

State dependent behavior and the Marginal Value Theorem

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The Marginal Value Theorem (MVT) is the dominant paradigm in predicting patch use and numerous tests support its qualitative predictions. Quantitative tests under complex foraging situations could be expected to be more variable in their support because the MVT assumes behavior maximizes only net energy-intake rate. However across a survey of 26 studies, foragers rather consistently “erred” in staying too long in patches. Such a consistent direction to the errors suggests that the simplifying assumptions of the MVT introduce a systematic bias rather than just imprecision. Therefore, I simulated patch use as a state-dependent response to physiological state, travel cost, predation risk, prey densities, and fitness currencies other than net-rate maximization (e.g., maximizing survival, reproductive investment, or mating opportunities). State-dependent behavior consistently results in longer patch residence times than predicted by the MVT or another foraging model, the minimize μ/g rule, and these rules fail to closely approximate the best behavioral strategy over a wide range of conditions. Because patch residence times increase with state-dependent behavior, this also predicts mass regulation below maximum energy capacities without direct mass-specific costs. Finally, qualitative behavioral predictions from the MVT about giving-up densities in patches and the effects of travel costs are often inconsistent with state-dependent behavior. Thus in order to accurately predict patch exploitation patterns, the model highlights the need to: (1) consider predator behavior (sit-and-wait versus actively foraging); (2) identify activities that can occur simultaneously to foraging (i.e., mate search or parental care); and (3) specify the range of nutritional states likely in foraging animals. Future predictive models of patch use should explicitly consider these parameters. *Key words:* marginal value theorem, predation risk, foraging, patch use, stochastic dynamic programming, state-dependent behavior. [*Behav Ecol* 12:71–83 (2001)]

Optimal foraging theory is an important tool for increasing our understanding of animal behavior. One optimality model that has been particularly widely used is the Marginal Value Theorem (MVT), which predicts the behavior of foraging animals collecting energy within patches. Patch depletion will eventually force the animal to move. If the animal’s goal is to maximize net rate of energy intake, it should leave a patch when its foraging rate drops to the overall average intake for the entire habitat (Charnov, 1976). The MVT further predicts that if an animal encounters a series of patches of varying quality, it should bias its foraging efforts such that eventually all patches are depleted to an equal prey density. The prey density at which a forager leaves a patch is known as the giving-up density, or GUD, and therefore optimal foraging should result in all exploited patches having similar GUDs.

The MVT has been extensively applied and tested. Many studies have shown good qualitative support for MVT predictions such as animals preferring richer food patches over poorer ones and patch residence time (PRT) correlating with patch quality (see Stephens and Krebs, 1986: Table 9.1). However, quantitative tests of MVT predictions have been less successful in that observed behavior often deviates measurably from predicted behavior. One reason why quantitative predictions may be less accurate is due to the difficulty of objectively measuring payoff rates of various behavioral options. This is a significant problem for both the foraging animal (which may often need to sample changing or unpredictable environments), and for the researcher in determining and measuring the fitness of behaviors.

Methodological problems aside, a review of quantitative tests of the MVT shows a definite pattern (Table 1). When quantitative predictions of the MVT fail it is far more common for animals to stay longer in patches than predicted. In 23 of 26 studies, quantitative observations differed from the predicted MVT optima. In most studies there was considerable variance in patch usage across subjects and across trials within subjects. Some stayed too long while others left too early. However, in 19 studies the more common or average deviation from MVT predictions was to stay too long. In two cases both leaving too early or too late were relatively equally observed either for individual animals or across sets of conditions. In the other two cases, the average deviation was in leaving patches too quickly. In another seven studies the results could not be entirely consistent with MVT quantitative predictions (e.g., animals stayed equal lengths of time in good and poor patches), but the direction in which the animals deviated could not be determined.

Consistent patterns in deviations from a model’s predictions strongly suggest that instead of mere imprecision resulting in random errors, something fundamental is missing. Two major aspects of biological realism are absent from the MVT. First, animals are probably simultaneously doing more than just searching for food. For example, patch use patterns may often be affected by predators, either through their physical presence or by the foragers having to be vigilant for their appearance (Brown, 1988; Lima and Dill, 1990; Newman, 1991; Nonacs and Dill, 1990). Besides negative factors such as predation risk, foragers may also be looking for positive benefits such as mating opportunities.

The effect of predation risk on optimal foraging strategies has been extensively modelled, with the general result that net intake-rate maximization is not always the best strategy. Instead, strategies that maximize long-term survival trade off between foraging gain and exposure to risk do better (Mc-

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Table 1
Summary of studies testing quantitative predictions of the Marginal Value Theorem

Study: Species	Location	Experimental design	Results
Survival			
Alonso et al. (1995): European crane (<i>Grus grus</i>)	Field	Patches are farm fields and variable in quality, patch quality estimated by distance from roost.	Correlations between initial and quitting intake rates across patch qualities. Suggests birds either left good patches too quickly or bad patches too slowly. Flock size increases patch residence. (?)
Cassini et al. (1990): Armadillo (<i>Chaetophracus vellerosus</i>), Guinea pig (<i>Cavia porcellus</i>)	Lab	Two patches, with one better than the other. Animals must move between patches.	Consistent with qualitative MVT predictions in most trials. Errors always in staying too long. Overall, stayed too long in 10/21 trials with better environment, 5/21 trials in poorer. (+)
Cassini et al. (1993): Guinea pig (<i>C. porcellus</i>)	Lab	Design similar to above.	In 12 trials, quantitative predictions of MVT met; in 6 trials foragers stayed too long. (+)
Cowie (1977): Great tit (<i>Parus major</i>)	Aviary	Several patches all of equal initial quality. Travel times and costs varied.	PRTs are variable, with both longer and shorter times than predicted by the MVT. Longer PRTs more common. (+)
Crowley et al. (1990): Bluegill (<i>Lepomis macrochirus</i>)	Ponds	Four patches of equal initial density. Fish made to move sequentially between patches. Different prey densities across trials.	Variable PRTs, but on average, fish stayed 4–157% longer than predicted by the MVT. (+)
Cuthill et al. (1990): Starlings (<i>Sturnus vulgaris</i>)	Lab	Patches of equal quality, with variable travel times within a trial.	PRTs respond to short-term variation in travel time (e.g., birds stay longer if last travel time was longer), while MVT predicts no effect. (?)
Cuthill et al. (1994): Starlings (<i>S. vulgaris</i>)	Lab	Patches of equal quality, with variable travel times within a trial.	PRTs identical to MVT predictions in 11 of 12 birds (0)
Formanowicz (1984): Diving beetle (<i>Dytiscus verticalis</i>)	Aquaria	Constant density of prey within a trial. Patch = prey item, with measure being how much prey to consume.	Beetle larvae partially consume prey as predicted at high densities, but handle too long at low prey densities. (+)
Gaines (1989): Tree sparrow (<i>Spizella arborea</i>)	Field	Five patch qualities, energetic costs related to daily temperatures.	Birds spend, on average, equal time in patches of all qualities, but PRTs are highly variable. Cannot estimate under- or overuse relative to MVT, but observations cannot be quantitatively correct. (?)
Hansen (1987): Pigeon (<i>Columbia livia</i>)	Lab	Single patch, measuring how long animal stays.	On average, stay too long in all patches, but more so in better patches. (+)
Hansen and Green (1989): Pigeon (<i>C. livia</i>)	Lab	Can switch within a trial between richer and poorer patches.	Stay too long in all patches, but with high variance in PRTs. Trend is exaggerated when overall habitat quality is poorer. (+)
Howell and Hartl (1980, 1982), Schulter (1982): Bat (<i>Leptonycteris sanborni</i>)	Field	20-artificial flower patches, all with equal initial volumes. Departure rules estimated relative to patterns observed.	On average, stayed too long. (+)
Hubbard and Cook (1978): Parasitoid wasp (<i>Nemeritis canescens</i>)	Lab	Measured departure time from patch. Variable densities of hosts across patches.	Excessive use of less profitable patch which declines with experience. (+)
Kacelnik and Todd (1992): Pigeon (<i>C. livia</i>)	Lab	Identical patches across trials, but with travel times having different variances.	Patch residence times respond to short-term variation in travel time (i.e., birds affected by last travel time experienced) rather than the mean travel time as predicted by MVT. (?)
Kamil et al. (1988): Bluejay (<i>Cyanocitta cristata</i>)	Lab	Patches are either empty or contain one prey item. PRTs measured for the empty patch.	Stay longer than predicted in empty patch if rate-maximizing. (+)
Kamil et al. (1993): Bluejay (<i>C. cristata</i>)	Lab	Same as above, except travel times varied.	Stay too long in empty patches and travel time has an effect when it should not. Prefeeding increases overstay (i.e., birds not underestimating environment). (+)
Kotler et al. (1994): Ibex (<i>Capra ibex</i>)	Field	Three patch qualities, but only one type presented per day.	GUD correlates with initial patch density, contrary to MVT predictions, but cannot estimate under- or overuse relative to MVT. (?)
Lima (1984): Downy woodpecker (<i>Picoides pubescens</i>)	Field	Pairs of patches presented, one empty and one with variable amount of prey. Predicted PRTs in empty patch.	Birds, on average, sampled too many holes on empty patches. Effect more pronounced when overall habitat is richer. (+)
Lima (1985): Starling (<i>S. vulgaris</i>)	Aviary	Pairs of patches presented, one empty and one with variable amount of prey. Predicted PRTs in empty patch.	Highly variable PRTs with both over and understaying. On average, birds stayed too long. (+)

