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A habitat selection game of interactions between rodents and their predators

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I developed a game theoretic model for habitat selection of prey and a generalist predator. In the model, both prey and predator may choose between either a simple or a complex habitat. A second predator is restricted to hunting only in the simple habitat. The model is applied to a system of rodents and their predators: snakes (the generalist predator) and owls. The simplest version of the model predicts that snakes and rodents distribute themselves among the two microhabitats according to the relative magnitude of risk for rodents. Under various conditions (moonlight, competition among rodents and dilution of the risk) the model predicts that snakes distribute themselves among habitats in a way that dampens rodent reactions to variation in owl predation risk and to effects of competition. When rodents are abundant the model predicts that snakes will show a weaker reaction to moonlight. The predictions of the model are qualitatively comparable to field data of microhabitat use of kangaroo rats and sidewinders from the Mojave Desert. The model can also describe a habitat selection game at a larger scale (e.g., movements of snakes into a rich desert oasis). Although a game between predators and prey may not be the cause for all their movements among habitats in the field, a game perspective may contribute explanations for what would otherwise be unintuitive habitat shifts.

Introduction

The constraints imposed by predators on the activity of prey have often been addressed, and evidence for their importance is accumulating (Sih 1980, Lima & Dill 1990, Lima 1998). Normally, models consider habitats as either safe or risky, and prey animals are assumed to consider the different levels of predation risk in each habitat. The risk in a habitat may depend on several factors; two important ones being the probability of encounter between predator and prey and the conditions which may facilitate or hinder predation (e.g., moonlight and vegetation cover, respectively). While the second element is a property typical of the habitat or of the conditions at a given time, the presence of predators in the habitat and their density during that time, is an important issue that is not easily addressed. Predators are often assumed to have a fixed distribution (e.g., Rahel & Stein 1988), but the density of predators is likely to be affected by habitat choices and relative densities of prey and vice versa. All else being equal, prey animals should benefit from using habitats in which the probability of being caught is relatively low. Predators, in turn, should be influenced by the habitat selection of prey. In order to find an appropriate distribution for both prey and predator, game theoretic methods need to be used.

Game theory and its special case, the evolutionarily stable strategy (ESS) (*see* Hammerstein 1998), have been successfully applied to many aspects of behavioral ecology including: escalating conflicts (e.g., Maynard Smith & Price 1973, Maynard Smith 1982, Riechert 1998), parental investment (e.g., Parker & MacNair 1978, Mock *et al.* 1998) cooperative behavior (e.g., Pulliam *et al.* 1982, Dugatkin 1998), and habitat selection (e.g., Fretwell 1972, Brown 1998). Models of games among several species have received less attention than games within a species (for exceptions *see* Lawlor & Maynard Smith 1976, Auslander *et al.* 1978, Riechert & Hammerstein 1983, Bell 1986, Brown 1998). It is in this context of interactions among more than one species that most predator-prey games are found. Even though the concept of games is very reasonable for analyzing ecological interactions, only a few models have been created that address games between predators and prey (Stewart 1971, Schwinning & Rosenzweig 1990, van Baalen & Sabelis 1992, Bouskila 1993, Hugie & Dill 1994, Bouskila *et al.* 1998, Sih 1998). Here I present a general model for microhabitat selection of predators and prey, and adjust it to describe a system in the Mojave Desert involving rodents, snakes and owls. The same model can be applied at different scales and to different systems with only minor modifications (e.g., an oasis in a desert environment).

Construction of the model

General considerations

The model deals with one prey species and two predator species, a generalist and a specialist, which differ in their habitat specificity. Two habitats provide foraging opportunities for the prey, and in both, the prey is exposed to risk of predation from the generalist predator. The habitats differ in structural complexity, and as a consequence, in predation risk. For example, the generalist predator is less visible when ambushing in the complex habitat. The specialist predator is restricted to the simple habitat, and because it cannot choose among habitats, it is not included as a player in the game. As in many other static game theoretic models, all individuals within a species are assumed identical, and to have full knowledge of model parameters and variables.

The payoffs to the players are presented as combinations of costs (energy loss and death) and benefits (energy gain) in the cells of a 2 × 2 matrix (Table 1). The payoff is the expected change in the eventual reproductive output of a player adopting one of the habitat choices when its opponent adopts the same or a different choice (Hines 1987). This definition allows one to treat energy gain, energy expenditure and death in a common currency. The loss or gain of energy is assumed to affect eventual reproductive output, and the cost of death corresponds to reducing future reproductive output to 0. Future reproductive output varies in nature with the age of the animal and its available energy reserves, but because all animals are assumed identical, the cost of death is constant (d).

The parameters in the payoff expressions can use any unit of time, but the same unit is used consistently for all parameters and for the predictions of the model. If the unit is one hour, for instance, the model predicts what proportion of animals will spend the hour active in each habitat.

The biological scenario

As an example for a system to which the model can be applied, I considered nocturnal desert rodents in the Mojave Desert and their predators (Bouskila 1995). The generalist predator is represented by the viperid snake, *Crotalus cerastes*, that hunts from ambush, either in the open (simple habitat) or in the bush (complex habitat). Kangaroo rats (*Dipodomys* spp.) forage in both habitats, and when in the open, are subject to predation not only from snakes, but also from owls, that specialize in preying on rodents only in the open (Longland & Price 1991).

Moonlight substantially increases the risk from owls because rodents are more vulnerable to visual predators under illuminated conditions (e.g., Clarke 1983, Kotler *et al.* 1988). However, snakes are not likely to be more successful in capturing rodents in moonlight because they rely mostly on senses other than vision (e.g., olfaction and in some groups, detection of infrared radiation [Schwenk 1995]). Moreover, on moonlit nights, rodents detect snakes more easily (Bouskila 1995), thus the predatory risk from snakes may be somewhat lower than on dark nights.

