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General results concerning the trade-off between gaining energy and avoiding predation

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CONTENTS

SUMMARY

When animals can choose from a range of feeding options, often those options with a higher energetic gain carry a higher risk of predation. This paper analyses the optimal trade-off between food and predation. We are primarily interested in how an animal's decisions and its state change over time. Our models are very general. They can be applied to growth decisions, such as choice of habitat, in which

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case we might consider how the state variable size changes over an animal's lifetime. Equally our models are applicable to short-term foraging decisions, such as vigilance level, in which case we might consider how energy reserves vary over a day. We concentrate on two cases: (i) the animal must reach a fixed state, its fitness depending on when this is attained; (ii) the animal must survive to a fixed time, its fitness depending on its final state.

In case (i) minimization of mortality per unit increase of state is optimal under certain baseline conditions. In case (ii) behaviour is constant over time under baseline conditions (the 'Risk-spreading Theorem'). We analyse how these patterns are modified by complicating factors, e.g. time penalties, premature termination of the food supply, stochasticity in food supply or in metabolic expenditure, and state-dependence in the ability to obtain food, in metabolic expenditure and in predation risk. From this analysis we obtain a variety of possible explanations for why an animal should reduce its intake rate over time (i.e. show satiation). We show how earlier work can be viewed as special cases of our results.

1. INTRODUCTION

The trade-off between energetic gain and the risk of predation is a topic of central interest in behavioural ecology. The general idea is that by varying some aspect of its behaviour an animal can control both its rate of energetic gain and the probability that it is killed by a predator. High rates of gain can be achieved only at the cost of a high rate of predation (e.g. Milinski 1986; Dill 1987; Sih 1987; Lima & Dill 1990). This trade-off can arise in various ways, including the following.

(*a*) *Choice of habitat*

The animal can forage in various areas or habitats. Each habitat has an associated rate of gain and danger of predation. The choice can occur on various spatial and temporal scales. For example, an animal may change its energetic gain and danger of predation both rapidly and repeatedly by changing the distance from cover at which it forages (e.g. Schneider 1984; Lima 1987; see also Werner & Hall 1988). In contrast, fledging in birds and metamorphosis in amphibians is an irreversible change of habitat that occurs once in the animal's life and may involve movement between widely separated habitats.

(*b*) *Level of vigilance*

In some species of animals foraging is incompatible with looking around for potential predators (e.g. Lima 1990; Elgar 1989). A high level of vigilance results in little danger of predation but also a low rate of energetic gain.

(*c*) *Group size*

Foraging in a group of animals has both costs and benefits. Although an animal may benefit from food found by other members of the group, it shares its food with them and thus may have a lower food intake than a solitary animal (Pulliam & Millikan 1982; Clark & Mangel 1984, 1986; Magurran 1990). It may also have a lower danger of being killed by a predator as group size increases, both because of the reduced probability that it will be the animal attacked by the predator (dilution effect) and because of the vigilance of other group members (e.g. Bertram 1978; Lima 1990; McNamara & Houston 1992*a*).

Further examples of the trade-off concern the distance that an animal allows a predator to approach before fleeing and the time spent in a safe place before returning to forage after a disturbance (see Ydenberg & Dill 1986; Lima & Dill 1990).

Although we present our results in terms of the trade-off between energetic gains and danger of predation, they are also relevant when other factors cause the mortality. For intertidal organisms, the mortality might result from desiccation. Swennen *et al.* (1989) suggest that oystercatchers can increase their intake rate at the cost of an increased probability of damage to the bill. Good feeding areas or easy prey such as snails might involve a high risk of parasitic infection.

As the trade-off between food and predation is both widespread and an important determinant of fitness, considerable effort has been devoted to models which predict the behaviour favoured by natural selection. One basic problem in formulating a model is to compare the benefits of feeding and the cost of predation. Early work on this topic (Sibly & McFarland 1976; Milinski & Heller 1978) used an *ad hoc* objective function or currency that was not obviously related to fitness. Subsequent work has attempted to use a currency that has an obvious interpretation in terms of fitness. The biological role of energy must first by identified. For a small bird in winter, feeding is important in maintaining fat at a level that enables it to avoid starvation when foraging is interrupted by darkness or bad weather (see Lima 1986; Blem 1990; McNamara & Houston 1990*a* and therein). Birds also build up levels of fat in order to migrate (e.g. Alerstam & Lindström 1990). Food can instead be used for growth, which may improve survival probability or enable the animal to reproduce.