Table 1, continued

Study: Species	Location	Experimental design	Results
Mellgren (1982): Rat (<i>Rattus norvegicus</i>)	Arena	Variable densities of food in patches.	Rats visit all patches, which results in an overuse of bad patches and underuse of good patches. (\pm)
Munger (1984): Horned lizard (<i>Phrynosoma cornutum</i> , <i>P. modestum</i>)	Field	Patches are ant colonies and variable in quality.	Large variance in PRTs across individuals, with a mean close to the MVT prediction. On average, animals stayed slightly too long. (+)
Podolsky and Price (1990): Kangaroo rat (<i>Dipodomys deserti</i>)	Field and lab	Large and small seed patches of varying densities presented together.	GUD equal across patches in field, but contrary to the MVT, correlated with initial densities in the lab. No estimate to compare with MVT. (?)
Roitberg and Prokopy (1982): Roitberg (1990): Fruit fly (<i>Rhagoletis pomonella</i>)	Large flight cage	Hawthorn trees with set numbers of fruit, but different distances apart across trials.	Variation in individual fly behavior, with some consistently staying too long in trees (up to 25 \times longer than predicted) and others leaving too early. Staying too long is more common. (+)
Todd and Kacelnik (1993): Pigeon (<i>C. livia</i>)	Lab	Two patches with different mean travel times.	High variability in PRTs, but on average birds stay too long. No reduction in PRT variance with experience. (+)
Tome (1988): Ruddy duck (<i>Oxyura jamaicensis</i>)	Pool	Either single or two patch densities per trial.	Close to MVT prediction. Misses usually from staying too long. (+)
van Alphen and Gallis (1983): Parasitoid wasp (<i>Asorbara tabida</i>)	Lab	Variable number of hosts across trials, but single density in patch within a trial.	Concludes too much time spent in low density patches, but quantitative basis for prediction unclear. (+)
Ydenberg (1984): Great tit (<i>P. major</i>)	Lab	Patches of high or low quality and bird decides when to leave to go to next patch.	On average, birds leave rich patches too quickly and poor patches too slowly. (\pm)
Reproduction			
Best and Bierzychudek (1982): Bumblebee (<i>Bombus flavifrons</i>)	Field	Natural patches of flowers.	Number of flowers visited not different from MVT predictions, although prediction is a range and individual variance is high. (0)
Hodges and Wolf (1981): Bumblebee (<i>B. appositus</i>)	Field	Individual flowers with variable nectar levels.	Queen bees left patches slightly too fast although quantitative difference is not significantly different from MVT. (-)
Kacelnik (1984): Starling (<i>S. vulgaris</i>)	Field	Single patch delivering mealworms at a declining rate.	Large variability in PRTs. Behavior best predicted by birds maximizing energy for chick growth. Birds stayed too long more often than left too early relative to MVT. (+)
Pyke (1978): Hummingbird (<i>Selasphorus rufa</i> , <i>S. platycercus</i>)	Field	Artificial inflorescences in patches with identical nectar contents.	Close to MVT prediction, with some staying longer than predicted, others shorter than predicted. (0)
Mating			
Grether et al. (1992): Gibbons (<i>Hyllobates lar</i> , <i>H. syndactylus</i>)	Field	Fruit trees variable in time and space.	Contrary to MVT predictions, entry and exit foraging rates of patches are correlated, but cannot estimate under- or overuse of patches. Pairs may be patrolling territories. (?)
Parker (1978): Dung fly (<i>Scatophaga stercoraria</i>)	Field	Patch = female, measured length of time spent in copulation.	Males understay in copulation by 14%, but no range of values was given. (-)

“Survival” refers to studies in which the forager is most likely maximizing its survival or a parasitoid that is maximizing its rate of host encounters. “Reproduction” refers to studies where the foragers are likely to have dependent offspring. “Mating” refers to studies where the forager appears to be maximizing encounters with mates or territorial intruders. Experimental location varied in degree of artificiality ranging from free-foraging natural populations (Field), to captive animals in simulated field conditions in aviaries and ponds, to operant-trained animals responding to lights and bar presses (Lab). The results are categorized as consistent with MVT quantitative predictions (0); having foragers stay too long (+); having foragers leave too early (-); or staying too long and leaving too early occurring about equally (\pm). In some studies, the results could not be consistent with quantitative MVT predictions, but the direction of the error could not be determined (?). In the majority of studies, a range of behavior was observed with foragers both over and understaying, but the study was categorized as best as possible in relation to the authors’ conclusions about the general trend in quantitative errors. No effort was made to check the accuracy of the assumptions and calculations presented in the studies.

Namara, 1990). Consequences of such trade-offs have been predicted to affect: (1) the amount of fat foragers were willing to accumulate (Bednekoff and Houston, 1994; Clark and Ekman, 1995; Houston and McNamara, 1993; Houston et al., 1997; Lima, 1986; McNamara and Houston, 1990); (2) activity regimes over a day (Clark, 1994; Houston et al., 1993; McNamara et al., 1994); (3) reproductive and mating strategies (Houston and McNamara, 1986; McNamara and Houston, 1997) and (4) population-level mortality rates (Houston and McNamara, 1993; McNamara and Houston, 1987, 1990).

Most of the above examinations of predation risk and foraging gain have numerically solved for optimal behavior. A different analytical approach in combining foraging gain with avoiding predation risk yields the minimize μ/g rule (Werner et al., 1983). Over a given time period, foragers maximize their survival by choosing the patch that has the smallest ratio of expected predation rate (μ) to growth rate (g), subject to the constraints that g is positive and there is no opportunity for reproduction. Although the minimize μ/g rule does not predict optimal behavior under conditions of strong seasonal effects or discrete time horizons (Ludwig and Rowe, 1990), patch choice decisions in juvenile fish have been accurately predicted in several species (Gilliam and Fraser, 1987; Werner et al., 1983). However, the extent to which the qualitative and quantitative predictions of the MVT and minimize μ/g rules differ has not been rigorously examined.

A second aspect of biological realism lacking in the MVT is that all animals are not the same. Foragers differ in their hunger states, energy reserves, susceptibility to predators, and parental demands. Environments can also vary over time in their harshness, stability, or predictability, so that the animal's expectation of overall patch quality may be continually in flux. Although for any animal facing any given set of circumstances, a unique MVT prediction can be derived, in practice the model has been applied only to the average animal in relation to the average state of the environment (Stephens and Krebs, 1986). When a forager's fitness depends on more than the food it collects, state-dependent behavior may again be a better strategy than rate maximization (Houston, 1990; McNamara et al., 1987).