The basic model

I start with a simple game between the generalist predator and the prey, with no interactions between conspecifics. Later, I add competition among prey and dilution of predation risk. Mathematically, the basic model with no intraspecific interactions is equivalent to a model for one predator and one prey individual, but it may represent also a situation in which several rodents have non-overlapping home ranges.

Assumptions

The payoffs for the basic model (Table 1) are based on the definitions of parameters in Table 2 and on the following assumptions:

1. The payoff for a snake foraging in the same microhabitat used by the rodent is e when the prey is caught, occurring with probability P_{sb} (if in the bush, cell [1]) or P_{so} (if in the open, cell [4]). A foraging cost for the snake, β is also added. When the snake and the rodent forage in different microhabitats, the cost β is the only component of payoff for the snake.
2. The probabilities that a snake captures a rodent in the bush is larger than that in the open ($P_{sb} > P_{so}$).
3. A rodent in the open is under risk of predation from both the snake (P_{so}) and the owl (P_{oo}). If the snake and the rodent are both in the open (cell [4]), the probability that a rodent survives is $(1 - P_{so}) \times (1 - P_{oo})$. Because both probabilities for predation were small (< 0.04), I used the simpler approximation $1 - (P_{so} + P_{oo})$ without significant effect on the result.
4. A rodent gets a payoff $-d$ if caught by either predator. If it is not caught, it gets a payoff ρ_b (in the bush, cells [1] and [2]) or ρ_o (in the open, cells [3] and [4]) less the cost for for-

Table 1. Payoff matrix in the basic version of the predator-prey habitat selection game. The numbers in square parentheses are used as a reference to the cells in the text. In each cell, the top expression represents the payoff for the predator and the bottom expression, for the prey.

		Snake	
		Bush	Open
Rodent	Bush	[1] $P_{sb}e - \beta$ $P_{sb}(-d) + (1 - P_{sb})(\rho_b - \alpha)$	[2] $-\beta$ $\rho_b - \alpha$
	Open	[3] $-\beta$ $P_{oo}(-d) + (1 - P_{oo})(\rho_o - \alpha)$	[4] $P_{so}e - \beta$ $(P_{so} + P_{oo})(-d) + [1 - (P_{so} + P_{oo})](\rho_o - \alpha)$

aging, α.

5. In the basic model, which assumes no competition, the payoff for the rodent due to energy intake is equal in both microhabitats: $\rho_b = \rho_o$.
6. There is no predation risk for the snakes.
7. The activity of the players includes only foraging. Information acquisition, territorial behavior, mate acquisition, reproduction etc., are ignored.

Results with pure strategies

Each one of the cells [1–4] represents a combination of two pure strategies, one for each species. An optimal solution exists at the Nash equilibrium, the combination of strategies which if used by all players, optimizes the payoffs for each one of them. Any deviation from the optimal solution will decrease the payoff to the deviator (Nash 1951). To find the equilibrium, one compares the payoffs in each cell to the alternative cells. Only a cell that maximizes the payoff for both players can be the Nash solution. In Table 1, we see that only cell [1] includes a combination of pure strategies that can be a Nash equilibrium. Solving the condition for the rodent to choose cell [1] leads to a requirement which is likely to occur only if $P_{oo} > P_{sb}$. This means that, when the risk from owls in the open is larger than the risk from snakes in the bush, all snakes and all rodents should select the bush microhabitat. No other cell provides a stable solution.

Results with mixed strategies

According to the previous section, in all cases where the risk from owls in the open is smaller

Table 2. Parameters used in various versions of the model. All parameters (except for *d*) are per one time unit. Costs and payoffs are the expected changes in eventual reproductive output. The units of reproductive value (rep. val.) need not be specified (*see* Appendix 2).

Symbol	Units	Description
d	rep. val.	Cost of death for a rodent, when captured by a snake or by an owl (equivalent to its future reproductive value).
P_{sb}		Probability that snake captures rodent, if the rodent and the snake are in the bush.
P_{so}		Probability that snake captures rodent, if the rodent and the snake are in the open.
P_{oo}		Probability that owl captures rodent, if a rodent is in the open.
α	rep. val.	Cost (due to energy loss) for a rodent in either microhabitat.
β	rep. val.	Cost (due to energy loss) for a snake in either microhabitat.
ρ_b	rep. val.	Payoff for energy gained by a foraging rodent in the bush, given it survives predation (without competition).
ρ_o	rep. val.	Payoff for energy gained by a foraging rodent in the open, given it survives predation (without competition).
F_b	rep. val.	Payoff due to the per-capita amount of food eaten in the bush, when all rodents forage in that habitat and divide the food.
F_o	rep. val.	Payoff due to the per-capita amount of food eaten in the open, when all rodents forage in that microhabitat and divide the food.
e	rep. val.	Payoff for energy gained by a foraging snake, if rodent is captured.
a	indiv.	Determines the intensity of the dilution effect.
k	indiv.	Number of rodents in the home range of an owl (for the dilution effect).

