

# Patch Choice under Predation Hazard

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In this paper we study optimal animal movement in heterogeneous environments consisting of several food patches in which animals trade-off energy gain versus predation risk. We derive a myopic optimization rule describing optimal animal movements by fitness maximization assuming an animal state is described by a single quantity (such as weight, size, or energy reserves). This rule predicts a critical state at which an animal should switch from a more dangerous and more profitable patch to a less dangerous and less profitable patch. Qualitatively, there are two types of behavior: either the animal switches from one patch to another and stays in the new patch for some time before it switches again, or the animal switches between two patches instantaneously. The former case happens if animal state growth is positive in all patches, while the latter case happens if animal state growth is negative in one patch. In particular, this happens if one patch is a refuge. We consider in detail two special cases. The first one assumes a linear animal state growth while the second assumes a saturating animal state growth described by the von Bertalanffy curve. For the first model the proportion of time spent in the more profitable and more risky patch increases with profitability of this patch when state growth is positive in both patches. On contrary, if state growth is negative in the less profitable and safer patch, animals spend proportionally less time in the more profitable and more risky patch as its profitability increases. As a function of the predation risk in the more profitable patch the time spent there proportionally decreases. When animal state growth is described by the saturating curve, time spent in the more risky patch is a hump-shaped curve if state growth is positive in both patches. Our results extend the  $\mu/f$  rule, which predicts that animals should behave in such a way as to minimize mortality risk to resource intake ratio. © 2000 Academic Press

**Key Words:** adaptive behavior; heterogeneous environment; switching; predation risk; ideal free distribution; von Bertalanffy curve.

## 1. INTRODUCTION

Spatial heterogeneity has been known to be an important factor for understanding animal distribution in space, where animals can trade off energy gain versus mortality risk (Werner and Hall, 1974; Werner and Hall, 1979; Sih, 1980; Cerri and Fraser, 1983; Werner *et al.*, 1983; Werner and Gilliam, 1984; Sih *et al.*, 1985; Fraser and Huntingford, 1986; Sih, 1986; Dill, 1987; Fraser and

Gilliam, 1987; Gilliam and Fraser, 1987; Mittelbach and Chesson, 1987; Sih, 1987; Gilliam and Fraser, 1988; Holbrook and Schmitt, 1988; Mangel and Clark, 1988; Pitcher *et al.*, 1988; Lima and Dill, 1990; Ludwig and Rowe, 1990; Werner, 1991; Sih, 1992; Werner and Anholt, 1993; Anholt and Werner, 1995; Diehl and Eklöv, 1995; Eklöv and Persson, 1995; Abrams *et al.*, 1996; Werner, 1996; Cowlshaw, 1997; Sih, 1997). To build a predictive theory which describes animal distribution across space we must understand the effects of

such trade-offs on animal behavior. In behavioral ecology a common currency which is assumed to be maximized is animal fitness, which combines animal survival and reproduction. Models describing animal distribution in heterogeneous environments consisting of two or more habitat patches therefore depend crucially on the choice of the particular form of the fitness function. Animal fitness has two components, (i) animal survival and (ii) animal reproduction, which is usually assumed to be directly related to resource acquisition. Because patches with high standing crop are often dangerous compared with less profitable patches, mortality risk associated with foraging must be accounted for in any reasonable choice of fitness function. Animals that die because of starvation or predation before they can reproduce have zero fitness. Reproductive output measured as the number of offspring is a function of animal state. The main question posed by behavioral models is: What optimal strategy maximizes fitness? Typically, these models are based either on deterministic or on stochastic dynamic programming (Mangel and Clark, 1988; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991, McNamara and Houston, 1992; Houston *et al.*, 1993; Houston and McNamara, 1999). A major difficulty with these models is that they are analytically intractable because they require long-term optimization and therefore predictions are based more often on numerical simulations than on qualitative analysis. This makes functional relations between model parameters and model outcomes difficult to understand.

In this article we consider the case where animals choose their strategy instantaneously and no future insights are assumed. We call such a strategy myopic. First, we formulate a general model which describes animal movement in space (modelled by 2 or  $n$  patches), together with the animal state. Following the approach advocated by Houston and McNamara (1989) and Ludwig and Rowe (1990) (reviewed in Houston and McNamara, 1999) we derive a general rule that specifies optimal animal movement depending on instantaneous position and state. Our model predicts that there exists a switching value of state such that animals whose state is below this critical value are risk-prone (they move to more dangerous but also more profitable areas), while animals with a state above the switching value are risk-averse (they move to safer and less profitable places). This general result does not depend on the particular choice of the fitness function. Our modelling approach allows us to estimate the proportion of times animals stay in each patch. We show two examples for particular fitness functions. The first example considers the case in which both state growth rate and mortality risk are fixed

in each patch. This corresponds to the case in which a patch is not depleted by foraging and/or animals do not reach saturation. For this case Gilliam and Fraser (1987) derived a formula (called the  $\mu/f$  rule) which predicts that animals should move to the patch which minimizes mortality rate per foraging rate. We show that our approach leads to the same formula but in addition, it allows estimation of the time that animals should spend in each patch. The second example considers the case in which animal state follows the von Bertalanffy curve, which corresponds to situation of animal satiation. We compare predictions from these two models with respect to food level and mortality risks in the more profitable but riskier patch. We consider two cases: (i) animal state growth is positive in both patches, and (ii) animal state decreases in the safer patch. In the former case our constant rate model predicts that the proportion of time spent in the more profitable patch increases with patch profitability. In contrast, if state growth is negative in the safer patch, animals spend proportionally less time in the more profitable patch as its profitability increases. If animal growth is saturated, time spent in the more profitable patch is a hump-shaped curve if animal state increases in both patches. If it decreases in the safer patch, the proportion of time spent in either patch follows qualitatively a pattern similar to that for the constant rate model.