Despite the tacit consensus that natural foraging situations are much more complex than net rate of energy-intake maximization, qualitative predictions that follow from the MVT are still often made and tested (e.g., the studies in Table 1). Some of these include: (1) better food patches are used more than poorer patches; (2) giving up densities are equalized across foraged patches, with the corollary that unequal GUDs imply particular cognitive processes or predation risk differences in the patches; and (3) increased patch residence time and lower GUDs with both increased travel costs or decreased overall prey density. However, few theoretical extensions of foraging models have directly compared the expected fitness of foraging as predicted by the MVT versus the more complex and realistic state-dependent models. If foraging according to the MVT performs poorly, it can be said to have a high canonical cost and it would be predicted that significant selection would favor behavior different from pure net-rate maximization (McNamara and Houston, 1986). With high canonical costs, it is possible that some of the qualitative predictions of the MVT will also not hold.

In this article, I will derive sets of optimal behaviors for a foraging animal that is faced with simultaneous problems of survival (i.e., gaining food and avoiding predators) and provisioning young or finding mates. I will compare the relative fitness of hypothetical foragers that use either state-dependent behavior (SDB), a strategy predicted by the MVT, or a strategy predicted by the minimize μ/g rule. The goal is to identify sets of conditions under which the MVT or the minimize μ/g

rule either approximate optimal behavior or do not have high canonical costs. Additionally, if the quantitative predictions significantly diverge, I will test if the qualitative predictions of the MVT are also inconsistent with more complex behavior.

Models of patch choice

My model uses Stochastic Dynamic Programming (as described in Clark and Mangel, 2000; Mangel and Clark, 1988) to predict the optimal set of strategies for a foraging animal under a wide variety of conditions and assumptions. The elements of the baseline conditions are as follows.

Food patches

All food patches are assumed to have 20 possible hiding places (slots) for prey items. A forager staying in a patch randomly hunts in one slot per time period. Foragers do not systematically search through the patch, so revisits of empty slots are possible. The patches are either rich (initially 12 prey items scattered in the 20 slots); medium (eight prey items); and poor (four prey items). Rich, medium and poor patches occur at equal frequency. Once in the patch, the forager is assumed to be able to recognize and track its overall quality, but not which slots contain food. If a forager encounters a prey item during time t , the number of prey in the patch at time $t + 1$ is decreased by one. Patches do not replenish during a forager's visit and overall habitat quality is stable within a simulation. Foragers traveling between patches encounter the three types randomly and have to spend at least one time period in each encountered patch (i.e., they cannot recognize a poor patch before entering and thus avoid it). This can be thought of as a sampling constraint. There is only one prey type and it contains 5 units of energy. The forager expends 1 unit of energy per time period as a basal metabolic rate (BMR), independent of what it is doing.

Predation risk

This situation is modeled as if a sit-and-wait predator is present in only some of the patches and infrequently moves between them. Therefore the longer a forager is in a patch without encountering a predator, the more likely it is that the patch has no hidden predator. This decline in probability of encountering a predator with patch residence time is set as an exponential function, so that: $p_t = ae^{-b(t-1)}$, where $a = 0.1$ and $b = 0.2$. The minimum predation risk is set as p_t at $t = 30$, so that patches never become totally safe. Any encounter with a predator results in death for the forager.

Traveling between patches

Travel between patches occurs instantaneously, in that the forager does not spend a given number of time steps in transit. Travel costs are therefore incorporated as added energetic demands on top of BMR. Because fitness results directly from net foraging intake, when the model reaches stationarity (see below) traveling-cost effects are identical if considered either as an extra energy expenditure rather than several time steps in which the animals reserves decline due to not foraging. However, it is computationally much easier to have a single cost rather than simultaneously considering the effects of decisions over multiple time steps. Travel has an added predation risk of a 0.05 probability of dying while moving between patches.

State variable

The forager's energy resource (S) is the state variable, from which its fitness will be determined. S can have integer values

from 0 to a maximum of 50. If $S = 0$ the individual has starved and is dead.

Fitness functions

The model finds the set of state-dependent behaviors that maximize fitness under three different assumptions. The first function maximizes the forager's long-term probability of survival. The terminal fitness function is positive and equal for all energy states greater than zero (i.e., there is no benefit for surviving at a larger size). There are no mating or reproductive opportunities. These "Survival" conditions approximate the classic problem of a "bird in winter," whose only goal is to survive (e.g., Lima, 1986; McNamara and Houston, 1990; McNamara et al., 1994). Maximizing fitness is thus a matter of avoiding predators and starvation. If there is no predation risk then the optimal solution approximates the maximization of net intake rates. An analogous situation described by this model would be for a parasitoid that lays eggs on individual hosts, so that instead of maximizing caloric intake rates, the animal should maximize the number of hosts encountered over its lifetime.

The second fitness function, "Reproduction," assumes a parent caring for offspring, where fitness is maximized by collecting the most food over a lifetime to invest in offspring. Thus, the animal must avoid starvation and predation (as in the Survival model), and provision offspring. The terminal fitness function is zero for all final states in this model because animals can accrue fitness through reproduction at every time step rather than reproducing after a set period of foraging. In constructing the set of optimal behaviors, a successful foraging animal must decide between eating the prey itself or provisioning young. Once a prey item is obtained, the eat/feed decision is maximized for lifetime reproductive output identically for the SDB, MVT, and μ/g strategies. Therefore, the three strategies differ only in regards to patch use patterns and are independent of allocation strategy to self versus offspring. The Reproduction conditions are also applicable to parasitoids that both feed and lay eggs on the same host. Such a parasitoid also faces a similar trade off in that the more it eats (and improves its condition), the less there is for its offspring.

The third fitness function, "Mating," assumes an animal that is searching a patch for both prey and mating opportunities. Each patch contains four possible mates in the 20 slots (i.e., rich prey patches do not have more potential mates). The probability of successfully mating, if a potential mate is encountered, is a linear function of size so that large animals are more likely to be successful than are small animals. Thus under these conditions, fitness accrues as a function of mate encounter rate, foraging success, and predator avoidance. As with the Reproduction function, fitness accrues at each time step rather than at the end through a terminal fitness function. The Mating conditions are also applicable to territorial animals that must patrol for intruders. Successful guarding of territory boundaries is likely to be a function of both the territory holder's physical state and search strategy.

Running the simulations

In all cases, the models were iterated backwards for 250 time steps. An individual in a patch has two options: it can continue to forage in that patch, or it can travel on to the next patch. On the last day of the model ($t = 250$), the stay/go decisions are numerically solved for every combination of the forager's energy state ($1 \leq S \leq 50$), possible number of food items still in the patch (0 to a maximum of 12), and the level of risk (from $t = 1$ to 30) in the patch. The optimal decision is the one which gives the highest expected fitness and it is recorded in an optimal decision matrix. The process is repeated step-

wise for $t = 249$, which uses the t_{250} decision matrix as its fitness function, and then for $t = 248$, and so on.

The optimal decision matrix at t_1 has reached stationarity, where patch residence decisions are affected only by processes occurring within the time step and are no longer affected by the initial terminal fitness function at $t = 250$. Therefore, the optimal behavior for any given set of states and options does not change from one time step to the next (Clark and Mangel, 2000; Mangel and Clark, 1988). Given this fact, I could use t_1 matrices to simulate the equilibrium behavior and success of hypothetical populations of foragers. When simulating behavior at stationarity, the results are independent of the assumed terminal fitness function.

In the simulations I started 20,000 foragers, with S drawn randomly from values between 10 and 40 and having just entered a randomly-determined new patch ($t = 1$). Each forager stays or leaves patches depending on the rule they are following (see below). Foraging success, patch type encounters and predator encounters were stochastically drawn from the expected probability distributions. For each individual, the simulation ran until it starved or was killed by a predator. There was no upper limit to the number of patches potentially encountered. Across the 20,000 simulations I calculated:

- (1) Mean fitness in the assumed currency
- (2) The mean and distribution of patch residence times in the three patch types
- (3) The mean giving-up densities at which foragers chose to leave patches for each patch-entry state.

For comparing the overall mean GUDs of the different patch types, I simulated behavior from the decision matrices, but without predation so that foragers would not die. I started 1000 foragers at every possible state (from one to 50) in each patch type and calculated the mean GUD. In calculating the equilibrium energy reserves, I started 1000 foragers at randomly drawn states between 10 and 40, in randomly-determined patches and let them forage for 250 time steps (again with no predation to assure survival). Mean equilibrium energy state was defined as the average energy reserves over the last 50 days.