than the risk from snakes in the bush, one should search for a solution in which a proportion of prey and/or predators use both microhabitats. These proportions can be also regarded as the probabilities that an individual animal will use each microhabitat. The probability that a rodent or a snake is in the open is p_{Rop} and p_{Sop}, respectively. For each species, the condition for equilibrium is that the weighted payoff in the bush is equal to that in the open. To obtain the probability that a rodent is in the open (p_{Rop}) one can use the payoffs for the snakes from Table 1:

$$-\beta p_{\mathrm{Rop}} + (P_{\mathrm{sb}}e - \beta)(1 - p_{\mathrm{Rop}}) = -\beta(1 - p_{\mathrm{Rop}}) + (P_{\mathrm{so}}e - \beta)p_{\mathrm{Rop}} \qquad (1)$$

Similarly, to obtain the probability that a snake is in the open (p_{Sop}) the payoffs of the rodent are used:

$$\begin{gathered}(\rho_{\mathrm{b}} - \alpha)p_{\mathrm{Sop}} + \\ [P_{\mathrm{sb}}(-d) + (1 - P_{\mathrm{sb}})(\rho_{\mathrm{b}} - \alpha)](1 - p_{\mathrm{Sop}}) = \\ [P_{\mathrm{oo}}(-d) + (1 - P_{\mathrm{oo}})(\rho_{\mathrm{o}} - \alpha)](1 - p_{\mathrm{Sop}}) + \qquad (2) \\ \{(P_{\mathrm{so}} + P_{\mathrm{oo}})(-d) + [1 - (P_{\mathrm{so}} + P_{\mathrm{oo}})](\rho_{\mathrm{o}} - \alpha)\}p_{\mathrm{Sop}}\end{gathered}$$

Solving Eq. 1 for p_{Rop} leads to

$$p_{\mathrm{Rop}} = \frac{P_{\mathrm{sb}}}{P_{\mathrm{sb}} + P_{\mathrm{so}}} \qquad (3)$$

Assuming that $\rho_{\mathrm{b}} = \rho_{\mathrm{o}}$, solving Eq. 2 for p_{Sop} leads to

$$p_{\mathrm{Sop}} = \frac{P_{\mathrm{sb}} - P_{\mathrm{oo}}}{P_{\mathrm{sb}} + P_{\mathrm{so}}} \qquad (4)$$

Eqs. 3 and 4 offer a convenient way of looking at the probabilities that rodents and snakes are in the open, using only the relative magnitude of the different predation risks. One implication is that the proportion of rodents in the open depends on the relative magnitude of predation risk from snakes. When $P_{\mathrm{sb}} = P_{\mathrm{so}}$, the rodents should be distributed equally between the two microhabitats. But as stated above, the risk from snakes in the bush should be higher than that in the open. More rodents should forage in the open than in the bush.

Because the probability that snakes will be in the open (p_{Sop}) cannot be negative, there are no mixed strategy solutions if the risk from snakes in the bush is smaller than the risk from owls in the open (Eq. 4; $P_{\mathrm{sb}} < P_{\mathrm{oo}}$). Under these conditions, only the pure strategy of all snakes and rodents in the bush is stable. The model in this basic form predicts mixed solutions only for systems in which snake predation in the bush is at least as important as owl predation in the open.

Effects of moonlight

On illuminated nights, the increase in the risk from owls (P_{oo}), and the reduction in the risk from snakes (P_{sb} and P_{so}), reduces the probability that snakes will ambush in the open (Eq. 4). Moonlight should have no effect on the distribution of rodents, as long as moonlight affects P_{sb} and P_{so} by the same proportion. The advantage afforded by moonlight to rodents in the detection of snakes, however, is likely to be more prominent near the bush, because in the open, rodents can detect snakes fairly well even in the dark (pers. observation). If rodents get a greater advantage from moonlight near the bush, the ratio $P_{\mathrm{so}}/P_{\mathrm{sb}}$ will be larger during moonlit nights, and from Eq. 3, moonlight will decrease the proportion of rodents in the open, p_{Rop}. If, however, the advantage to rodents is greater in the open, moonlight will increase the proportion of rodents in the open.

Including intraspecific interactions

Different energy gains in habitats

Habitats may often vary in productivity ($\rho_{\mathrm{b}} \neq \rho_{\mathrm{o}}$). The probability that rodents will forage in the open remains unchanged because ρ_{b} and ρ_{o} do not appear in Eq. 1. Habitat choice by snakes does change, however, because ρ_{b} and ρ_{o} do not cancel out of Eq. 2. Solving for the probability that snakes will forage in the open we obtain:

$$p_{\mathrm{Sop}} = \frac{P_{\mathrm{sb}}(\alpha - d - \rho_{\mathrm{b}}) - P_{\mathrm{oo}}(\alpha - d - \rho_{\mathrm{o}}) + \rho_{\mathrm{b}} - \rho_{\mathrm{o}}}{P_{\mathrm{sb}}(\alpha - d - \rho_{\mathrm{b}}) + P_{\mathrm{so}}(\alpha - d - \rho_{\mathrm{o}})} \qquad (5)$$

The partial derivative of p_{Sop} with respect to ρ_{b} is always negative, as long as $P_{\mathrm{sb}} \geq P_{\mathrm{oo}}$. An increase in productivity in the bush habitat will drive the snakes into the bush.

Effects of competition

Resource competition can be added to the basic model by modifying the payoff for a surviving rodent. Without competition, the payoff included a positive component, due to the energy gained (ρ_b or ρ_o, depending on the microhabitat), and the negative cost of foraging ($-\alpha$). When rodents compete, the per-capita amount of food available in each microhabitat depends on the proportion of rodents choosing each microhabitat.