Once the biological role of energy has been identified, a variety of modelling techniques can be used to find the policy which maximizes fitness. Stochastic dynamic programming has been widely used in this context (e.g. McNamara & Houston 1986; Mangel & Clark 1986, 1988; Mangel 1990; McNamara 1990; McNamara & Houston 1990*b*; Szekely *et al.* 1991). Houston & McNamara (1988) argue that realistic models of starvation require a stochastic approach. In contrast, growth has been investigated using deterministic optimal control theory (e.g. León 1976; Alexander 1982; Gilliam 1982; Sibly *et al.* 1985).

Gilliam (1982) considered an animal that had to grow to a certain size before it could reproduce and showed that the animal should minimize the predation per unit of growth. This simple and intuitively appealing result depends on the assumption that fitness does not depend on the time of reproduction. Ludwig & Rowe (1990) and Rowe & Ludwig (1991) have considered the effects of time constraints on optimal behaviour. Their work (which we review below) is based on an animal switching between habitats, and their results concentrate on the timing of such switches. Sibly *et al.* (1985) are concerned with patterns of growth. They model foraging activity by a control variable u which can vary continuously; they find the optimal time course of u and the resultant pattern of growth.

We develop a general approach which incorporates the models of Gilliam (1982), Ludwig & Rowe (1990), and Sibly *et al.* (1985). Our approach is to derive general results by analytical means, although this is not possible in all cases and we then resort to numerical computations. Different qualitative forms of the link between energetic gain and predation risk are considered. We also specify how both predation risk and energetic gain depend on size (or reserves). From these relationships we deduce how behaviour and size (or reserves) should change over time. We will be concerned with how these results are modified by time constraints, interruptions, refuges from predators and stochasticity in the food supply.

We establish conditions under which Gilliam's criterion does give the optimal policy and show how it must be modified under other conditions. In the simplest cases it is optimal for foraging activity to remain constant, a result we call the 'Risk-spreading Theorem'. We consider this as a null case and identify conditions under which foraging activity increases over time and conditions under which it decreases.

2. THE MODEL

(*a*) *The control variable*

The variable that characterizes the animal's behaviour is u, where $0 \leqslant u \leqslant 1$. A large value of u corresponds to high energetic gain and high predation. The options available to an animal may form a continuum, as with distance from cover, or may be discrete, as with choice of habitat. u provides a way of ranking the available options in terms of their food supply. $u=0$ then corresponds to the choice of the option with the least food, and $u=1$ corresponds to the choice of the option with the most food.

We will often consider an animal which is performing two activities between which it can switch. We then focus on the proportions of time spent performing each activity over a short period of time. We take u to be the proportion of time spent on the activity that provides the higher rate of energy gain. For example, when an animal has a choice between two habitats in which to forage, u will be the proportion of time in the habitat with the better food supply. When we are modelling vigilance behaviour of an animal, we envisage the animal as switching between being vigilant and feeding on a time scale of a minute or less. u is then the proportion of time spent feeding over a longer period (e.g. an hour) and $1-u$ is the proportion of time for which the animal is vigilant.

The animal's options sometimes include a special habitat in which the animal is safe from predators. We refer to this habitat as a refuge.

(*b*) *State*

The animal's state is characterized by the variable x. For a bird foraging over a day we would take x to be its level of energy reserves (McNamara & Houston 1982, 1986), whereas for a fish moving between habitats over a period of months (Werner & Gilliam 1984; Werner & Hall 1988), x would represent the body mass of the fish or some transformation of it, such as the logarithm of the mass.

We assume that the mean increase in x per unit time is

$$\gamma(u,x) = a(x)u - b(x), \qquad (1)$$

i.e. u is scaled so that mean gain is linear in u. The exact form and interpretation of $a(x)$ and $b(x)$ depend on the animal that we are studying. We have set up our model so that $a(x)$ is always positive, but $b(x)$ may be positive or negative. When there are two habitats, with a gain $g_0(x)$ in Habitat 0 and a gain $g_1(x)$ in Habitat 1, then

$$\begin{aligned}\gamma(u,x) &= (1-u)g_0(x) + ug_1(x) \\ &= (g_1(x) - g_0(x))u + g_0(x),\end{aligned} \qquad (2)$$

which has the same form as equation (1). We assume that Habitat 1 is better in terms of food, so that $a(x) = g_1(x) - g_0(x)$ is positive. In this case, $b(x) = -g_0(x)$ is negative.