For contrast to state-dependent behavior, I repeated the simulations for foragers behaving as predicted by either the MVT (i.e., maximizing the long-term net rate of energy intake in the environment), or the minimize μ/g rule where a forager leaves a patch when the patch's ratio exceeds the expectation averaged across randomly encountered new patches.

Other models of patch choice

Two previous models also examined how patch choice might differ from MVT predictions when there are trade-offs between foraging gain and predation risk or other activities. Methodologically, however, there are significant differences between these models and the one presented here. First, Brown (1988) considered trade-offs in terms of energy (e.g., how much foraging success is an animal willing to give up to be safer?). Thus, the optimal predicted harvest rate at which an animal quits a patch (H) would be the sum of the energetic cost of foraging (C), energetic equivalent for predation risk (P), and the energetic equivalent of missed opportunity costs (MOC) for personal maintenance, mating opportunities, or finding alternative food sources.

If the values of P and MOC are known or biologically reasonable functions that can be estimated, then analytical solutions give the optimal patch exploitation pattern. In practice, however, quantitative predictions from the $H = C + P + MOC$ rule may be difficult to obtain (Brown, 1992). Nevertheless, by holding all variables except one constant, the model does predict qualitative shifts in patch use patterns. Tests of the model in kangaroo rats (Brown, 1988) and fox squirrels (Brown et al.,

Table 2
Sets of simulation conditions

Simulation condition	Travel cost	Travel risk	Maximum predation risk			Decline in risk with PRT
			Rich patch	Medium patch	Poor patch	
Baseline*	1	0.05	0.1	0.1	0.1	rapid
MVT conditions*	1	0	0.05	0.05	0.05	none
Low overall risk	1	0.005	0.01	0.01	0.01	rapid
Travel effects						
No travel cost	0	0.05	0.1	0.1	0.1	rapid
High travel cost	4	0.05	0.1	0.1	0.1	rapid
No travel risk*	1	0	0.1	0.1	0.1	rapid
Patch effects						
80% rich patches	1	0.05	0.1	0.1	0.1	rapid
80% poor patches	1	0.05	0.1	0.1	0.1	rapid
Constant risk in patch	1	0.05	0.05	0.05	0.05	none
High risk	1	0.05	0.1	0.1	0.1	slow
Risk trade-off	1	0.05	0.1	0.05	0.025	rapid
Constant risk + trade-off	1	0.05	0.1	0.05	0.025	none

MVT conditions are sets of values most similar to the assumptions of the Marginal Value Theorem.

* These conditions also simulated with a refuge patch (no food and no risk) for the Survival scenario.

1992) found that, as predicted, patch use went down with increased predation risk and missed opportunity costs. Neither result would be predicted by the MVT because of its insensitivity to factors other than the net rate of food intake.

Brown's model, however, is based on the assumptions of the MVT. If predation risk and missed opportunities are absent or are equal across patches then both the quantitative and qualitative predictions are identical to MVT. The model does not predict behavior in currencies of fitness besides energy gain. Instead, it assumes the animal will "pay" for gaining safety or non-foraging opportunities by sacrificing energy intake rate. Although optimal behavior can be observed and measured in this context, a priori predictions about quantitative patterns of patch use are difficult to make. Therefore, the SDB model presented here is a numerical method of analyzing optimal behavior conceptualized in the Brown model under conditions where P and MOC may or may not vary across patches.

Newman (1991) used an SDB model to predict foraging behavior under predation hazard and to see how similar the predicted behavior might appear to an MVT model. The techniques employed by Newman are similar to those presented here, but there are substantial differences in the assumptions and goals of the models. Major differences in the Newman model are: (1) only two patches are available in any simulation, a refuge and a foraging patch; (2) predation risk does not change within patches and there are no predation costs for travelling; (3) behavior is modelled to the end of set time period, so the terminal fitness function has an effect; and (4) only survival is used as a fitness currency. One model should not be thought of as being better than the other, as they are geared towards different problems. Newman's model predicts foraging behavior over 1 day, while the one presented here is designed more towards identifying longer term patterns.

Sensitivity analyses

Food patches

I examined the effects on the predicted behaviors of overall habitat quality by changing the probabilities of encountering various patch types (Table 2). In a good habitat, rich patches occurred 80% of the time, medium patches and poor patches

each 10% of the time. In a bad habitat there are: 80% poor, 10% medium, and 10% rich patches.

Predation risk

Six quantitative and qualitative changes in the predation risk functions were examined.

1. Low predation risk, where risk in the patch and traveling were each reduced by a factor of 10.

2. High risk, where risk in a patch declined inversely to the baseline exponential function resulting in an initial slow decline in risk with patch residence time.

3. Constant risk per any time period across all patches, with $a = 0.05$ and $b = 0$. This is analogous to the predator also being an active forager moving frequently between patches.

4. A predation-risk/foraging-gain trade-off, where: $a = 0.1$, 0.05 or 0.025 for rich, medium and poor patches, respectively. This simulates a situation where a forager's predators and prey are most likely to be found in the same place.

5. Constant predation risk ($b = 0$) with $a = 0.1$, 0.05 or 0.025 for rich, medium, and poor patches, respectively.

6. No predation risk in traveling between patches.

Traveling between patches

Three quantitative changes to traveling were examined. First, travel costs were set to zero, so that it cost the forager no extra energy above BMR to switch patches. Second, travel costs were set high ($= 4$ units), so that travel + BMR would cost one captured prey item. Note that this would be equivalent in time to where foragers can instantly switch patches or have to take four time steps to move.

Marginal value theory conditions

As a reference point for all other simulations, all parameters were set to most closely resemble the basic assumptions of the MVT. These are: (1) a constant per time predation risk of 0.05 so that neither patch choice or residence times have effects on mortality from predation; (2) no added predation risk for traveling; and (3) a constant travel cost of one unit plus BMR. Under such conditions, the state-dependent solution should be very similar if not identical to the solution from the MVT.

Table 3

Percentage fitness for foraging as predicted by the Marginal Value Theorem (MVT) or μ/g rules relative to the SDB strategy, under scenarios where survival, reproduction or mating opportunities are maximized

Simulation condition	Survival		Reproduction		Mating	
	MVT	μ/g	MVT	μ/g	MVT	μ/g
Baseline	21.27	32.18	77.97	86.72	45.00	60.36
MVT conditions	98.19	98.09	98.81	98.58	91.24	89.75
Low overall risk	75.03	86.37	79.16	78.78	97.14	89.40
Travel effects						
No travel cost	17.68	31.18	63.87	85.95	40.43	59.93
High travel cost	41.39	36.04	71.25	69.15	68.18	54.93
No travel risk	23.62	35.36	81.61	90.66	50.86	65.96
Patch effects						
80% Rich patches	16.63	28.69	76.49	86.16	42.86	62.73
80% Poor patches	42.38	39.68	76.03	70.48	64.60	56.72
Constant risk in patch	77.92	79.77	96.10	96.76	84.36	86.33
High risk	72.69	74.33	96.61	95.87	89.38	86.70
Risk trade-off	18.63	28.16	69.34	75.00	35.04	45.33
Constant risk + trade-off	41.44	50.81	68.74	75.18	53.73	67.13

RESULTS

There are four main outcomes from the simulations:

1. Behaving as predicted by the MVT or the μ/g rule often substantially reduces survival, mating opportunities, or offspring production.

2. Predation risk strongly influences patch use patterns if foragers can affect the level of risk by their patch residence times.

3. Qualitative predictions from the MVT concerning patch depletion patterns, GUDs, and the effects of travel costs do not often result from state-dependent behavior.

4. Mass regulation occurs in foragers (i.e., maintaining body mass below an obtainable maximum). This regulation results from indirect rather than direct costs of predation risk. Fatter birds were never assumed to be directly more at risk because of their weight. Rather, body mass is regulated through decreasing dangerous foraging activity.