The payoff for a surviving rodent foraging in the open is defined now as $Y_o - \alpha$, where Y_o is the payoff due to energy intake for a rodent in the open, and α is the cost of foraging. To introduce density dependence I assumed that there is an inverse linear relationship between the number of rodents in a microhabitat and the per-capita amount of food collected by each rodent. The payoffs due to energy intake in the open and in the bush, respectively, are:

$$Y_o = \rho_o - p_{\mathrm{Rop}}(\rho_o - F_o) \quad (6)$$

$$Y_b = \rho_b - (1 - p_{\mathrm{Rop}})(\rho_b - F_b) \quad (7)$$

where ρ_o is the payoff in the open for a rodent which is under no competition, and F_o is the payoff due to the per-capita amount of food eaten in the open when all rodents forage in that microhabitat. The intensity of competition is determined in two ways: by the values chosen for F_o and F_b (depend on habitats and population density) and by the proportion of rodents foraging in the habitat (calculated by the model).

The addition of competition among rodents has no effect on the probability that rodents select the open (Eq. 1 unchanged). When competition is intensified, however, snakes shift their activity towards the bush (Appendix 1). Increasing competition reduces the payoff for rodents in the open more than it reduces the payoff in the bush. Equal payoffs for the rodents across habitats can be maintained only if snakes shift their activity to the bush.

The dilution effect

The per-capita risk to individual prey may be lower in larger groups than in smaller ones (the dilution effect; Foster & Treherne 1981, Morgan & Godin 1985, Treherne & Foster 1982, Wrona & Dixon 1991). If a group does not attract predators in proportion to prey number (Turner & Pitcher 1986, Morgan & Godin 1985), the dilution effect is likely to operate and it is relevant to ask how might the dilution of risk alter the distribution of prey.

The probability of being killed by an owl in the open, when the dilution effect is operating, is now defined as $P_{oo}' = P_{oo}m$, where $m \leq 1$ and represents the reduction in risk due to the dilution effect. To calculate m I divided the number of rodents captured per unit time in an owl's home range (N_r) by the number of rodents active in the open habitat in that area:

$$m = \frac{N_r}{kp_{\mathrm{Rop}}} \quad (8)$$

where k is the total number of rodents active in the home range of an owl (in both habitats).

The number of rodents captured per unit time by owls can be described by a type 2 functional response (Korpimaki & Norrdahl 1989):

$$N_r = \frac{kp_{\mathrm{Rop}}a}{kp_{\mathrm{Rop}} + a - 1} \quad (9)$$

where $a \geq 1$ and controls the steepness of the curve. Substituting N_r in Eq. 8 by the expression in Eq. 9, we obtain:

$$m = \frac{a}{kp_{\mathrm{Rop}} + a - 1} \quad (10)$$

The parameter m is not only inversely related to the number of rodents active in the open, but also to the size of the population (this property is used in the next section).

In contrast to owls, ambushing snakes are extreme sit-and-wait predators and they have very low capture rates (Mushinsky 1987, personal observation). As a consequence, prey capture rate by snakes is proportional to the density of prey and the dilution effect does not operate (Holling 1959, Murdoch & Oaten 1975). Accordingly, I added to the habitat choice model the dilution effect only in the case of risk from owls. I substituted the diluted risk from owls,

P_{oo}', for P_{oo} in Eq. 4 to find the equilibrium for the proportion of animals in the different microhabitats. As in the effect of competition, the dilution of risk from owls affects only the distribution of snakes, because P_{oo} does not appear in Eq. 3. The new expression for the probability that snakes will ambush in the open is now:

$$p_{\mathrm{Sop}} = \frac{P_{\mathrm{sb}} - \dfrac{P_{\mathrm{oo}}a}{kp_{\mathrm{Rop}} + a - 1}}{P_{\mathrm{sb}} + P_{\mathrm{so}}} \qquad (11)$$

The partial derivative of p_{Sop} with respect to a is negative, as long as one or more rodents forage in the open habitat. This means that when dilution of risk approaches its maximum value (at $a = 1$), more snakes shift to the open microhabitat. The dilution of risk from owls creates an advantage to the rodents in the open, and the shift of snakes to that microhabitat acts to offset this advantage.

Effect of population density

The model operates only on the relative number of predators and prey in the two microhabitats, and one cannot model changes in population density directly (*see* Appendix 3). Nevertheless, combining an increase in the dilution effect with an intensification of competition simulates the main effects of an increase in the population of rodents. To increase the dilution effect I multiplied the number of rodents in the home range of an owl (k) by 2, 4, and 8. Competition was intensified by dividing the per-capita food available (F_o and F_b) by the same values. The results are plotted in Fig. 1a; no competition or dilution operates at the basic population size (N). With the increase in rodent density, snakes react less to moonlight, and the differences between full moon and new moon are diminished.

Summary of predictions from the microhabitat choice model

The effects of moonlight, competition and dilution are summarized in Fig. 2. When moonlight is assumed to increase risk to rodents from owls, and diminish risk from snakes, the snakes ambush more in the bush. There is almost no effect on the rodents. The shift of snakes to the bush on moonlit nights is an indirect reaction to the change in risk to rodents: according to the model assumptions, there is no risk to snakes from owls. Where such a risk exists, the shift of the snakes should be even more extreme. When productivity is increased in one of the habitats (the open, in the example in Fig. 2), only the snakes react, by shifting to the enriched habitat.

When competition among rodents is included the proportion of snakes in the open declines. By contrast, when the risk from owls is diluted, the proportion of snakes in the open increases. When both competition and dilution operate (e.g., when the density of rodents increases) the snakes still shift towards the open, but less than with dilution only. The difference in the proportion of snakes in the open between full moon and new moon is reduced at high rodent density.