## 2. OPTIMAL PATCH CHOICE

We consider an animal in a heterogeneous environment consisting of  $n$  patches. Animal state is described by a state variable  $s$  (such as gut fullness, animal weight, size, or energy reserves) and animal position is described by function  $u_i(t)$ ,  $i = 1, \dots, n$ . The control  $u_i$  is equal to 1 if at time  $t$  the animal is in the patch  $i$  ( $u_j = 0$  for  $j$  different from  $i$ ). Because we assume that animals move between patches infinitely fast we have

$$u_1(t) + \dots + u_n(t) = 1.$$

The instantaneous rate of change of the animal state in patch  $i$  is  $S_i(s)$  (which we call patch profitability) and the model for time evolution of the animal state is given by the differential equation

$$\frac{ds}{dt} = S_1(s) u_1(t) + \dots + S_n(s) u_n(t), \quad s(0) = s_0, \quad (1)$$

where  $s_0$  denotes the initial state of the animal.

Let  $\mu_i(s)$  be the instantaneous mortality risk of an animal in state  $s$  in patch  $i$ . Ignoring terms of higher order, the probability that an animal survives from time  $t$  until time  $t + \Delta$  is

$$1 - \Delta \sum_{i=1}^n \mu_i(s(t)) u_i(t).$$

Let  $F(s)$  be the reproductive value of an animal which is in state  $s$ . We assume that  $F$  is a non-negative and increasing function of animal state  $s$ . Then animal fitness at some final time  $T$  is given by the reproductive value  $F(s(T))$  at that time multiplied by the probability of survival to time  $T$  (Houston and McNamara, 1989; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Houston and McNamara, 1999). Myopic optimization assumes that animals maximize their fitness over the time interval  $(t, t + \Delta)$  where  $\Delta$  is small. This gives

$$\left(1 - \Delta \sum_{i=1}^n \mu_i(s(t)) u_i(t)\right) F(s(t + \Delta)) \rightarrow \max.$$

Using a Taylor expansion of  $F(s(t + \Delta))$  and neglecting higher order terms, our maximization problem leads to the selection of a strategy which maximizes

$$\sum_{i=1}^n \left( \frac{dF}{ds}(s) S_i(s) - F(s) \mu_i(s) \right) u_i.$$

Observe that  $\frac{dF}{ds}(s) S_i(s) - F(s) \mu_i(s)$  is the rate of fitness increase in patch  $i$ , so the above formula suggests animals will move to the patch where this rate is maximized.

## 2.1. The Case of Two Patches

If there are only two patches we get the following strategy:

- (a) If  $\frac{dF}{ds}(s)(S_2(s) - S_1(s)) - F(s)(\mu_2(s) - \mu_1(s)) > 0$  then animals prefer the second patch ( $u_1 = 0, u_2 = 1$ ).
- (b) If  $\frac{dF}{ds}(s)(S_2(s) - S_1(s)) - F(s)(\mu_2(s) - \mu_1(s)) < 0$  then animals prefer the first patch ( $u_1 = 1, u_2 = 0$ ).

Let us consider two simple cases. If the risk of predation in both patches is the same ( $\mu_1 = \mu_2$ ) then our criterion suggests that foragers should move to the more profitable patch (because we assume that the reproductive value increases with animal state, i.e.,  $\frac{dF}{ds}(s) > 0$ ). If both patches are equally profitable ( $S_1 = S_2$ ) then foragers should move to the less dangerous patch. This prediction qualitatively agrees with observations although an "all or none" switch is not observed in

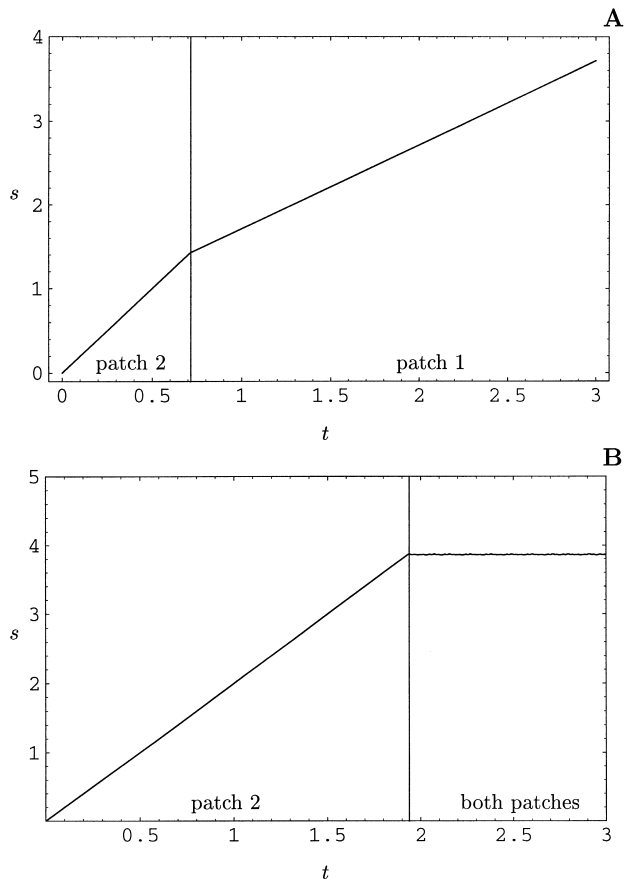
reality (Holbrook and Schmitt, 1988). This is understandable because our model assumes omniscient foragers that react instantaneously.