Fitness consequences

The behaviors predicted by the SDB model always have higher fitness than behaviors predicted by the MVT and minimize μ/g strategies (Table 3). If the foraging situation approximates the assumptions of the MVT model, then there are small canonical costs to deviating from state-dependent behavior. However, when these assumptions are relaxed, state-dependent behavior does considerably better in increasing survival, mating opportunity and reproductive success. In all cases, the SDB strategies have higher fitness through equal or longer patch residence times in at least one of the three patch types than predicted by the MVT. The fact that the SDB model consistently predicts longer PRTs than the MVT under all scenarios fits with the predominant trend in the quantitative tests of the MVT (Table 1).

Not surprisingly, because the μ/g rule was derived to include both predation risk and foraging gain in patch use, behavior that minimizes μ/g is intermediate in fitness between the MVT and SDB under most simulation conditions of the Survival scenario (Table 3). Minimizing μ/g is generally a better behavioral strategy than net-rate maximization without traveling costs or risks or when risk in the patches is intermediate or constant. It is a poorer strategy whenever μ/g predicts shorter PRTs than does the MVT. However, overall the

difference in success between following a μ/g strategy or a MVT strategy is small. Minimizing μ/g does not approximate state-dependent solutions significantly better than does the MVT.

Predation risk

Predation risk greatly affects foraging patterns when behavior is state-dependent. SDB foraging reduces risk through staying longer in patches and moving less often. SDB also predicts that within-patch risk has greater effects than risk associated with moving between patches, in that GUDs change more from the baseline conditions when the dynamics of risk within patches are altered than when traveling risk is removed. Although the addition of predation risk in these models predicts patch use patterns quite different from the MVT, the canonical cost for non-optimal behavior is not equal across all levels of risk. When risk levels are high or low, the MVT and μ/g rules predict much higher GUDs than the SDB model, but all patch use patterns have relatively similar fitnesses (Table 3).

In the above simulations there were no explicit refuge patches where the animal cannot forage but is also absolutely safe from predators. Although foragers make patches refuge-like with long stays, it may be that such behavior would not be predicted with a true refuge possibility. Thus, for three sets of conditions in the Survival scenario (Table 2), I added a refuge as third option for a foraging animal (i.e., stay in current foraging patch, go to another foraging patch, or use a refuge). Under baseline and the no predation risk while traveling conditions, there is a trivial effect of the refuge. Overall, the animals spend only 0.5 and 4.9% of their time in the refuges. There is no effect on patch use patterns during time spent foraging. Under MVT conditions, however, animals spend 47.9% of their time in the refuge. If predation risk is reduced from 0.05 to 0.01 per time step, there is almost no effect on the use of the refuge with MVT conditions (animals spend 49.3% of their time in the refuge). This latter result further reinforces the finding that changes in risk with time spent in patches are more important than the absolute level of risk within a patch.

Qualitative predictions

State-dependent foraging behavior does not predict the same general results as the MVT. First, giving-up densities are not

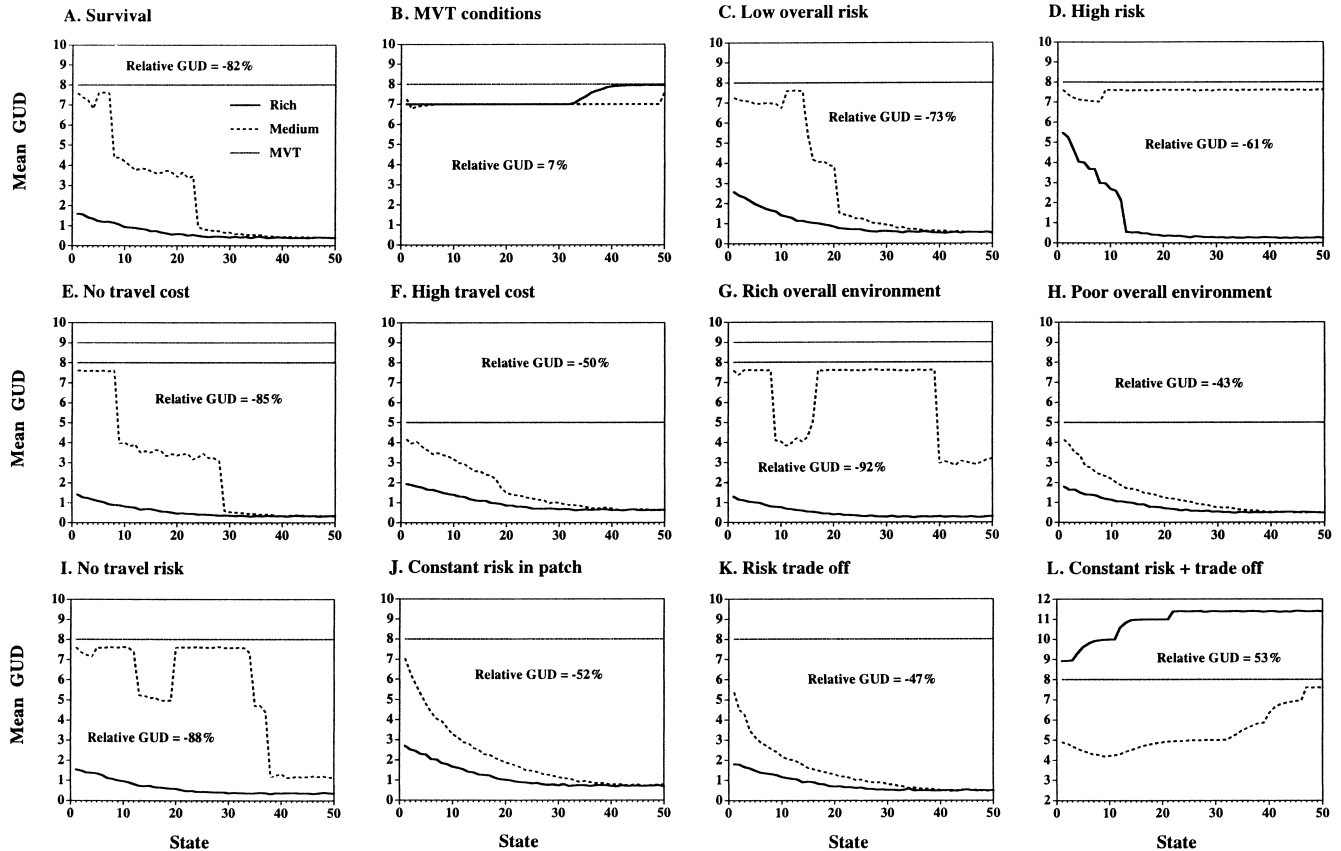


Figure 1

Mean giving-up densities in rich and medium patch types under the SDB and MVT models for all possible states under the various sets of conditions (see Table 2). In graphs where there are two dotted lines for MVT predictions, the higher value is for the predicted GUD in the rich patch, the lower for the medium patch. The fitness currency is survival for the longest period of time. Mean GUD in the rich patch is given relative to mean GUD in the medium patch, calculated from the simulations of lifetime fitness of 20,000 foragers [relative GUD = $(\text{GUD}_{\text{rich}} - \text{GUD}_{\text{medium}}) / \text{GUD}_{\text{rich}}$]. All simulations begin with a rich patch having 33% more prey than a medium patch.

equalized across the utilized patches. In the simulations, the MVT predicted differences in GUD's between the rich and medium patches in the range from 0–16% of remaining prey density. However, state-dependent behavior produced larger mean differences in the majority of simulations (Figures 1–3). Furthermore, the expected GUDs for both the rich and medium patches were strongly affected by energy state of the forager and the effects of state differed across simulations. Thus, increasing a forager's state can either increase or decrease the difference in expected GUDs as well as switch which patch would be expected to be the more heavily exploited. When GUDs are equalized across patches, it most often results from foragers staying much longer than predicted by the MVT in rich and medium patches and reducing both to very low prey densities. This effect is also state-dependent with generally lower GUDs in all patches when foragers have high energy reserves.

Second, GUDs are affected by environmental quality and foraging costs, but the effects are not always in the direction predicted by the MVT. Consistent with the MVT, increasing travel costs decreased GUDs where increasing overall environmental quality increased GUDs in medium quality patches (panels E versus F and H versus G in Figures 1–3). However contrary to MVT predictions, GUDs always slightly increased in good patches with increased travel costs and decreased with overall environmental quality in both the Survival and Mating scenarios.