When u represents the proportion of time that an animal spends feeding, as opposed to being vigilant, and x is energy reserves, the interpretation of b depends on how foraging intensity u affects metabolic expenditure. If expenditure is independent of u, $b(x)$ is the mass-dependent metabolic rate and $a(x)$ is the rate at which energy is gained per unit time spent feeding. When expenditure increases linearly with u, $b(x)$ is the metabolic expenditure when $u=0$ and $a(x)u$ is the rate at which energy is gained per unit of time minus the additional metabolic cost incurred by feeding at intensity u. In birds, under both these interpretations it is reasonable to assume that the the cost of flight means that $b(x)$ increases with energy reserves (e.g. McNamara & Houston 1990*a*). We also expect $a(x)$ to either be constant or to decrease with x. When x corresponds to the body mass of a growing organism, $a(x)$ is likely to be an increasing function of x.

(*c*) *The danger of predation*

The probability that the animal is killed by a

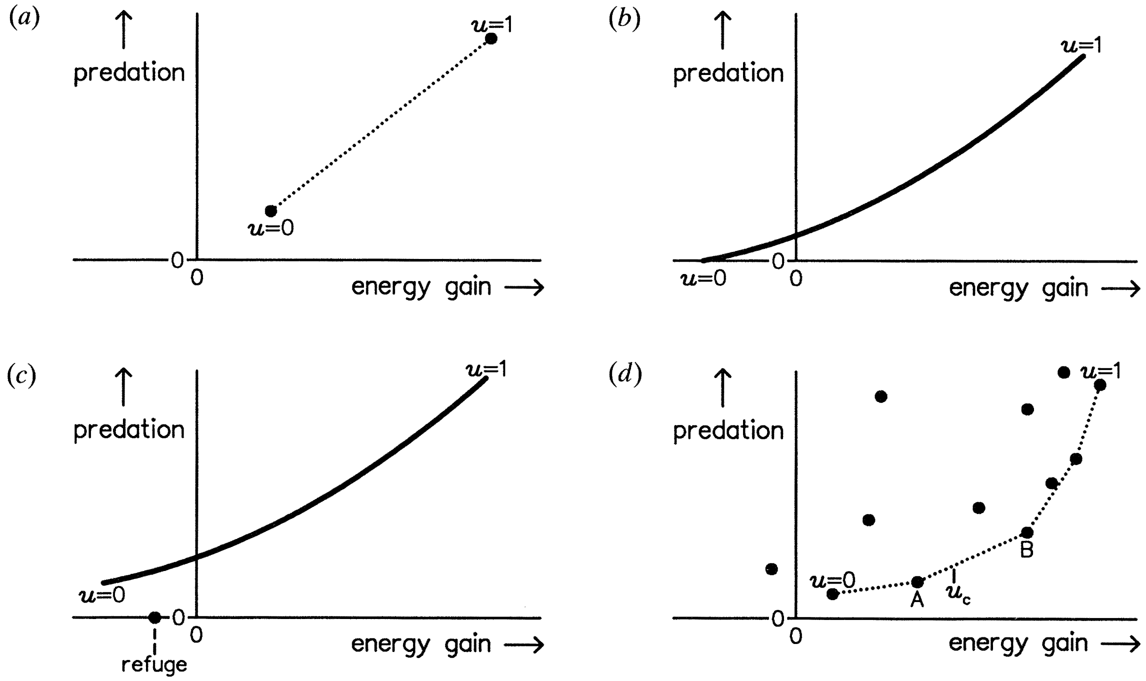

Figure 1. Possible trade-offs between predation risk and energy gain as described in the text. Closed circles represent discrete options; dotted lines correspond to taking some proportion of discrete options. Solid lines represent a continuum of options. (*d*) also illustrates the analysis of Gilliam & Fraser (1987); u_c is the constant value of u sufficient to attain x_c at final time T. u_c will thus depend on the starting value, $x(0)$. To achieve the value u_c only options A and B are used.

predator per unit time is $M(u,x)$. For fixed x we assume that $M(u,x)$ is an increasing function of u. Various forms of the relationship between M and u are considered. We illustrate these forms in figure 1.