Let us assume that the equation

$$\frac{dF}{ds}(s)(S_1(s) - S_2(s)) - F(s)(\mu_2(s) - \mu_1(s)) = 0$$

has one solution which we denote by  $s^*$ . Then  $s^*$  is called a switching state, because at this value animals change their habitat. Two types of behavior can occur when an animal state reaches the switching state  $s^*$ . Either the animal state increases in both patches when  $s = s^*$ , i.e.,  $S_1(s^*) > 0$  and  $S_2(s^*) > 0$ , and then the animal switches from one patch to another and stays there forever (Fig. 1A). For example, if  $s$  describes the size of the animal then there will be only one habitat switch along the ontogenetic trajectory. The situation changes qualitatively if the animal state decreases in one patch. This happens, for example, if one patch is a refuge which is safe but with not enough food, so animals which stay there are well protected against predators but cannot survive because of lack of food. Assume that patch one is the refuge; in other words,  $S_1(s) < 0$  and  $\mu_1 = 0$ . This implies that animals with a state lower than  $s^*$  enter the food patch, where their state will increase until it reaches  $s^*$ . At this moment  $S_1(s^*) < 0$  and  $S_2(s^*) > 0$ , which leads to a conflicting situation in which the animal should start to switch instantaneously back and forth between the two patches, which keeps its state constant and equal to  $s^*$  (Fig. 1B). The instantaneous switching along the critical value  $s^*$  is referred to as the switching regime. Naturally, animals are not able to switch between the two patches instantaneously and therefore some oscillations of animal state around the switching value occur. Such behavior could correspond, for example, to a consumer which attacks its prey from a refuge. The instantaneous switching between the refuge and the food habitat keeps the consumer state approximately constant. We are interested in knowing the proportion of time the animal spends in the refuge, because this is a measurable quantity in experiments. Let us assume that the system is in the switching regime so that the initial animal state  $s(0)$  equals  $s^*$  and let us consider a time interval of length  $T$ . Let  $T_1$  denote the time that an animal spends in the refuge and  $T_2$  the time it spends in the other patch. Then, in the switching regime, we have

$$\begin{aligned} s^* &= s^* + \int_0^T S_1(s^*) u_1(t) + S_2(s^*) u_2(t) dt \\ &= s^* + T_1 S_1(s^*) + T_2 S_2(s^*). \end{aligned}$$



**FIG. 1.** Evolution of animal state for the model with linear state growth. Animals with zero initial state move first to the more hazardous but also more profitable patch 2 where their state increases quickly. When their state reaches the switching value  $s^*$  animals switch to the safer patch 1. Figure A describes the case in which state growth is positive in both patches, in B the state decreases in patch 1 (refuge). In this latter case animals use both patches which keeps their state equal to  $s^*$ . Parameters for A:  $r_1 = 1$ ,  $r_2 = 2$ ,  $\mu_1 = 0.3$ ,  $\mu_2 = 1$ . Parameters for B:  $r_1 = -0.5$ ,  $r_2 = 2$ ,  $\mu_1 = 0.3$ ,  $\mu_2 = 1$ .

The proportion of total time of the switching regime that the animal will spend in the refuge is

$$\tau_1 = \frac{S_2(s^*)}{S_2(s^*) - S_1(s^*)} \quad (2)$$

and the proportion of time it will spend in the food patch is

$$\tau_2 = \frac{S_1(s^*)}{S_1(s^*) - S_2(s^*)}. \quad (3)$$

The preceding analysis can be easily extended to  $m$  patches when  $S_i$  and  $\mu_i$  are constant.

### 3. THE CASE WITH CONSTANT RATES

Here we consider  $m$  patches and we assume that neither animal state growth nor mortality risk depends on animal state; i.e.,  $S_i = r_i$  and  $\mu_i$  are constant. These assumptions allow us to predict explicitly which patch is optimal. First, we eliminate those patches that cannot be optimal. If  $r_i \geq r_j$  and  $\mu_j \geq \mu_i$  then

$$\frac{dF}{ds}(s) r_i - F(s) \mu_i \geq \frac{dF}{ds}(s) r_j - F(s) \mu_j,$$

which means that patch  $j$  is always worse than patch  $i$  and thus cannot be optimal. We eliminate such patches and also those which are not on the lower part of the boundary of the convex hull of points  $[r_j, \mu_j]$  (see also Gilliam and Fraser, 1987; McNamara and Houston, 1994; Houston and McNamara, 1999). We order the remaining patches so that

$$r_1 < \dots < r_n \quad (4)$$

and we define numbers

$$p_i = \frac{\mu_{i+1} - \mu_i}{r_{i+1} - r_i}, \quad i = 1, \dots, n-1. \quad (5)$$

These numbers are non-negative because we eliminated all patches  $[r_{i+1}, \mu_{i+1}]$  such that  $r_i \geq r_{i+1}$  and  $\mu_{i+1} \geq \mu_i$ . Moreover,  $p_1 \leq \dots \leq p_{n-1}$  because those patches which are on the lower part of the convex hull satisfy this inequality. The remaining patches also satisfy  $\mu_1 \leq \dots \leq \mu_n$ .

It follows that patch  $i$  is an optimal choice for an animal which is currently in state  $s$  if

$$p_{i-1} < \frac{dF(s)/ds}{F(s)} < p_i.$$

If

$$\frac{dF(s)/ds}{F(s)} < p_1$$

then the first patch is optimal and if

$$\frac{dF(s)/ds}{F(s)} > p_{n-1}$$

then the last patch is optimal.

We consider the evolution of animal position and state  $s(t)$  in time. Animal behavior will depend on the choice of the reproductive value function. As a prototype for this function we take a linear function  $F(s) = s$ . Then it follows that the function  $\frac{dF(s)/ds}{F(s)}$  decreases to zero as  $s$  increases and increases to infinity as  $s$  decreases to zero. First we assume that the state growth is positive in all patches ( $0 < r_1 < \dots < r_n$ ). When animal state is low,  $\frac{dF(s)/ds}{F(s)}$  will be high and the best patch for the animal is the most risky and most profitable patch  $n$ . As the animal state increases, the animal will switch to patch  $n - 1$  and so on, until finally it inevitably ends up in the first patch.

If  $r_1 < \dots < r_j < 0 < r_{j+1} < \dots < r_n$  then the animal will enter after some time the switching regime, in which it will use patch  $j$  and patch  $j + 1$  only. For simplicity we assume  $j = 1$ , which is the case considered by Gilliam and Fraser (1987). If the animal is in the switching regime then the proportion of time that the animal spends in each patch is as derived in Eq. (2) and (3) and animal switching state is

$$s^* = \frac{1}{p_1} = \frac{r_2 - r_1}{\mu_2 - \mu_1}. \quad (6)$$

In the long run (when we can neglect the time the animal needs to reach the switching regime), the proportion of time spent in either patch ( $\tau_i$ ) does not depend on the mortality risks. However, the animal switching state  $s^*$  depends on the mortality rates and it decreases as the difference between the two mortality rates increases. If patch one is an absolute refuge ( $\mu_1 = 0$ ) then our model predicts that in the long term, switching state  $s^*$  decreases as the mortality risk in patch 2 increases.