Relating the microhabitat choice model to field data

In a field study of kangaroo rats (*Dipodomys deserti* and *D. merriami*) and sidewinders (*Crotalus cerastes*) in the Mojave Desert, I investigated the habitat use of rodents and snakes. Habitat use of the rodents was quantified using the giving-up-density (GUD) method (Brown 1988) in trays located in bush, open and grass microhabitats. Each tray contained equal amount of seeds mixed with sand (*see* Bouskila 1995 for details of the field experiments). The amount of seeds left by the rodents in a tray after a night of foraging (the GUD) measures the foraging effort of the rodents in that tray and reflects costs of foraging as perceived by the rodents (Brown 1988). The habitat use of snakes was estimated from ambush sites that were located along the trails left by the snakes on the sand. The data on snakes and rodents were collected either during full moon nights or during new moon nights. No data were collected during intermediate moonphases in which the moon rises or sets during the night. Because the effect of rodent species was

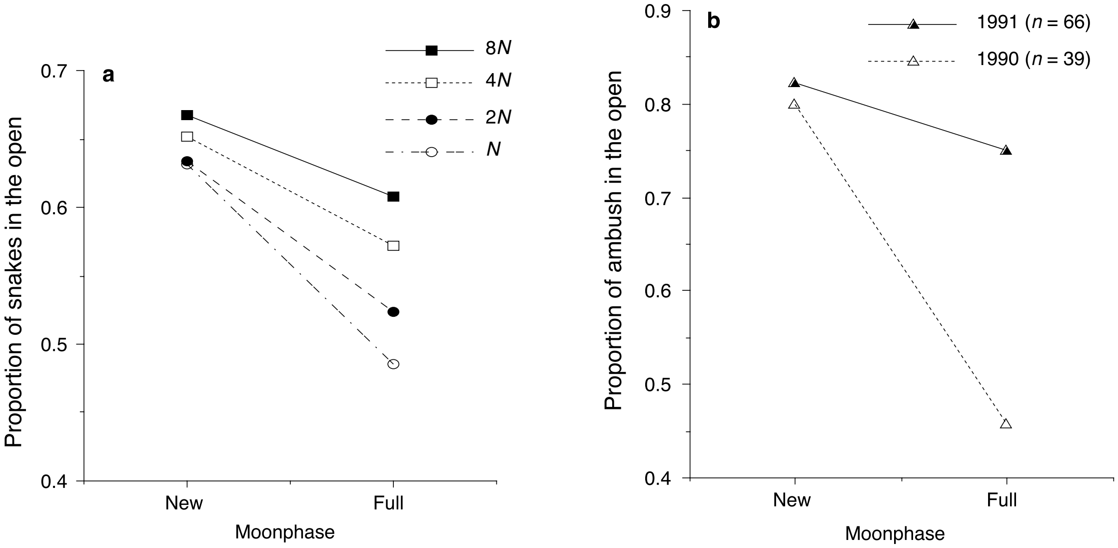

Fig. 1. Effects of rodent density on the proportions of snakes in the open at different moonphases. — **a**: Predictions of the model. *N* is the basic population density of the rodents, and the density increases up to 8N. — **b**: Proportion of ambush sites of snakes in the open measured in the Mojave desert (1990 and 1991). Rodent density was higher in 1991 than in 1990. Values of parameters in **a** are listed in Table 3. During moonlit nights, the risk from snakes was decreased (the values in the table for P_{sb} and P_{so} were multiplied by 0.75 and 0.85, respectively). To obtain the risk from owls under moonlight, P_{oo} was multiplied by 1.25.

not significant in the analysis presented here, and because both species are preyed upon by sidewinders, I treat both species of kangaroo rats together.

Use of microhabitat

The snakes and the rodents foraged substantially in all available microhabitats: creosote bush,

Table 3. Values of parameters used in Figs. 1a and 2. Parameter descriptions are listed in Table 2. Empty cells correspond to values for parameters that cancel out in specific versions of the model.

Symbol	Different scenarios in Fig. 1a (New moon)				Different scenarios in Fig. 2					
	N	2*N*	4*N*	8*N*	Basic	Moonlight	Rich open	Competition	Dilution	Comp. + Dilut.
d	1500	1500	1500	1500	–	–	1500	1500	1500	1500
P_{sb}	0.032	0.032	0.032	0.032	0.032	0.024	0.032	0.032	0.032	0.032
P_{so}	0.009	0.009	0.009	0.009	0.009	0.00765	0.009	0.009	0.009	0.009
P_{oo}	0.02	0.02	0.02	0.02	0.02	0.023	0.02	0.02	0.02	0.02
α	7	7	7	7	–	–	7	7	7	7
ρ_b	12	12	12	12	–	–	12	12	12	12
ρ_o	17	17	17	17	–	–	17	12	12	12
F_b	12	6	3	1.5	–	–	–	1.5	12	1.5
F_o	17	8.5	4.25	2.12	–	–	–	2.12	12	2.12
a	6	6	6	6	–	–	–	–	6	6
k	10	20	40	80	–	–	–	–	80	80

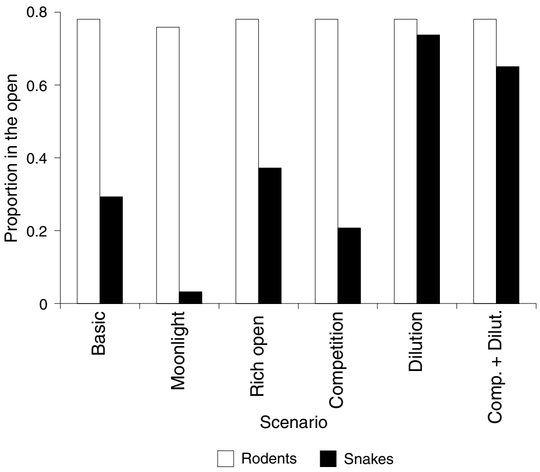

Fig. 2. Proportions of rodents and snakes that forage in the open habitat under different scenarios. Values of parameters are listed in Table 3.

