following the loss of 20% of the population of mountain lions, mule deer will immediately experience less overall predation risk. Within days, mule deer may respond by reducing their vigilance levels. As prey become easier to catch, the remaining mountain lions benefit almost immediately from the predator reduction. At 10–15 mountain lions, the unwary deer may buffer the lions from any further reduction. Furthermore, if the lions achieve a population of ca. 35, deer may be so hard to catch that the lions risk starvation, and some are obliged to emigrate. In such a system, territoriality by the mountain lions may not be as much a mechanism for social regulation of population sizes, as a means for mountain lions to protect catchability of their prey. A wayward mountain lion moving through another's territory may frighten the deer and cause a temporary decline in quality of the territory.

Our model suggests alternative strategies for monitoring and managing predator prey-systems that are μ-driven. In a μ-driven system in which the prey have imperfect information of the exact predator whereabouts, useful information for testing and applying the model include prey vigilance levels, feeding rates, giving-up densities (Altendorf, 1997), and the residency times of predators within prey patches. Vigilance and giving-up densities of the prey may provide a valuable behavioral indicator of the status of the predator population. For instance, by 1997 elk (*Cervus elaphus*) in regions of Yellowstone with wolves (*Canis lupus*) were conspicuously and significantly more vigilant than those in areas that had not seen wolves in >50 years (J. W. Laundré and K. B. Altendorf, in litt.). A sudden drop or increase in vigilance levels could be a valuable gauge of a collapse or surge,

respectively, in the predator population. Behavioral data on fierce-carnivore systems may be as useful and diagnostic as data on the respective population sizes of predator and prey.

For the last 30 years, the work of Rosenzweig and MacArthur (1963) has been valued for its mass-action model of predator-prey dynamics, and the work of MacArthur and Pianka (1966) has provided inspiration for studying foraging behaviors lines of evolutionary ecology to consider a model for how fierce-predator and prey systems might behave. Viewing predator-prey systems as foraging games of stealth and fear offers refreshing avenues for research and management.

LITERATURE CITED

ABRAMS, P. A. 1991. Life history and the relationship between food availability and foraging effort. Ecology, 72:1242–1252.

———. 1994. Should prey overestimate the risk of predation? The American Naturalist, 144,317–328.

ABRAMS, P. A., AND H. MATSUDA. 1993. Effects of adaptive predatory and anti-predator behavior in a two-prey-one-predator system. Evolutionary Ecology, 7:312–326

ALTENDORF, K. B. 1997. Assessing the impact of predation risk by mountain lions (*Puma concolor*) on the foraging behavior of mule deer (*Odocoileus hemionus*). M.S. thesis, Idaho State University, Pocatello.

BROWN, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology, 22:37–47.

———. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs, 59:1–20.

———. 1992. Patch use under predation risk: I. Models and predictions. Annales Zoologici Fennici, 29: 301–309.

———. 1999. Vigilance, patch use, and habitat selection: Foraging under predation risk. Evolutionary Ecology Research.

BROWN, J. S., AND P. U. ALKON. 1990. Testing values of crested porcupine habitats by experimental food patches. Oecologia, 83:512–518.

BROWN, J. S., AND R. A. MORGAN. 1995. Effects of foraging behavior and spatial scale on diet selectivity: A test with fox squirrels. Oikos, 74:122–136.

CASSINI, M. H. 1991. Foraging under predation risk in the wild guinea pig *Cavia aperea*. Oikos, 62:20–24.

CHARNOV, E. L. 1976. Optimal foraging and the marginal value theorem. Theoretical Population Biology, 9:129–136.

CHARNOV, E. L., G. H. ORIANS, AND K. HYATT. 1976. Ecological implications of resource depression. The American Naturalist, 110:247–259.

CRESSWELL, W. 1994. Flocking is an effective antipredator strategy in redshanks, *Tringa totanus*. Animal Behaviour, 47:433–442.

EMLEN, J. M. 1966. The role of time and energy in food preference. The American Naturalist, 100:611–617.

FRYXELL, J. M., AND P. LUNDBERG. 1994. Diet choice and predator-prey dynamics. Evolutionary Ecology, 8:407–421.