For short term experiments patch residence times may be strongly influenced by the fact that it will take some time for the animal state to reach the switching regime. We can predict times that an animal will spend in each patch whatever the initial animal state can be. For simplicity we consider only two patches and we distinguish two cases: (i) the animal state growth rate is positive in both patches, and (ii) the animal state growth rate is negative in one patch. We assume that at the initial time animal state  $s_0$  is low and we set  $s_0 = 0$ . Because we assume that the two patches are ordered so that  $r_1 < r_2$  and  $\mu_1 < \mu_2$  it follows that at the beginning of the experiment the animal always moves to the more profitable and more dangerous patch 2 where its state linearly increases.

The animal will stay there until its state reaches the switching value  $s^*$  which will last for

$$T^* = \frac{r_2 - r_1}{r_2(\mu_2 - \mu_1)}$$

time units.

### 3.1. Animal State Growth Is Positive in Both Patches

If animal state growth is positive in both patches then at time  $T^*$  the animal will switch to patch 1 and it will remain there for the rest of the time. If the total time for which animal behavior is observed lasts for  $T$  time units then the proportion of total time  $T$  that the animal spends in patch 1 is

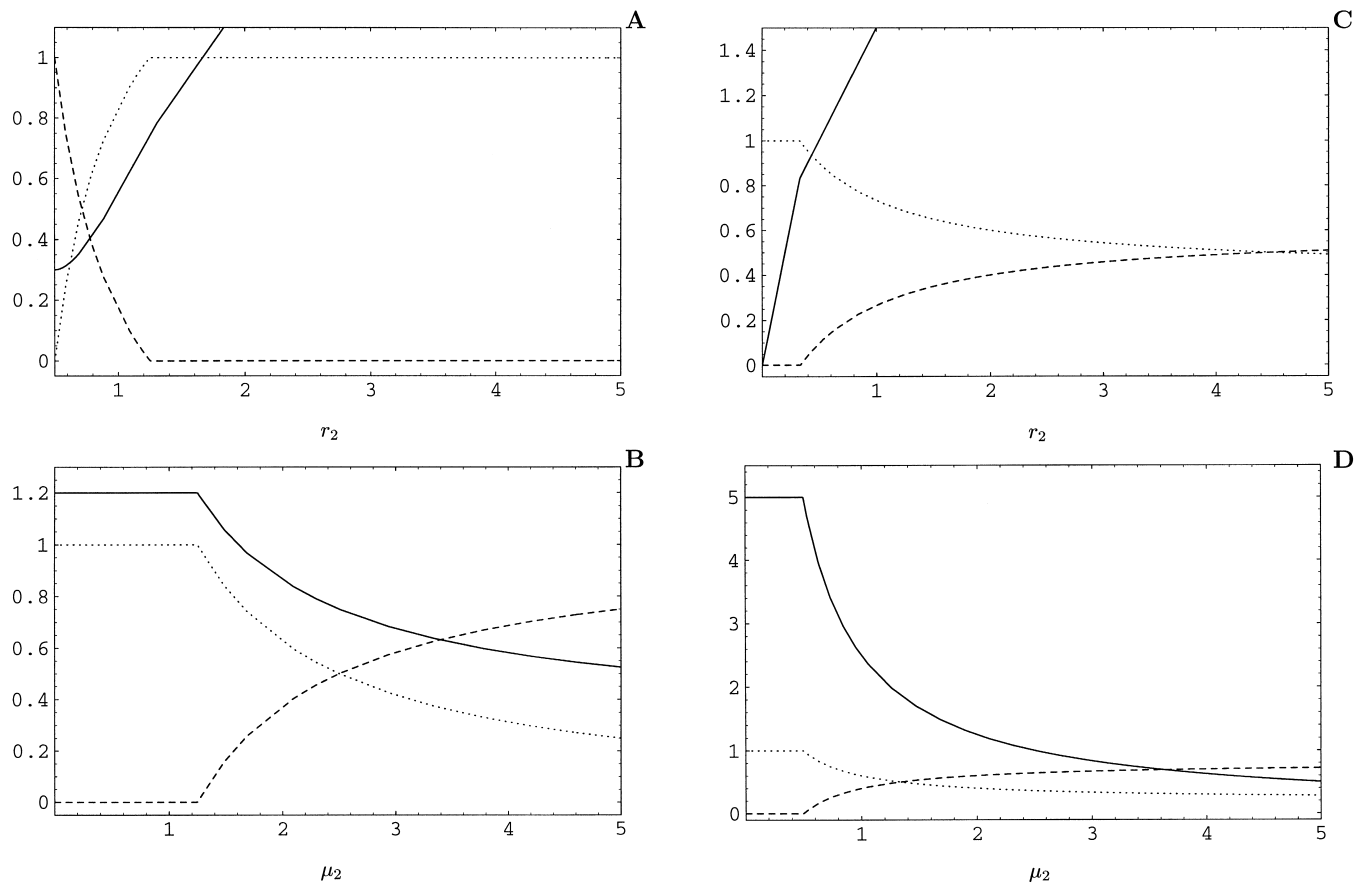
$$t_1 = \begin{cases} 1 - \frac{T^*}{T} & \text{for } T^* < T \\ 0 & \text{for } T^* \geq T, \end{cases} \quad (7)$$

and the proportion of time it spends in the food patch 2 is

$$t_2 = \begin{cases} \frac{T^*}{T} & \text{for } T^* < T \\ 1 & \text{for } T^* \geq T. \end{cases} \quad (8)$$

As profitability  $r_2 (> r_1)$  of the food patch 2 increases the animal state at final time  $s(T)$  (solid line in Fig. 2A) increases too and the animal will spend proportionally less time in patch 1 ( $t_1$ , dashed line in Fig. 2A). As  $r_2$  increases,  $T^*$  increases too and for  $r_2$  large enough  $T^* > T$  and the animal will spend all the time in patch 2 (dotted line in Fig. 2A). Thus its state at time  $T$  will be  $r_2 T$  and that is why for high values of  $r_2$  animal state increases linearly in Fig. 2A.