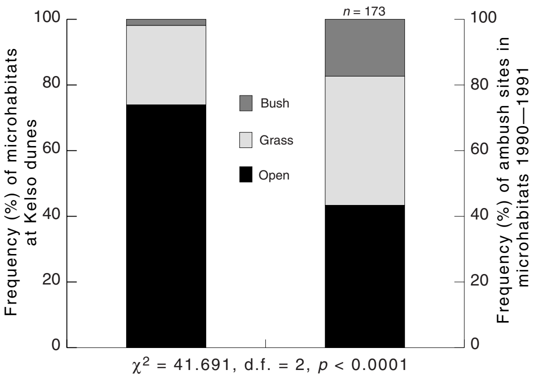

Fig. 3. Comparison between the available microhabitats and the distribution of ambush sites of the snakes for 1990 and 1991 combined. The snakes prefer to ambush near bushes and avoid the open.

open and perennial grasses. Direct observations indicated that individual snakes and rodents used all microhabitats, even during the same night. These results fit a mixed strategy, where each individual utilizes all available microhabitats, as predicted by all versions of the model as long as the risk from owls was lower than the risk from snakes in the bush. The snakes showed a preference for the use of the bush microhabitat, and they used it more frequently than its occurrence in random transects at the site (Fig. 3).

The preference of snakes for the bush was significant also when the comparison was restricted to open and bush microhabitats (χ^2 = 32.878, d.f. = 1, $P < 0.0001$). Rodents foraged more intensively in the open: they took more seeds from the trays in the open, leaving more unused seeds in the bush (d.f. = 1, $F = 8.048$, $P = 0.0252$; repeated measures ANOVA).

Effect of moonlight

As predicted, rodents did not forage less in the open on full moon nights than on new moon nights (d.f. = 1, $F = 1.228$, $P = 0.304$), the presence of snakes dampened the reaction of rodents to moonlight. When the same analysis was repeated with the data from the fall (when snakes were not active), the rodents avoided moonlight. Rodents foraged more in the bush than in the open (d.f. = 1, $F = 8.57$, $P = 0.0221$); foraging in the open was lower on full moon nights than on new moon nights (d.f. = 1, $F = 46.822$, $P = 0.0002$).

The snakes always preferred the bush microhabitat, but during full moon nights, the preference for the bush habitat was stronger (Fig. 1b), as predicted by the model (Fig. 1a).

Effect of prey density

A contingency table analysis on the habitat choice of the snakes during two years showed that the choice of habitat depends on both moonphase and the year ($\chi^2 = 10.432$, d.f. = 3, $P < 0.025$). During 1991, the shift of the snakes to the bushes on full moon nights was weaker, and the difference between new moon and full moon was smaller than in 1990 (Fig. 1b). In 1991 the density of rodents was extremely high (Bouskila 1995). I therefore compared the snakes' preference for microhabitats in 1991 with the predictions of the model at high prey densities (Fig. 1a and b). The qualitative similarity between the model's predictions and the results obtained in the field suggests that the different distribution of snakes in 1991 might have been associated with the increased density of rodents during that year.

Discussion

Lack of sensitivity of players in the game to their parameters

One consistent result from all versions of the model presented here is the lack of sensitivity of the prey to variables that intuitively should affect their choices, such as the distribution of food. Rather, prey distribution is mostly affected by the risk of predation from the generalist predator in each habitat. Moreover, even a change in the risk from the predator that is restricted to the simple habitat does not affect the distribution of prey. The reason for this result lies in the freedom of the generalist predators to choose among habitats, leading to their shift to the habitat that prey animals should move into. The lack of sensitivity to the distribution of food is manifested when predators do not interact. Bouskila (1993) showed that if predators compete, but prey animals do not, the predators would not be sensitive to changes in the intensity of competition: only the prey will adjust its behavior accordingly. This is a general result that was reached in other game theoretic models of predators and prey, even when different modeling approaches were used (van Balaan & Sabelis 1993, Hugie & Dill 1994, Sih 1998, Bouskila *et al.* 1998).

Shifts in rodent habitat use due to moonlight have been demonstrated in several studies. The shift has been attributed to increased risk from visual predators such as owls and mammals (Lockard & Owings 1974, Kotler 1984, Price *et al.* 1984, Bowers 1988, Travers *et al.* 1988, Wolfe & Summerlin 1989, Daly *et al.* 1992, Dickman 1992). Contrary to these studies, I found no moonlight effect on the intensity of activity and on microhabitat choice in *D. deserti* and *D. merriami* in the summer (Bouskila 1995). The response must have been caused by snakes. Using the same methodology, at the same site, I found in the fall (after the activity season of snakes was over) that on full moon nights, kangaroo rats took significantly less seeds in the open.

The microhabitat choice model developed here suggests an explanation for the exceptional results in the summer. Most studies of the effect of predators on habitat selection of rodents consider visual predators only, and therefore expect the rodents to react to moonlight (e.g., Wolfe & Summerlin 1989, for exceptions *see* Brown 1989, Longland & Price 1991). The model suggests that when the relative importance of risk from snakes is large enough, snakes will attenuate the effects of moonlight on the rodents. Some of the field studies that demonstrated an effect of moonlight on microhabitat use of rodents also used observations collected in winter (e.g., Daly *et al.* 1992, Lockard & Owings 1974, Price *et al.* 1984), when nocturnal snakes are not active. Other studies were performed in areas that are too cold for nocturnal snakes, even in summer (e.g., Kotler 1984, in the Great Basin Desert). In my study site in the Mojave Desert, the risk from snakes during the summer seemed to be important relative to the risk from owls, and might have affected the activity of rodents as predicted by the microhabitat choice model.