(i) *$M(u,x)$ increases linearly with u*

Suppose that there are two habitats with predation rates $\lambda_1(x)$ and $\lambda_2(x)$, and u is the proportion of time spent in Habitat 1. Then $M(u,x)$ is linearly dependent on u:

$$M(u,x) = u\lambda_1(x) + (1-u)\lambda_2(x).$$

(ii) *$M(u,x)$ is a strictly convex function of u, i.e. $\partial^2 M/\partial u^2 > 0$*

This form of function might be expected when u is the proportion of time a foraging animal spends feeding and $1-u$ is the proportion of time for which it is vigilant. The predation risk if every other minute is spent vigilant ($u = 0.5$) is likely to be less than half the predation risk if the animal is not vigilant at all ($u = 1$).

(iii) *$M(u,x)$ is strictly convex with $M(0,x) > 0$, but there is a refuge*

In this refuge the animal is safe from predators, i.e. there exists another option for which M is zero. For example, when there is a choice between feeding and vigilance, $u = 0$ corresponds to the bird being in the foraging area but spending all its time being vigilant. This may still involve some danger of predation. When the bird has a refuge it can leave the foraging area and go somewhere where there is no danger of predation.

(iv) *$M(u,x)$ is piecewise linear and convex*

Suppose an environment is composed of a number of distinct habitats. Each habitat is characterized by its net rate of energy gain and predation risk per unit time. The animal must choose the proportion of time it spends in each habitat. We may represent the energy gain and predation risk under each option diagramatically (figure 1*d*). It is clear that certain options will never be used. Those that are used can be parametrized by u where the option giving the lowest energy gain corresponds to $u = 0$ and the option giving the highest gain corresponds to $u = 1$. It can be seen from figure 1*d* that as u increases, $M(u,x)$ increases in a piecewise linear manner and that $M(u,x)$ is also a convex function of u.

(*d*) *The terminal condition*

In this paper, we look at two circumstances in which a trade-off between energetic gain and predation can occur.

(i) *Fixed state*

The animal has to get to one particular state, x_c, if it is to have any reproductive success. The reproductive value of reaching x_c may depend on the time t at which this state is reached. For example, in a population growing at rate λ, the reproductive value may be discounted by a discount factor $e^{-\lambda t}$, as in Sibly *et al.*(1985). Alternatively, it may be that young which are produced late in the season are less likely to survive to maturity, and hence the reproductive success associated with reading x_c may decline with t.

(ii) *Fixed time*

The animal's state at some fixed time, T, determines its reproductive success.

Although we analyse these cases separately, the results of one case can be relevant to the other. For example, suppose an animal must reach a fixed state x_c before it can reproduce. Under the optimal policy it attains this state at time t_F. Then often the optimal trajectory is the same as if it were a fixed-time problem with final time $T = t_F$.

In the discussion we relate our results to the case in which neither final state nor final time are fixed, there being a trade-off between the advantage of a high final state and the disadvantage of a late final time.

(*e*) *Optimal behaviour*

We will always denote the optimal strategy by $u_{OPT}(x,t)$. This function specifies the value of u used for each state x and time t. The behaviour of an animal following an optimal strategy is described in two ways. $x^*(t)$ specifies how the animal's state changes with time. This function is found by solving the equation $dx^*/dt = \gamma(u_{OPT}(x^*,t),x^*)$. $u^*(t)$ specifies how the value of u changes with time. This function is given by

$$u^*(t) = u_{OPT}(x^*(t),t).$$

The paper is organized so that we first analyse the fixed-state case in detail and then the fixed time.

3. FIXED STATE

In this section we will start by looking at the simplest case under which Gilliam's rule gives the optimal policy. We then allow an animal's reproductive success to depend on the time of reproduction. Penalizing late reproduction is shown to have the same effect as having a food supply which terminates unpredictably. Lastly, variability in food gain per unit time is considered.

(*a*) *Minimizing predation per unit increase in state*

The rule derived by Gilliam (1982) is to minimize mortality/gain; i.e. in our notation

$$M(u,x)/(a(x)u - b(x)), \tag{3}$$

is minimized (where u is restricted to values for which the gain is positive). This minimization is carried out independently for each state x, and gives a strategy $u_G(x)$ prescribing the value of u to be used in each state. Henceforth, u_G will always refer to the u prescribed by the Gilliam rule and will be referred to as the Gilliam rate. This strategy is an optimal one for reaching the fixed state provided there are no time constraints or time penalties and food options are deterministic (i.e. $u_{OPT}(x,t) = u_G(x)$ provided these conditions hold).