Next we consider the dependency of animal state  $s(T)$  together with time spent in either patch on the mortality risk in the food patch  $\mu_2$  (Fig. 2B). For low mortality risks in the food patch an animal will always prefer to stay there ( $t_2 = 1$ , dotted line in Fig. 2B) and its state reaches value  $r_2 T$  independently of the mortality risk. As mortality risk in the food patch increases, animal state will reach the switching value  $s^*$  in time interval  $(0, T)$  which leads to a switch to the less dangerous patch 1.



**FIG. 2.** The dependence of animal state ( $s(T)$ , solid line) at time  $T$ , proportion of time spent in refuge ( $t_1$ , dashed line) and in food patch 2 ( $t_2$ , dotted line) on the state growth rate parameter  $r_2$  (A and C) and on the mortality risk in the food patch  $\mu_2$  (B and D) for the model with linear state growth. (A and B) assume that state growth is positive in both patches while (C and D) assume negative state growth in patch 1. Parameters for (A):  $r_1 = 0.5$ ,  $\mu_1 = 0$ ,  $\mu_2 = 1$ ,  $T = 0.6$ ; for (B):  $r_1 = 0.5$ ,  $r_2 = 2$ ,  $\mu_1 = 0$ ,  $T = 0.6$ ; for (C):  $r_1 = -0.5$ ,  $\mu_1 = 0$ ,  $\mu_2 = 1$ ,  $T = 2.5$ ; for (D):  $r_1 = -0.5$ ,  $r_2 = 2$ ,  $\mu_1 = 0$ ,  $T = 2.5$ .

Animal state  $s(T)$  will decrease with increasing mortality risk in the food patch, because animals will spend less time there.

### 3.2. Animal State Growth Is Negative in the Refuge

If the animal state growth is negative in the refuge (patch 1,  $\mu_1 = 0$ ), then the animal enters at time  $T^*$  the switching regime (provided we assume that the observation time  $T$  is longer than  $T^*$ ) in which it will spend the rest of the time, i.e.,  $T - T^*$  time units. Thus the proportion of total time  $T$  that the animal spends in the refuge follows from expressions (2) and (3),

$$t_1 = \begin{cases} \frac{r_2}{r_2 - r_1} \left(1 - \frac{T^*}{T}\right) & \text{for } T > T^* \\ 0 & \text{for } T \leq T^*, \end{cases} \quad (9)$$

and the proportion of time it spends in the food patch is

$$t_2 = \begin{cases} \frac{r_1}{r_1 - r_2} \left(1 - \frac{T^*}{T}\right) + \frac{T^*}{T} & \text{for } T > T^* \\ 1 & \text{for } T < T^*. \end{cases} \quad (10)$$

Let us consider dependence of the animal state at final time  $s(T)$  on the profitability of the food patch  $r_2$  (solid line in Fig. 2C). For low profitabilities of the food patch, animal state does not reach the switching state in time interval  $(0, T)$  and it spends all time in the food patch 2 ( $t = 1$ , dotted line in Fig. 2C) where its state increases linearly. For high enough profitability of the food patch, animal state reaches the switching value in time interval  $(0, T)$  and as  $r_2$  increases, the animal will spend proportionally more time in the refuge (dashed line in Fig. 2C). Animal state  $s(T) = s^*$  will also increase with increasing

$r_2$  but with a lower slope due to the fact that the animal also uses the refuge, which decreases animal state growth.

Next we consider the dependency of animal state  $s(T)$  together with time spent in either patch on the mortality risk in the food patch (Fig. 2D). For low mortality risks in the food patch an animal will always prefer to stay there ( $\tau_2 = 1$ , dotted line in Fig. 2D) and its state reaches value  $r_2 T$ . As mortality risk in the food patch increases, animal state will reach the switching value in time interval  $(0, T)$  which leads to the use of both patches. Animal state  $s(T)$  will decrease with increasing mortality risk in the food patch, because animals will spend less time there. As  $T$  increases, the proportion of time spent in the refuge converges to

$$\tau_1 = \frac{r_2}{r_2 - r_1} \quad (11)$$

and the proportion of time spent in the food patch converges to

$$\tau_2 = -\frac{r_1}{r_2 - r_1}, \quad (12)$$

(see (2) and (3)).

When we compare the two cases we see that predictions of our models depend on the sign of the state growth parameter  $r_2$  in the less profitable but safer patch 1. If it is positive then our model predicts only one switch (Fig. 1A) and as the state growth parameter in the more dangerous patch increases, an animal will stay there proportionally longer time compared to the residence time in patch 1. On contrary, if state growth parameter in the safer patch is negative then our model predicts that an animal with state equal to  $s^*$  will be instantaneously switching between the two patches (Fig. 1B) and it will stay in the safer patch proportionally longer time as  $r_2$  increases.

The constant animal state growth is unrealistic, because of physiological constraints that prevent unbounded animal state growth. In the next section we study the case of a saturated animal state growth.