The distribution of risk from snakes

Snakes in the field study preferred the bush, but one cannot assume that this preference is independent of the distribution of prey. If rodents and snakes respond to each other's behavior when choosing microhabitats for foraging, as suggested by the model, the preference of snakes may be simply a result of the game between the two players, rather than an innate preference. Two of the potential causes for high use of bushes by snakes are (a) higher success rates in capturing rodents in the bush, and (b) the risk to rodents from owls, which is confined to the open. Additional factors may be the distribution of food for the rodents (e.g., if there is more food near the bushes), or the risk from the predators of the snakes (e.g., if snakes are captured more in the open). It is not clear whether these last two factors have any importance in the system that I studied. The model suggests that the preference of snakes for the bush can be entirely explained by the first two causes.

An effect of snakes on the foraging of rodents was also found by Kotler *et al.* (1993) who exposed gerbils in an enclosure to snakes. In the presence of snakes, *Gerbillus pyramidum* did not respond to artificial illumination, in contrast to previous experiments in the same enclosure without snakes (Kotler *et al*. 1991). Kotler *et al*. (1992) assumed that the snakes impose a risk in the bush, and thus described the role of snakes as driving the rodents "into the talons of the owls". The results from the present model and from my study in the Mojave Desert suggest that the microhabitat choice of snakes cannot be assumed to be rigid: sidewinders ambushed in all microhabitats, and their proportions in each microhabitat may be adjusted to maximize their capture success. To do that, they need to react to fluctuations in the risks to rodents from other predators. The snakes may not be just driving the rodents into the talons of the owls, rather, they may be equalizing the payoffs for the rodents in all microhabitats.

Effects of population size

During 1991, a year that was characterized by a high density of rodents, snakes reacted less to moonlight. The version of the model with increased rodent competition, but without dilution, does not explain the weaker reaction of snakes to moonlight: it predicts fewer snakes in the open during full moon nights, which is opposite to the results from the field. Only the version which included both competition and dilution effect predicted correctly the reaction of snakes in the field to moonlight. The dilution effect plays an important role due to the differences between risk from snakes and from owls. When rodents population expand, the importance of risk from snakes increases relative to the risk from owls, because only the risk from owls is diluted.

The model is not the only way to interpret the increased use of the open habitat by the snakes when the density of rodents was high. An alternative explanation involves information exchange among rodents, which cannot be incorporated in the present model. A high rodent density may have facilitated the awareness of rodents to the location of ambushing snakes. As a result, the snakes may have switched ambush sites more often, and since bushes are scarce in the dunes, they had to increase the use of the less preferred, but more common, habitat, the open. This explanation is not mutually exclusive of the effects of higher density of rodents on the game between rodents and snakes, and they could both act simultaneously in the same direction.

Future directions

The general predictions should apply to other systems of two predators and one prey, as long as one predator is limited to one habitat only. Potential examples include ground geckos-snakes-owls (Reichmann 1998) and scorpions as prey for their predators, hedgehogs and owls (Shamir 1999). The model can also describe a larger scale of habitats (*see* Appendix 4 for an example with rodents, snakes and owls), and it can also be adjusted to describe hyrax which are prey to leopards and raptors. The prey and the leopards may forage both in boulder habitat and in dense canopy, but the raptors are limited to the boulders.

Like most game theoretic models in behavioral ecology, the model presented here is static. In such models, one often assumes that all individuals are identical, and the state of the individuals is ignored. But the state of the players can not be ignored. Eshel (1978), for instance, suggested that predators of gregarious prey may be "cooperating" with superior prey against inferior prey individuals. The state of individuals can be incorporated in a genetic algorithm (*see* Bouskila *et al*. 1998 for an example with a predator-prey game). Dynamic games (Houston & McNamara 1988, Mangel 1990, Mangel & Clark 1988) also include the state of the animals involved. It will be interesting to see what new insights emerge from a dynamic version of the habitat selection game.

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Appendix 1

Snakes' proportion in the open when rodents compete

When rodents compete, ρ_o and ρ_b in Eq. 5 need to be replaced with appropriate expressions for energy gain in the open and in the bush, respectively, (Eqs. 6 and 7). Different energy gains in each microhabitat may not only result from the numbers of competing rodents, but also from different productivity in the bush and in the open. The Eq. for the probability that snakes will ambush in the open is thus

$$p_{\mathrm{Sop}} = \frac{P_{\mathrm{sb}}D_{\mathrm{b}} - P_{\mathrm{oo}}D_{\mathrm{o}} + F_{\mathrm{b}} - \rho_{\mathrm{o}} + p_{\mathrm{Rop}}(\rho_{\mathrm{o}} + \rho_{\mathrm{b}} - F_{\mathrm{o}} - F_{\mathrm{b}})}{P_{\mathrm{sb}}D_{\mathrm{b}} + P_{\mathrm{so}}D_{\mathrm{o}}} \tag{A1}$$

where

$$D_{\mathrm{b}} = \alpha - d - F_{\mathrm{b}} - p_{\mathrm{Rop}}(\rho_{\mathrm{b}} - F_{\mathrm{b}})$$

and

$$D_{\mathrm{o}} = \alpha - d - \rho_{\mathrm{o}} + p_{\mathrm{Rop}}(\rho_{\mathrm{o}} - F_{\mathrm{o}})$$

Note that because the productivity in the open, ρ_o, is not necessarily equal to ρ_b in the bush, also the value of F is not equal in the different microhabitats and we have to use F_o and F_b for the open and the bush, respectively. Eq. A1 collapses back to Eq. 4 when $\rho_o = \rho_b = F_o = F_b$ (i.e., rodents do not compete).