Mass regulation

By the choice of when to leave patches (and if to feed offspring), the forager directly controls its energy reserves, which can be considered as the animal's body size or fat reserves. Energy held in reserve is strongly affected by which fitness currency is assumed. Under the baseline conditions, the equilibrium energy states (out of a maximum of 50) for the Survival, Reproduction, and Mating scenarios are: 38.2, 8.3, and 41.5, respectively. In the Reproductive scenario energy is invested in offspring, while in the Mating scenario reproductive success is a positive function of size. These differences decrease and increase the equilibrium energy state relative to the Survival scenario. Under all three scenarios, however, the equilibrium energy state is 15–25% lower than the equilibrium reached by animals foraging according to the MVT. For the Survival scenario, I calculated the equilibrium energy states for all sets of the conditions in Table 2. Only if conditions approximate the assumptions of the MVT, is the maximum attainable energy state also the equilibrium energy state. For all other permutations, the equilibrium energy states range from a low of 66% (in the Constant risk + risk trade-off situation) to a maximum of 84% (in the Low overall risk situation) of the equilibrium predicted by the MVT.

These results show that mass regulation below maximum levels can occur without direct mass specific costs in increased predation risk. This is a contested point. McNamara (1990) found no mass regulation without mass specific costs and

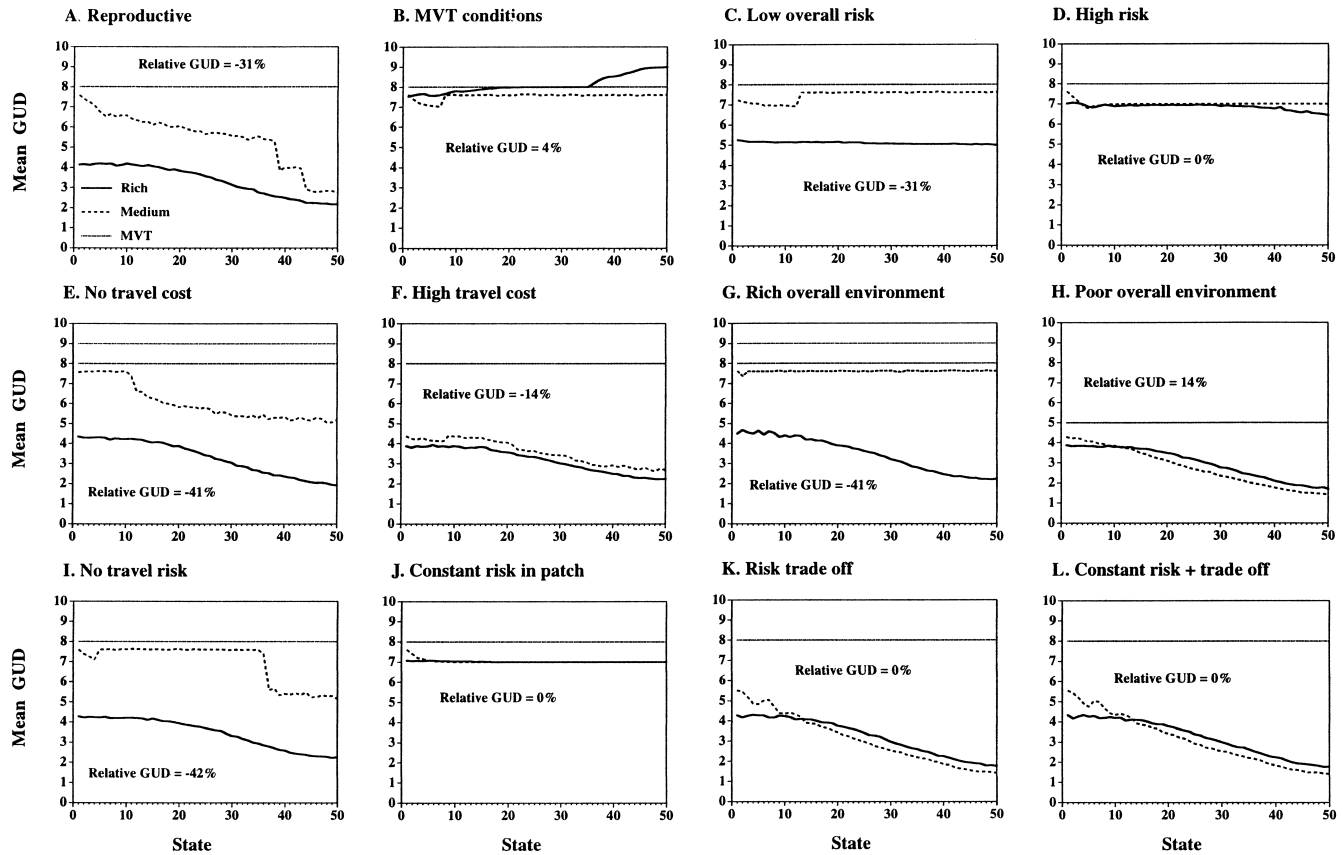


Figure 2 Mean giving-up densities in rich and medium patch types under the SDB and MVT models for all possible states under the various sets of conditions. Details same as Figure 1, except that the fitness currency is investment of resources in reproduction.

Houston et al. (1997) pointed out three errors in formulating SDB models that can produce results that mimic the appearance of mass regulation. These include: (1) numerical imprecision, in that after many iterations, differences in the outcomes between optimal and non-optimal behaviors can be rounded off to the same value, (2) choice of inappropriate time scales such that behavioral or physiological processes are not correctly modeled, and (3) sensitivity to the maximum energy state that can be achieved by a forager. The first two errors were suggested as explaining Clark’s (1994) results of mass-regulation through indirect costs. Error 1 may be present because foraging and resting have been rounded off to the same fitness value. Error 2 had birds with maximum energy reserves being able to survive for an unrealistic 267 days without foraging. Since the model ran for only 80 days, individuals with higher reserves never needed to forage. The first error was avoided in the Survival scenario by using double rather than single precision (see Houston et al., 1997). The other two scenarios (Reproduction and Mating) are immune to this problem because fitness is continually accrued at each time step rather than at the end of some time period. The second error is avoided by modelling behavior at a stage where the model is stationary in its patch choice predictions and foragers at the maximum energy state still have a non-zero chance for starving.

The models are, however, sensitive to the upper limit for energy reserves. For example, if maximum state is raised from 50 to 60, then the equilibrium state for the baseline Survival scenario increases from 38 to 46. Nevertheless, I would argue that the results are not simply a numerical artifact, but instead that the sensitivity to the upper limit illustrates an interesting

point. If the models are recast such that the maximum energy state is 10 or 30, the same mass regulation phenomenon emerges. As when $S_{max} = 50$, the equilibrium mass is always approximately 75% of the given maximum energy state (Figure 4). If the simulations are begun with all foragers at S_{max} , their states will converge on the same lower equilibria values. Finally, foragers can be simulated using optimal strategy sets derived from higher maximum energy state models (i.e., Figure 4A; a forager behaves as if it could reach an energy reserve of 70, but its actual maximum energy state is only 10). The equilibria energy states for such strategies also remain considerably below the states reached by foragers using MVT rules, and where they differ from the calculated optimal rule, their fitness is reduced (e.g., the lifespan of foragers behaving as if $S_{max} = 60$, when $S_{max} = 50$ is, on average, 97.2% that of optimal). In summary for the models presented here, the best long term strategy is to keep mass below the maximum attainable by behaving as predicted by the MVT.