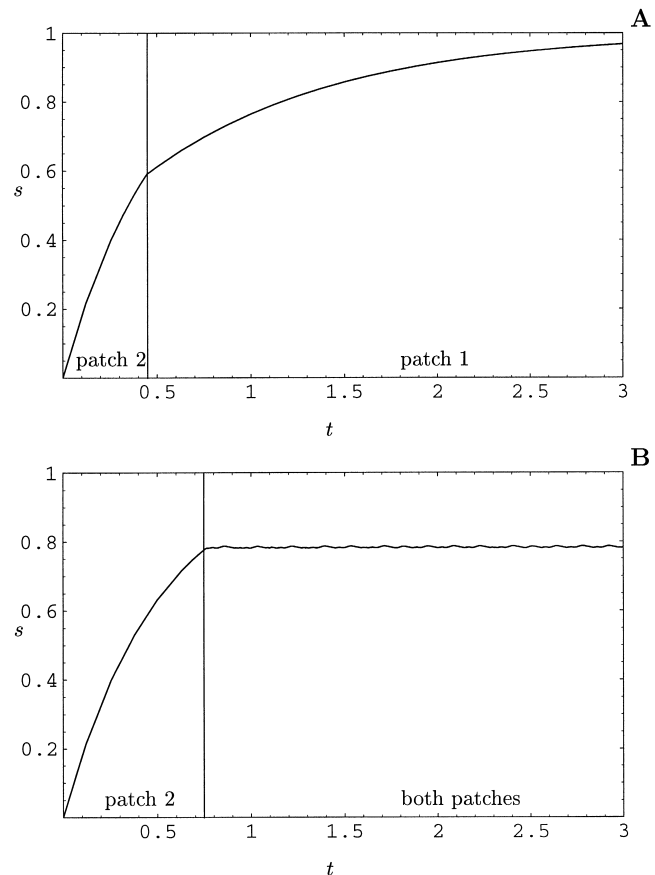
#### 4. LINEAR GROWTH RATES

The previous situation does not take into account the diminishing return due to animal satiation. Here we assume that the state of the animal is bounded from

above which can be described by the von Bertalanffy (1957) curve, i.e.,

$$S_i(s) = r_i \left( 1 - \frac{s}{K} \right)$$

where  $K$  is the maximal possible animal state. Because the animal state growth decreases with increasing animal state, this model describes a saturated animal state growth. We study how the saturated animal state growth influences results that we obtained for unbounded animal state growth in the previous part.



**FIG. 3.** Evolution of animal state for the von Bertalanffy saturated growth rate model. Animals with zero initial state move first to the more hazardous but also more profitable patch 2 where their state increases quickly. When their state reaches the switching value  $s^*$  animals switch to the safer patch 1. (A) describes the case in which state growth is positive in both patches; in (B) the state decreases in patch 1 (refuge). In this latter case animals use both patches which keeps their state equal to  $s^*$ . Parameters for (A):  $r_1 = 1$ ,  $r_2 = 2$ ,  $\mu_1 = 1$ ,  $K = 1$ . Parameters for (B):  $r_1 = -0.5$ ,  $r_2 = 2$ ,  $\mu_1 = 0.3$ ,  $\mu_2 = 1$ ,  $K = 1$ .

#### 4.1. Animal State Increases in Both Patches

We assume that the intrinsic per capita growth rate parameters are positive in both patches ( $0 < r_1 < r_2$ ), mortality risk is higher in the second patch ( $\mu_1 < \mu_2$ ) and the reproductive value is  $F(s) = s$ . The switching state is given by

$$s^* = \frac{(r_2 - r_1) K}{r_2 - r_1 + K(\mu_2 - \mu_1)}.$$

For  $K$  converging to infinity the switching state for saturated growth converges to the switching state for the unsaturated state growth given by (6). We remark that the switching state  $s^*$  is lower than is the switching state for the constant rate model. Animals with low states  $s < s^*$  move to patch 2 while animals with high state stay

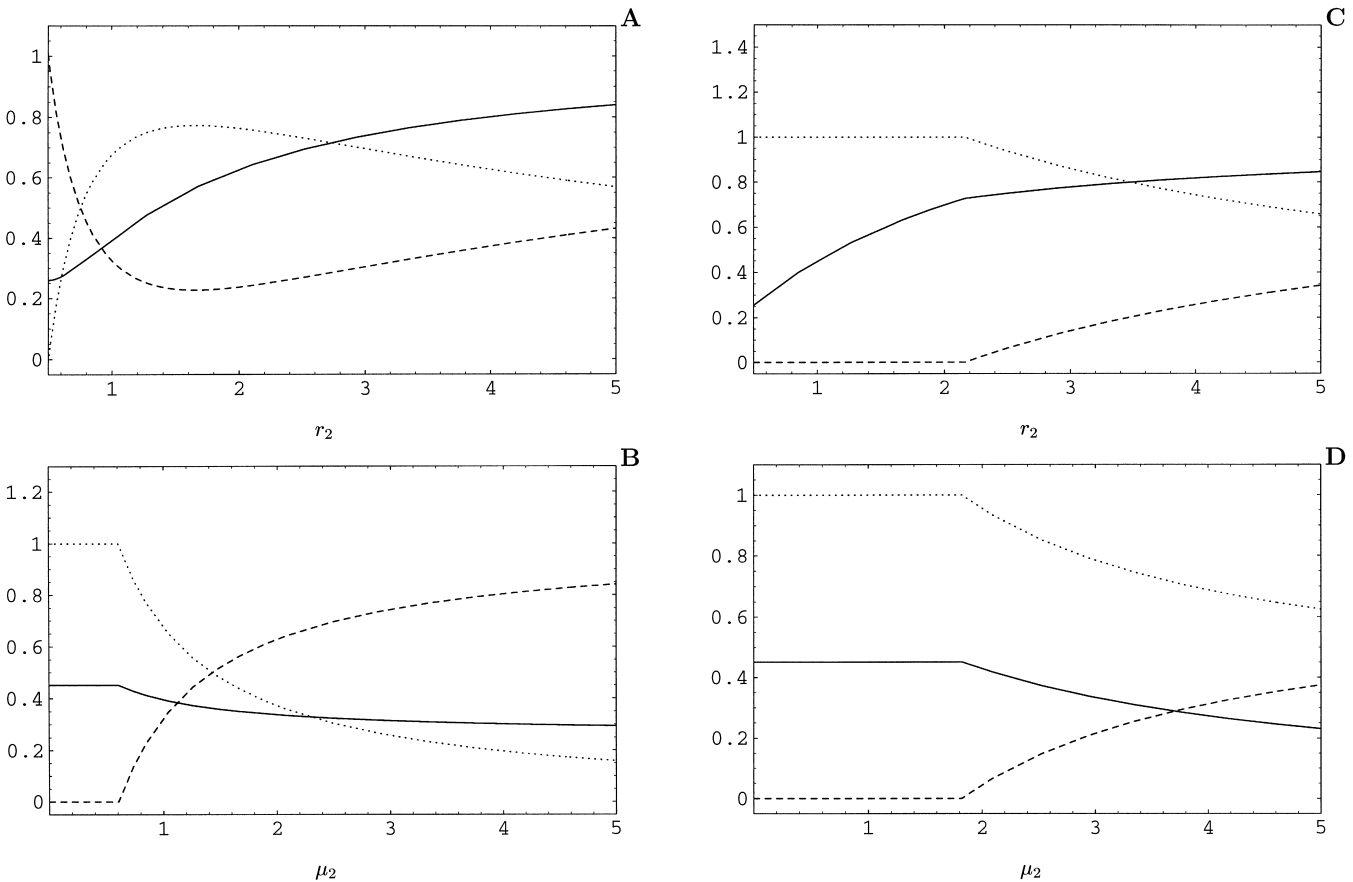
in patch 1. Let us consider an animal with a zero initial state. This animal prefers the more dangerous and more profitable patch 2 and the animal state is described there by