Gilliam developed the M/γ rule in the context of the ontogenic movement of sunfish between habitats (see Werner *et al.* 1983; Werner & Gilliam 1984; Werner & Hall 1988; Turner & Mittlebach 1990). It has also been applied to the timing of metamorphosis in amphibians (Werner 1986) and to the levels of fat carried by migrating birds (Alerstam & Lindström 1990).

We illustrate this rule with a simple example.

(i) *Example 1*

Let the state variable x be the animal's body mass. We interpret u as the proportion of time spent feeding. $a(x)$ can then be interpreted as the rate of mass increase per unit time spent foraging due to food acquisition and $b(x)$ can be interpreted as the rate of mass loss due to metabolic expenditure. We suppose mortality can be expressed as

$$M(u,x) = \alpha(x)u^2. \tag{4}$$

Here $\alpha(x)$ specifies how predation risk changes with body mass. When M has this form, minimization of expression (3) is equivalent to minimization of $u^2/(a(x)u - b(x))$.

By differentiating with respect to u it can be verified that this quantity is minimized by setting $u = u_G$ where

$$u_G(x) = 2\ b(x)/a(x). \tag{5}$$

One immediate conclusion is that in this example the form of mass dependence $\alpha(x)$ in the predation risk has no influence on the optimal policy. This point is discussed further below. As growth increases x, $u_G(x)$ will change, and the direction of change will determine whether $u^*(t)$ is an increasing or decreasing function of time. Equation (5) shows that the relative scaling of the gain rate and metabolic expenditure determines the direction of change. If metabolic expenditure increases faster than the gain rate, u^* will increase over time; if the gain rate increases faster than expenditure, u^* will decrease.

An animal using the Gilliam rule will grow at rate $dx^*/dt = \gamma(u_G(x^*),x^*)$. Substituting for $u_G(x^*)$ from equation (5) gives

$$dx^*/dt = b(x^*), \tag{6}$$

so that, rather suprisingly, in this special case the growth curve depends only on metabolic expenditure.

Once the growth curve $x^*(t)$ has been found from integrating equation (6), we can substitute in equation (5) to find $u^*(t) = u_G(x^*(t))$.

Of course the above analysis assumes that $u_G(x)$ can be found by differentiation. Care must be taken that the value of $u_G(x)$ found from equation (5) does not exceed 1. If it does the analysis needs to be modified.

The metabolic rate of fish increases with mass raised to a power between 2/3 and 1 (Ursin 1967). To illustrate our results, let $b(x) = b_0x^{0.75}$ and suppose that $a(x) = a_0x^d$. Thus the gain rate increases faster than metabolic expenditure if $d > 0.75$. Figure 2 illustrates u_G as a function of x and u^*, and x^* as functions of t for various values of d.

(ii) *Three conditions under which u_G is independent of certain parameters*

In the above example the Gilliam rate u_G did not depend on the way in which predation risk changed with body mass. More generally, if $M(u,x)$ can be expressed as a function of x times a function of u, so that $M(u,x) = \alpha(x)N(u)$, then minimization of $M(u,x)/\gamma(u,x)$ is equivalent to minimization of $N(u)/\gamma(u,x)$ and u_G does not depend on $\alpha(x)$.