———. 1998. Individual behavior and community dynamics. Population and Community Biology, Chapman and Hall, London, United Kingdom, 20:1–202.

GILLIAM, J. F., AND D. F. FRASER. 1987. Habitat selection under predation hazard: a test of a model with foraging minnows. Ecology, 68:1856–1862.

HASSELL, M. P. 1978. The dynamics of arthropod predator prey-systems. Princeton University Press, Princeton, New Jersey.

HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada, 45:1–60.

HOLT, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology, 12:197–229.

HOLT, R. D., AND J. LAWTON. 1994. The ecological consequences of shared predators. Annual Review of Ecology and Systematics, 25:495–520.

HORNOCKER, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs, 21:1–39.

HOUSTON, A. I., J. M. MCNAMARA, AND J. M. C. HUTCHINSON. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society of London, Series B, 341:375–397.

HUGIE, D. M., AND L. M. DILL. 1994. Fish and game: a game theoretic approach to habitat selection by

predators and prey. Journal of Fish Biology, 45 (Supplement A):151–169.

HUNTLY, N. J. 1987. Influence of refuging consumers (Pikas: *Ochotona princeps*) on subalpine meadow vegetation. Ecology, 68:274–283.

ILLIUS, A. W., AND C. FITZGIBBON. 1994. Costs of vigilance in foraging ungulates. Animal Behaviour, 47: 481–484.

KOTLER, B. P. 1992. Behavioral resource depression and decaying perceived predation in two species of coexisting gerbils. Behavioral Ecology and Sociobiology, 30:239–244.

KOTLER, B. P., AND R. D. HOLT. 1989. Predation and competition: the interaction of two types of species interactions. Oikos, 54:256–260.

KOTLER, B. P., L. BLAUSTEIN, AND J. S. BROWN. 1992. Predator facilitation: the combined effects of snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici, 29:199–206.

KOTLER, B. P., J. S. BROWN, AND O. HASSON. 1991. Owl predation on gerbils: the role of body size, illumination, and habitat structure on rates of predation. Ecology, 71:2249–2260.

KOTLER, B. P., J. E. GROSS, AND W. A. MITCHELL. 1994. Applying patch use to assess aspects of foraging behavior in Nubian ibex. The Journal of Wildlife Management, 58:299–307.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology, 68:619–640.

MACARTHUR, R. H., AND E. L. PIANKA. 1966. On optimal use of a patchy environment. The American Naturalist, 100:603–609.

MILLS, M. G. L., AND T. M. SCHENK. 1992. Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. The Journal of Animal Ecology, 61:693–702.

MURDOCH, W. W., AND A. OATEN. 1975. Predation and population stability. Advances in Ecological Research, 9:1–131.

ROSENZWEIG, M. L., AND R. H. MACARTHUR. 1963. Graphical representation and stability of predator-prey interaction. The American Naturalist, 97:209–223,

SCHALLER, G. B. 1972. The Serengeti lion, a study of predator-prey relations. The University of Chicago Press, Chicago, Illinois.

SCHMITZ, O. J., A. P. BECKERMAN, AND K. M. O'BRIEN. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food webs. Ecology, 78: 1388–1399.

SCHWINNING, S., AND M. L. ROSENZWEIG. 1990. Periodic oscillations in an ideal-free predator-prey distribution. Oikos, 59:85–91.

SIH, A. 1980. Optimal behavior: can foragers balance two conflicting demands. Science, 210:1041–1043.

———. 1984. The behavioral response race between predator and prey. The American Naturalist, 123: 143–150.

TAYLOR, R. J. 1984. Predation. Chapman and Hall, Inc., New York.

VAN BAALAN, M., AND M. W. SABELIS. 1993. Coevolution of patch strategies of predator and prey and the consequences for ecological stability. The American Naturalist, 142:646–670.

VINCENT, T. L., AND J. S. BROWN. 1988. The evolution of ESS theory. Annual Reviews of Ecology and Systematics, 19:423–443.

WERNER, E. E. 1992. Individual behavior and higher-order species interactions. The American Naturalist, 140:S5–S32.