$$s(t) = K(1 - e^{-r_2 t/K}).$$

Because  $K > s^*$  then the animal stays in patch 2 until its state reaches the switching value  $s^*$  at time

$$T^* = -\frac{K}{r_2} \ln \left( 1 - \frac{s^*}{K} \right)$$

and the animal switches to patch 1 where its state will converge to  $K$  because of the positive state growth in patch 1. The animal will remain in this patch forever (Fig. 3A). The proportions of total time  $T$  which the



**FIG. 4.** The dependence of animal state ( $s(T)$ , solid line) at time  $T$ , proportion of time spent in refuge ( $t_1$ , dashed line) and in food patch 2 ( $t_2$ , dotted line) on the state growth rate parameter  $r_2$  (A and C) and on the mortality risk in the food patch  $\mu_2$  (B and D) for the model in which animal state growth is described by the von Bertalanffy curve. (A and B) assume that state growth is positive in both patches while (C and D) assume negative state growth in patch 1. Parameters for (A):  $r_1 = 0.5$ ,  $\mu_1 = 0$ ,  $\mu_2 = 1$ ,  $K = 1$ ,  $T = 0.6$ ; for (B):  $r_1 = 0.5$ ,  $r_2 = 1$ ,  $\mu_1 = 0$ ,  $K = 1$ ,  $T = 0.6$ ; for (C):  $r_1 = -0.5$ ,  $\mu_1 = 0$ ,  $\mu_2 = 1$ ,  $K = 1$ ,  $T = 0.6$ , for (D):  $r_1 = -0.5$ ,  $r_2 = 1$ ,  $\mu_1 = 0$ ,  $K = 1$ ,  $T = 0.6$ .



animal spends in either patch are given by (7) and (8). As  $r_2$  increases,  $s(T)$  will converge to  $K$  (Fig. 4A, solid line). Proportion of time spent in the food patch 2 is a hump-shaped curve (Fig. 4A, dotted line). This is because due to the saturating effects of the Bertalanffy curve the food intake rate decreases with increasing animal state. Therefore, animals with high state stay proportionally longer time in the safe patch.

Dependence of animal state and proportion of time spent in each patch on mortality risk in patch 2 is qualitatively similar to the case of constant rates (cf. Fig. 4B vs Fig. 2B).

#### 4.2. Animal State Decreases in the Refuge

Next we assume that animal state growth parameter  $r_1$  is negative in the refuge ( $r_1 < 0 < r_2$ ). In this case our model predicts that when reaching the switching state  $s^*$  the animal should start to switch instantaneously between the two patches, similarly as in the case of constant rates (Fig. 3B). In this case the proportion of total time  $T$  which the animal spends in either patch is given by (9) and (10). Dependence of animal state and proportion of time spent in each patch on  $r_2$  and mortality risk in patch 2 are qualitatively similar to the case of constant rates and they are shown in Figs. 4C and D (see Appendix).

## 5. DISCUSSION

In this article using a myopic optimality we have described adaptive animal movement in heterogeneous environments, assuming that animals can trade-off resource acquisition versus mortality risk. The problem of animal optimal movement between patches is often considered in the literature in the context of optimal foraging theory (Fretwell and Lucas, 1970; Stephens and Krebs, 1986; Sutherland, 1996). If animals are free to move between patches and they have complete information on quality of patches then the Ideal Free Distribution paradigm (IFD) (Fretwell and Lucas, 1970) tells us they will distribute in such a way that by moving to another patch an individual animal cannot increase its resource acquisition. The mechanism which drives the system to IFD is based on density dependence because the food intake rate is assumed to decrease due to patch exploitation and/or animal interference. IFD does not consider animal state (e.g., size, energy reserves, etc.). However, animal state is an important factor that influences animal decisions. For example, hungry

animals more readily move to patches with high reward where mortality risk is also high while animals with high state prefer safer, less profitable patches.

Following the approach of state dependent modelling (Gilliam and Fraser, 1987; Mangel and Clark, 1988; Houston *et al.*, 1988; Ludwig and Rowe, 1990; Houston *et al.*, 1993; Houston and McNamara, 1999) in this article we have considered simple models which predict animal movements in a heterogeneous environment consisting of two or more habitat patches, dependent solely on animal current state. We assumed that animals are able to estimate mortality risk associated with feeding and they instantaneously balance this mortality risk with reward obtained in a given patch and the animal current state. This myopic optimization provides us with a general explicit rule for animal patch choice depending on the animal current state. In the case of two patches this rule gives us a critical animal switching state such that those animals whose state is below this value prefer more risky and more rewarding patches while animals with a state above the switching value prefer less risky and less profitable patches. Qualitatively, there are two possibilities: (i) either animal state growth is positive in both patches, or (ii) animal state growth is negative in the refuge. In the former case, our model predicts that there will be only one switch from the more dangerous and more profitable patch to the less dangerous and less profitable patch. For the latter case, our model predicts that when the switching state is reached, the animal should switch instantaneously between the two patches which keeps its state at the level of the switching state. This roughly corresponds to consumers which attack their prey from a refuge. Our model allows us to estimate the animal state and times spent in each patch. If we do not consider any bound on the animal state then, as a function of the food patch productivity  $r_2$ , animal state  $s(T)$  is increasing (solid line in Figs. 2A and C) and proportion of time spent in the risky food patch increases when state growth is positive in both patches (dotted line in Fig. 2A). On contrary, if state growth is negative in the refuge, animals should spend proportionally less time in the food patch as  $r_2$  increases (dotted line in Fig. 2C). As a function of the predation risk in the food patch ( $\mu_2$ ) animal state decreases as the time spent in the food patch proportionally decreases (Fig. 2B and D).