As the maximum energy state decreases, the degree of apparent mass regulation decreases as well. When $S_{max} = 10$, the SDB equilibria energy state is 89.8% that of MVT state, while with $S_{max} = 50$, the SDB strategy is 79.7% of the MVT strategy. This suggests that the degree to which an optimally foraging animal exhibits mass regulation is dependent on the scale at which it usually changes its energy state. The finer the scale of this control, the more evident mass regulation should be. Therefore, I ran the Survival scenario again under baseline conditions, but with patches containing one, two, or three prey items of size 20, so that the amount of food per patch type and overall environment is the same, but it come in much bigger pieces. With this set of conditions, the equilib-

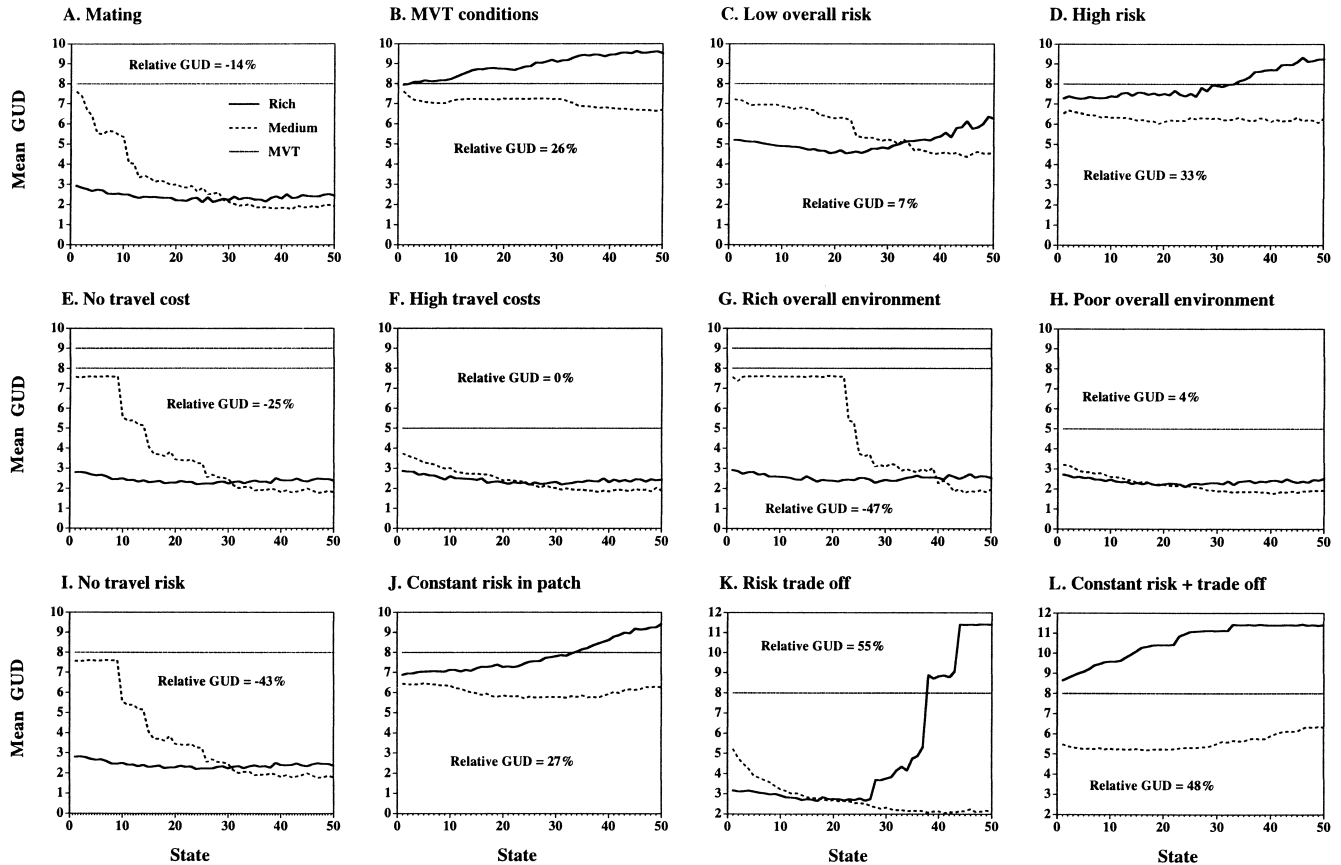


Figure 3 Mean giving-up densities in rich and medium patch types under the SDB and MVT models for all possible states under the various sets of conditions. Details same as Figure 1, except that the fitness currency is maximizing mating opportunities.

rium energy states for SDB and MVT rules were 35.6 and 39.1, respectively. Thus, the SDB strategy equilibrium was 91% that of the MVT when control of energy state was more coarse-grained. This result is consistent with previous models on mass regulation: An increase in environmental variability favors carrying closer to the maximum possible levels of fat (Bednekoff and Houston, 1994; Houston and McNamara, 1993; Lima, 1986).

DISCUSSION

The Marginal Value Theorem predicts patch use patterns based on maximization of long term net energy-intake rates. However, quantitative predictions of the MVT differ from other theoretical models that include avoiding predation (Bednekoff and Houston, 1994; Houston and McNamara, 1993; Houston et al., 1993; Lima, 1986; McNamara, 1990; McNamara and Houston, 1990) or reproductive behavior (Houston and McNamara, 1986; McNamara and Houston, 1997). Experiments with the MVT also show consistent deviations from quantitative predictions (Table 1). Thus, it is not surprising that state-dependent behavior does better than “simpler” behaviors predicted from the MVT or the μ/g rules. What is important, however, are the wide range of conditions that predict poor performance for foragers following those rules. Only under limited conditions are they good “rules of thumb” that approach optimal behavior. Furthermore, qualitative general predictions that follow from the MVT about patch residence times and giving up densities may also often be inconsistent with state-dependent behavior. The results affect five predictions about foraging behavior.

In the SDB model, patch residence times are longer, resulting in significantly lower GUDs than predicted by the MVT. The MVT and state-dependent strategies are more likely to predict similar behavior or to have similar fitness when food is immediately invested in reproduction, predation risk is either very low or high, foragers cannot reduce risk by moving less often between patches, foragers have low energy reserves; or food comes in large pieces. As in the majority of tests of the MVT such factors are not explicitly described, it is difficult to correlate how any of these factors affect the outcome of the tests. For example, a clear need in quantitative tests of foraging models is to examine more situations where animals are either feeding offspring or simultaneously looking for mating opportunities as these type of situations are greatly underrepresented in the existing tests of patch use (Table 1).

Decreased travel costs or an increase in overall environmental quality may result in more frequent moves between poorer patches as predicted by the MVT. However, a forager exhibiting SDB may treat the best patches as predation refuges, moving less often between them than predicted by the MVT (which does not incorporate predation risk).

The likelihood of observing equal giving-up densities across patches depends on how closely the situation corresponds to MVT assumptions. Unequal GUDs are an almost ubiquitous consequence of state-dependent foraging and can result from various departures from MVT assumptions. For example, differences in GUDs are predicted and observed across patches that differ in predation risk (Bouskila, 1995; Brown, 1988; Brown et al., 1992; Kotler, 1997). However, an observation that GUDs differ across two patches does not mean they must dif-