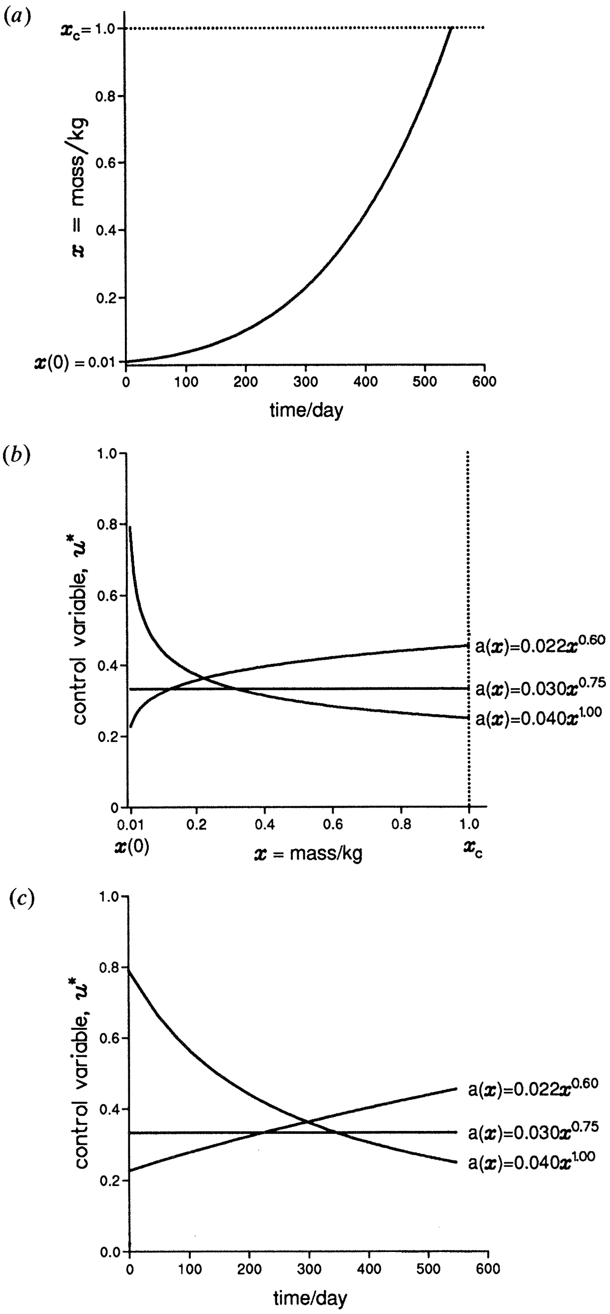

Figure 2. Illustration of Example 1 in which a hypothetical fish must grow from 10 g to 1 kg before it can reproduce. There are no time constraints, so that the optimal policy minimizes the mortality risk per unit increase in mass. Predation $M(u,x) = \alpha(x)u^2$ for any function of body mass $\alpha(x)$. Metabolic expenditure, $b(x) = 0.005x^{0.75}$. We show three cases differing in how the rate of food acquisition $a(x)$ scales with body mass. The actual scaling for a particular species may depend on, for example, whether it is a filter feeder or stalks its prey. (*a*) the growth curve is the same in all three cases (equation (6)). (*b*) The dependence of $u_{\mathrm{OPT}}(x,t) = u_{\mathrm{G}}(x)$ on mass (equation (5)). (*c*) From (*a*) and (*b*) we can calculate how $u^*(t)$ depends on time t.

Even if $M(u,x)$ cannot be expressed in the above form we can write $M(u,x) = \lambda_{\mathrm{A}}\, M_{\mathrm{A}}(u,x)$, where λ_{A} is the overall rate at which predators attack, and M_{A} is the mortality rate given that an attack occurs. It is clear that the value u that minimizes M/γ does not depend on λ_{A}.

To examine the dependence of u_{G} on feeding parameters, consider the case when u is the proportion of time feeding. Then if metabolic expenditure can be ignored, we have $\gamma(u,x) = a(x)u$, so that u_{G} does not depend on the gain rate, $a(x)$. As we demonstrate below, this result no longer holds when an animal reproduces at a fixed time rather than at a fixed state.

McNamara & Houston (1992*a*) derive the latter two results when reviewing models of vigilance behaviour. They show that the model of vigilance proposed by Pulliam *et al.* (1982) is based on minimizing M/γ and that this results in optimal behaviour being independent of both the rate at which attacks by a predator occur and the food supply. They further show that these results follow from the absence of time constraints or time costs.

(*b*) *Including a time penalty*

Minimizing M/γ is optimal if the time at which the critical state is reached has no influence on reproductive success. A more general assumption is that the animal must reach some critical state, but if this state is reached at time τ then the animal's reproductive success is $\mathrm{Rep}(\tau)$ which decreases as τ increases. The animal's expected reproductive success is the probability that it survives to the critical state x_c multiplied by the resulting reward:

$$\exp\left\{-\int_0^{\tau} M(u,(t),x(t))\,\mathrm{d}t\right\}\mathrm{Rep}(\tau).$$

It is now convenient to define quantities R_0 and $\theta(\tau)$ by $R_0 = \mathrm{Rep}(0)$ and $\theta(\tau) = -\log(\mathrm{Rep}(\tau)/\mathrm{Rep}(0))$, so that $\mathrm{Rep}(\tau) = R_0 \exp(-\theta(\tau))$. As $\mathrm{Rep}(\tau)$ is decreasing in τ, $\theta(\tau)$ is a non-negative increasing function of τ. The formula for reproductive success can then be rewritten as

$$\exp\left\{-\int_0^{\tau}(M(u(t),x(t)) + \theta'(t))\,\mathrm{d}t\right\}R_0,$$

which generalizes a result of Sibly *et al.* (1985).