When animal state growth is described by the von Bertalanffy curve the animal state as a function of  $r_2$  is described by a saturating curve (Fig. 3). Contrary to the constant rate model, time spent in the more risky patch is a hump-shaped curve (cf. dotted line in Fig. 4A vs. Fig. 2A) if state growth is positive in both patches. This is due to the decreased consumption rate as the animal

state approaches its satiation level  $K$ . Therefore, animals with higher state pay more attention to the mortality risk and therefore they spent proportionally less time in the more profitable but more risky patch 2 (see Fig. 4A).

If animal growth is negative in the refuge then proportion of time spent there increases with increased  $r_2$  (Fig. 4C) which is qualitatively similar to the unbounded animal growth. As a function of mortality risk in the more profitable food patch  $\mu_2$ , animal state decreases as it spends proportionally less time in the food patch (Figs. 4B and D).

Our results can be also interpreted at the population level. Let us consider a population in an environment consisting of two patches. Its distribution across patches is given by the proportion of times each individual spends in either patch. Because we computed these times explicitly, we can deduce that the population will distribute between the patches in the same ratio given by  $t_1/t_2$ . Figures 2 and 4 (with the meaning of dashed line denoting the fraction of the population in patch 1, dotted line in patch 2) then give the distribution of the population between the two patches for various values of  $r_2$  and mortality risks  $\mu_2$ . This population distribution does not take into account any population density effects such as interference or patch depletion which are the main driving forces in most models of IFD (Fretwell and Lucas, 1970; Sutherland, 1983; Kennedy and Gray, 1993; Křivan, 1997; van der Meer and Ens, 1997; Křivan, 1998).

Our model extends the work of Gilliam and Fraser (1987) who considered a similar problem of a patch choice but their model does not account for the animal state. They considered  $n$  habitat patches, each of them characterized by gross foraging rate and mortality risk. In their setting, one patch was a refuge which did not contain either foragers or food. They assumed that foragers move between patches in order to minimize their mortality risk subject to a constraint that the animal gets a certain minimal amount of food over a given period. They showed that the optimal strategy is to use the refuge and the food patch which has minimal ratio  $(\mu_i - \mu_R)/(h_i - h_R)$  where index R denotes the refuge and  $h_i$  is the net foraging rate, i.e.,  $f_i = h_i + m$  where  $m$  is the metabolic rate (assuming that minimum food requirement is met when feeding continuously in the food patch). Because the refuge was assumed to be absolute ( $\mu_R = 0$ ) this simplifies to the following rule: use the refuge and the patch which has minimal ratio mortality/gross foraging rate among all other patches. They manipulated the gross foraging rates by changing food density in patches and with the mortality risks and they showed that juvenile creek chub switched between

patches in a pattern which was consistent with their model. However, their derivation does not allow for estimation of times that the animal should stay in the food patch and in the refuge. Our derivation which considers animal state and which assumes a different fitness function provides us with the same criterion for patch choice when mortality and state growth rates are constant, but in addition it also allows us to estimate times that an animal should stay in each patch. Moreover, our approach is more general because it applies also to the case where mortality and state growth rates depend on the animal current state. We remark that the data provided in Gilliam and Fraser (1987) do not allow us to estimate the proportion of time spent in each patch because the authors work with gross foraging rates which do not include metabolic rate. This allows us to predict the switching state  $(S_2 - S_1)/(\mu_2 - \mu_1)$  because this value equals  $(f_2 - f_1)/(\mu_2 - \mu_1)$ , where  $S_i = f_i - m$  and  $m$  is the metabolic cost which is assumed to be the same across patches. To estimate durations that the animals should spend in each patch we would need to know the net foraging rates  $S_i$ .

Our models predict that foragers should spend more time in the refuge as the mortality risk in the food patch increases (Figs. 2B, 2D and 4B, 4D), which agrees with experimental observations (Fraser and Huntingford, 1986; Holbrook and Schmitt, 1988). Gilliam and Fraser (1987) and Holbrook and Schmitt (1988) also observed that the proportion of time spent in the more profitable and more risky patch increased with the food level in this patch. The other patch(es) contained some positive food densities which roughly corresponds to our models with a positive state growth rate in the less profitable patch. We conclude that their observations of patch residence time on the profitability of the food patch agree with our predictions (Figs. 2A and 4A, dotted line). On contrary Fraser and Huntingford (1986) did not observe any effects on the patch residential times when they changed food densities in the more profitable patch. In their experimental setting one patch was a refuge without any food which roughly corresponds to our model with a negative state growth in that patch. For this case our models predict that proportion of time spent in the more profitable patch is either constant or decreasing function of that patch profitability (Figs. 2C and 4C, dotted line) which again roughly corresponds with the experimental observations.

Both our models suggests a clear decrease of the proportion of time animals will spend in the more profitable and more risky patch as predation risk increases. The effects of food level in the risky patch on the proportion of time spend in this patch depend on

parameters of the model and functions chosen for the model description. We hope that our analysis will stimulate more empirical research in this direction.

## APPENDIX

For the saturated animal state growth we have

$$\frac{\partial s^*}{\partial r_2} = \frac{K^2(\mu_2 - \mu_1)}{[r_2 - r_1 + K(\mu_2 - \mu_1)]^2}$$

and

$$\frac{\partial \tau_2}{\partial r_2} = \frac{r_1}{(r_1 - r_2)^2}$$

which are positive as we assume that  $\mu_2 > \mu_1$ .

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