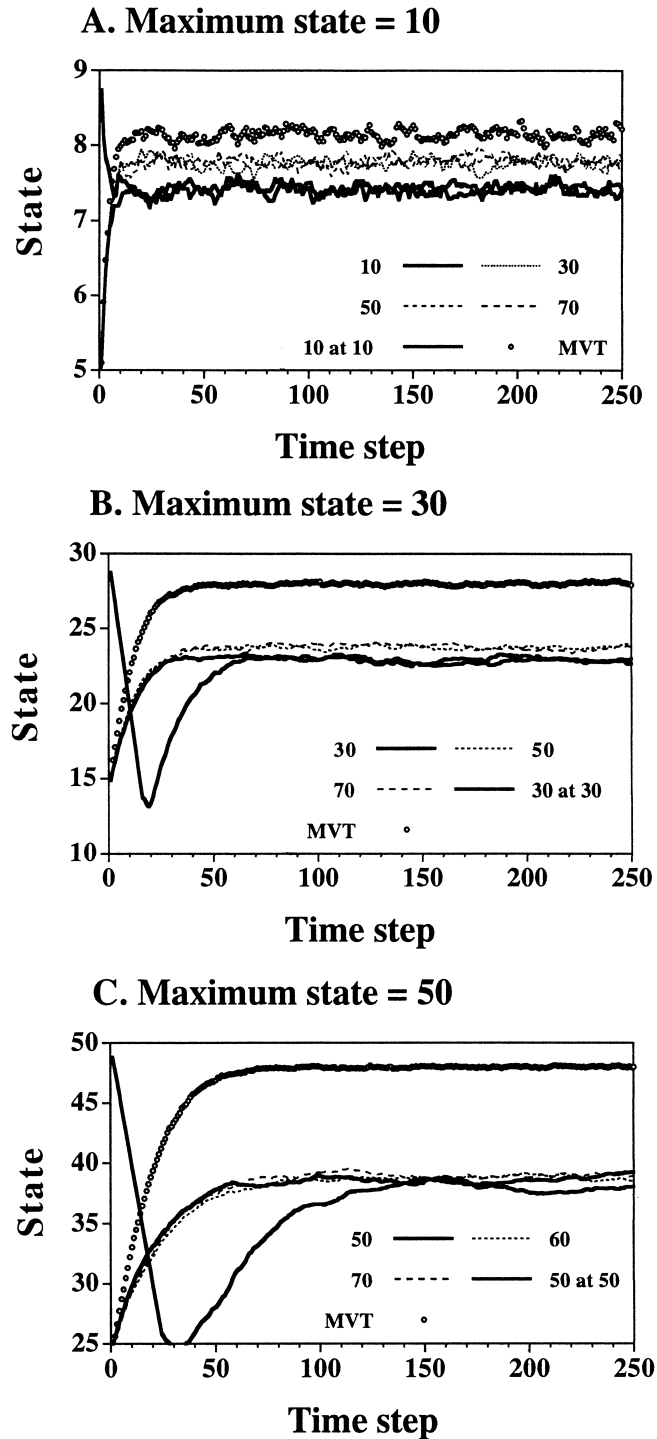


Figure 4
The equilibrated energy reserves for foragers that maximize survival or forage as predicted by the MVT. In (A), the maximum energy reserves = 10 and the state versus time relationships are plotted for the optimal strategy (10), state-dependent strategies that derived from situations where maximum energy reserves range from 30 to 70, and the MVT strategy. Initial energy reserves are randomly assigned with values between 10 and 40, except for where all foragers follow the optimal strategy but begin at the maximum state (e.g., 10 at 10). (B) and (C) are as (A) except the maximum state is 30 or 50, respectively.

fer in predation risk or other non-foraging opportunities. If perceived predation risk declines with time in a patch, unequal GUDs are likely to result without any difference in initial predation risk across the patches. The better patches will simply also function as predation refuges.

Equal GUDs are more likely with foragers that have significant energy reserves, but quantitatively this results from staying in patches far longer than predicted by the MVT and thus reducing them to similar, very low densities. When patches are not reduced to similar GUDs, correlations between initial prey density and final density result. The correlations are negative if the forager overuses the rich patch relatively more than the other patches and positive if vice versa. Positive correlations between initial patch density and the GUD have been proposed to indicate that foragers are Bayesian in their estimation of overall habitat quality (Alonso et al., 1995; Valone, 1991). However, positive correlations are also predicted when conditions are similar to the assumptions of the MVT, when there are trade-offs between risk and food, so that the best food patches are also perceived as the most risky, or when the foragers are simultaneously searching for food, mates, or territory intruders. In all of these situations, animals with higher energy reserves might appear Bayesian in their behavior, without actually being so.

Predation risk strongly affects patch use patterns, but only if there are time-dependent or movement-dependent effects. The overall level of risk for foraging has little effect, if it cannot be decreased by staying longer in patches or moving less often between them. This is complementary to results found by Newman (1991) and Bednekoff and Houston (1994), who also predict no effect of increasing risk per time unit of foraging activity. In total this suggests that patch use may be greatly influenced by how a forager expects to encounter its predators. The response to ambush or sit-and-wait predators may be to stay longer in individual patches, but not reduce the overall time spent foraging. Conversely, the response to actively foraging predators may be rate-maximizing GUDs, but reduced overall foraging and more time spent in refuges. As a hypothetical example, desert rodents may spend more time foraging with lower GUDs per patch if they are avoiding rattlesnakes rather than owls. Predation risk from snakes would be reduced by staying longer in patches, and predation risk from owls would be reduced by hiding in refuges.

Mass regulation below an attainable maximum follows from behavioral patterns that reduce foraging activity in order to reduce encounters with predators (similar results are found in Clark and Ekman, 1995; Lima, 1986; and Newman, 1991). As such, these conclusions are contradictory to those made by Bednekoff and Houston (1994) and Houston et al. (1997) who predict mass regulation only with direct mass-specific costs. The differences between these findings may relate to how the effect of predation risk is interpreted or how maximum attainable weight is defined.

Bednekoff and Houston (1994) found a large effect of mass-dependent risk and almost no effect of increasing per unit exposure risk over four orders of magnitude. However, all their simulations included a mass-specific predation cost, which may have masked the effects of increased exposure risk. Thus, it is appropriate to conclude that variation in mass-dependent costs predicts larger effects than variation in exposure costs, but not that exposure, per se, has no effect. The latter would only be true if the mass of a forager experiencing no risk at all were similar to those experiencing exposure risk. Houston et al. (1997) reject Clark and Ekman's (1995) conclusion about mass regulation from exposure costs based on the sensitivity of the predicted optimal body mass to the upper constraint in maximum body mass. However, the predicted optimum remains consistently proportional to the upper con-

straint (see Houston et al., 1987: Figure 2). Thus, as in the models presented here, Clark and Ekman's predictions may be valid if viewed as a proportion of attainable body mass rather than a specific value. Without comparing Clark and Ekman's results to the expected body mass with no predation risk, it cannot be concluded that mass regulation was truly absent.

Mass regulation without direct cost should not be taken to imply that such mass-specific costs do not exist. There are certainly ample reasons to believe that carrying extra weight imposes metabolic and agility costs on animals (e.g., Witter et al., 1994) and in theoretical considerations such costs have always predicted large behavioral effects (Bednekoff and Houston, 1994; Lima, 1986). However, one cannot infer direct mass-dependent costs if foragers in a Survival-type scenario are simply observed to "not keep reserves at the maximum possible level" (e.g., Houston et al., 1997: 331). This convenient shortcut to the difficult proposition of measuring the survival costs of extra weight in natural situations is not justified.

The Marginal Value Theorem has served as a valuable heuristic tool in behavioral ecology, but there is too large of a disconnection between the modeling and the testing of the foraging process. Models strongly suggest that optimal behavior is not synonymous with net intake-rate maximization, but rarely explicitly examine the degree to which the MVT may fail. Experimenters may realize that the quantitative predictions of the MVT are unlikely to be upheld in the field but continue to assume that the qualitative patterns of the MVT will hold. The goal of this article is to bring these issues into focus.

A state-dependent approach to describing foraging is, by its nature, unlikely to generate broadly applicable predictions about patch use as does the MVT. The model presented here identifies sets of conditions where particular types of behavior may occur, but the testing of these predictions will be case-specific in adapting the model. The experimenter may have to know the nature of predation risk, what is important to the forager besides its food, the general quality of the environment that determines the forager's access to resources, and the likely energy state the tested animal will have. This is not as daunting a task as it may seem and including state-dependent behavior can certainly lead to new insights. An example of this approach is Roitberg's (1990) work with fruit flies (*Rhagoletis pomella*). Female flies lay eggs on fruit hosts and there is considerable variation in search times within trees across females. With an SDB model, Roitberg predicted decisions as a function of: (1) current and average patch qualities, (2) patch densities, (3) time of day, and (4) egg load. He also varied fly behavior in terms of whether flies used a rule of thumb that over or underestimated their rates of locating patches ("optimists" versus "pessimists"). Overall, both strategies performed nearly as well as the optimal behavior, when the patch estimate errors were small or moderate. However, as errors increased in magnitude, pessimists did worse than optimists, which led Roitberg to further predict (and confirm by observation) that the rule of thumb for optimistic behavior is more common in natural fly populations than pessimistic behavior. In summary, state-dependent optimality models create logical constructs against which actual behavior can be matched to test the validity of the assumptions (Nonacs and Dill, 1993). Models like the MVT are a reasonable starting point, but natural complexity has to be incorporated in both the derivations of foraging and patch use predictions and their tests.

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