Appendix 2

Model structure

In general, the abundance of a species is treated in this model as constant. Riechert and Hammerstein (1983) showed that the relative numbers of individuals from each species play an important role in interspecific games, and these models should be either investigated for a specific relative-abundance of species or, alternatively, by including the variation in the relative numbers in the model. In the habitat selection game, the proportion of animals emerging from their shelter may be subject to another predator-prey game (developed in Bouskila 1993). The current model deals only with the choice of habitats after the number of active animals has been determined. A similar approach was used by Schwinning and Rosenzweig (1990).

Payoffs were defined in the model as the expected changes in eventual reproductive output. The time unit need not be specified, because one should be concerned only with the relative costs and benefits of any choice made by the animals. This allows one to use a general unit of reproductive value, without specifying its precise translation into offspring or energy. When the fitness of rodents is calculated at equilibrium, one may obtain negative values with the parameters used in this model. This is the result of the large cost of death (relative to other costs and benefits) that was assumed to operate. I assumed the rodents to be in a non-reproductive period. Negative payoffs may be interpreted in this case as a reduction in the expected reproductive output, because a rodent that defers its reproduction to the future may be killed before it realizes the potential fitness.

Appendix 3

Model stability

The solutions for the various scenarios described by the model were based on finding Nash equilibria

(Nash 1951) by comparing the first derivative of the fitness of a species with respect to the proportion of animals in the habitats. Whether the equilibrium is stable or not is determined by the second derivative: stability is maintained when the second derivative is negative. In analyses of the expressions obtained by the different versions of the model, negative second derivatives occur only in the models with intraspecific competition. I assumed that only rodents compete. It follows that there are two implications for the stability: (a) if rodents choose to deviate from equilibrium, they will suffer a reduction in fitness due to the density dependence in the competitive relations among them. (b) If snakes choose to deviate from equilibrium their fitness is not reduced. At equilibrium, when rodents use the habitats in the optimal proportions, snakes' fitness is constant, regardless of the habitat they choose. This suggests that snakes may deviate from equilibrium without penalty.

Stability may still be maintained, if the rodents and the snakes differ in their rate of information gain. Rodents may take longer to realize that the snakes have deviated from equilibrium, because the snakes are rarely encountered when hidden in ambush, and such encounters may often be fatal to the rodents. Thus rodent reaction to deviations by snakes are likely to be gradual and to lag behind the shift of the snakes. In contrast, the daily movements of snakes before choosing the ambush site (Bouskila 1995) may provide them with a good indication of habitat selection by rodents, through the density of scent trails left by the rodents. This means that snakes can immediately detect shifts in the proportions of rodents in each habitat, and they must react by shifting back towards equilibrium. If this lag indeed maintains the stability of the system, we should expect the variability around the equilibrium to be larger among snakes than among rodents.

Appendix 4

The application of the model to large scale habitats

The model presented here was constructed to describe a game in microhabitat selection. Nevertheless, it can be easily interpreted at the scale of whole habitats. Consider, for instance, the spatial relationships of snakes around the oasis of Ein-Gedi, in the Judean Desert, Israel. The oasis attracts many prey species of a viperid snake, *E. coloratus,* (rodents, but also birds, frogs and geckos) probably due to the abundance of food and water, moderate microclimate and shelter from avian predators provided by the dense canopy of trees. Nevertheless, intensive weekly surveys (resulting in 195 encounters with *E. coloratus*) showed that none of the 36 different snakes was permanently found in the oasis. Moreover, on any given survey, the number of snakes found ranged between 1–5 per night (Hawlena & Bouskila 2001). Two hypotheses can explain the absence of most snakes from the oasis: (a) snakes spend most of their time in shelters and (b) the snakes wander most of the time in the dry rocky habitat, outside the boundary of the oasis. The second hypothesis suggests that the oasis serves as a source of occasional food for a large number of snakes that do not permanently reside within its boundary. It implies that a game, similar to that described by the microhabitat selection model, may operate. One may treat the oasis as the bush microhabitat and the arid surroundings, as the open microhabitat. The foraging characteristics of *E. coloratus* (low capture rates, better camouflage under vegetation and the option for each snake to ambush in any of the two habitats) is reminiscent of the foraging of sidewinders in American deserts. The basic concepts developed in the microhabitat selection game are applicable, and the proportion of snakes in the two habitats may be the consequences of the costs and benefits associated with each habitat. If snakes stay in the oasis only temporarily, as part of a mixed strategy, the same individuals should also forage outside the oasis. The appropriate densities needed to maintain optimal proportions of rodents and snakes in the oasis may determine the long absences of each snake from the rich habitat.

During the third season of the study, we fitted six *E. coloratus* that were captured within the oasis with miniature transmitters and released them at the site of capture. We then attempted to relocate them daily for as long as they retained the transmitters. All the snakes moved eventually out of the oasis, and in one case, more than 300 meters away from it. These preliminary observations are not sufficient to demonstrate that the snakes and their prey operate according to the game theoretic model, but they suggest that the concept of subsidies between habitats (Polis *et al*. 1997) involves a game between the predators and the prey.