This formula shows that the inclusion of a time penalty results in a problem equivalent to reaching a state x_c under the time-dependent mortality pressure

$$\tilde{M}(u,x,t) = M(u,x) + \theta'(t),$$

where the reproductive success on reaching x_c is R_0 and is not discounted by time.

In this case it is not necessarily optimal to minimize $\tilde{M}/\gamma$ at each time because of the time dependence. But when $\theta(t) = \theta_0 t$, and thus $\theta'(t) = \theta_0$, we have $\tilde{M}(u,x) = M(u,x) + \theta_0$, which is independent of t, and the optimal policy is to minimize $\tilde{M}/\gamma$. In other words, Gilliam's rule then gives the best behaviour provided that the 'mortality' rate is modified by adding θ_0. The general effect of this modification of the mortality rate is to increase u^* compared to the value of u that minimizes M/γ.

Figure 3 illustrates the effect of including a time penalty on the growth of a hypothetical mammal. The illustration is of a case where M and γ do not depend on x. As is shown below, the Risk-spreading Theorem then implies that an animal should use a constant value of u in reaching x_c. Thus the trajectories giving an animal's state as a function of time are straight lines. When there is no time penalty, trajectories from different initial states are all parallel. When $\theta(t) = \theta_0 t$, trajectories are still parallel but have a greater slope. When $\theta(t) = \theta_0 t^2$ trajectories from different initial states are no longer parallel: when an animal starts in a high state, its feeding intensity is similar to that when there is no time penalty; when its initial state is low it has to work much harder than when there is no time penalty. The figure considers different initial states, but a similar result holds when different initial times are considered. Under no time penalty the start time has no effect. Under a penalty of the form $\theta(t) = \theta_0 t^2$, the later an animal starts the harder it should work to obtain food.

Effect of attack rate

Let $M(u,x) = \lambda_A M_A(u,x)$ where, as before, λ_A is the predator attack rate. We have seen that λ_A has no effect on the optimal behaviour when there is no time penalty. When there is a time penalty, the animal should minimize

$$\int_0^\tau (M(u(t),x(t)) + \theta'(t))\mathrm{d}t,$$

which is equivalent to minimizing

$$\int_0^\tau (M_A(u(t),x(t)) + \theta'(t)\lambda_A^{-1})\mathrm{d}t.$$

Thus the effect of increasing λ_A is effectively to decrease the time penalty and hence to reduce the feeding intensity u^* (c.f. McNamara & Houston 1992*a*).

(*c*) *Premature termination of foraging*

Our analysis so far has assumed that the forager will not be interrupted before it reaches the critical level x_c. There are, however, many circumstances in which random interruptions are likely. For example, the foraging of a small bird in winter may be interrupted by bad weather which prevents it foraging until dusk (e.g. Lima 1986). The growth of insects or amphibians in their aquatic phase may be halted by sudden drying out of their pond or stream (e.g. Wilbur & Collins 1973; Wilbur 1980, 1984; McLachlan 1983; Hildrew 1985; Petranka & Sih 1987). In a hibernating animal, the onset of winter may prevent further feeding. Different types of interruptions have different durations. Here we consider interruptions lasting sufficiently long that the animal is prevented from attaining the critical level x_c if an interruption occurs. We refer to this as premature termination. (We will also consider premature termination later when there is a fixed final time.)

In the context of models of vigilance, McNamara & Houston (1992*a*) show that, when there is the possibility of termination, the level of foraging should be higher than the level predicted by minimizing M/γ. Let $\theta'(t)$ be the rate of termination at time t. We can relate $\theta(t)$ to the above analysis in two ways. Premature termination can be taken to result in an increase in mortality of $\theta'(t)$. Alternatively, premature termination can be thought of as introducing time discounting (e.g. McNamara & Houston 1987), with $\theta(t)$ acting as a discount factor. Whichever way we think of premature termination, it will increase u^*.

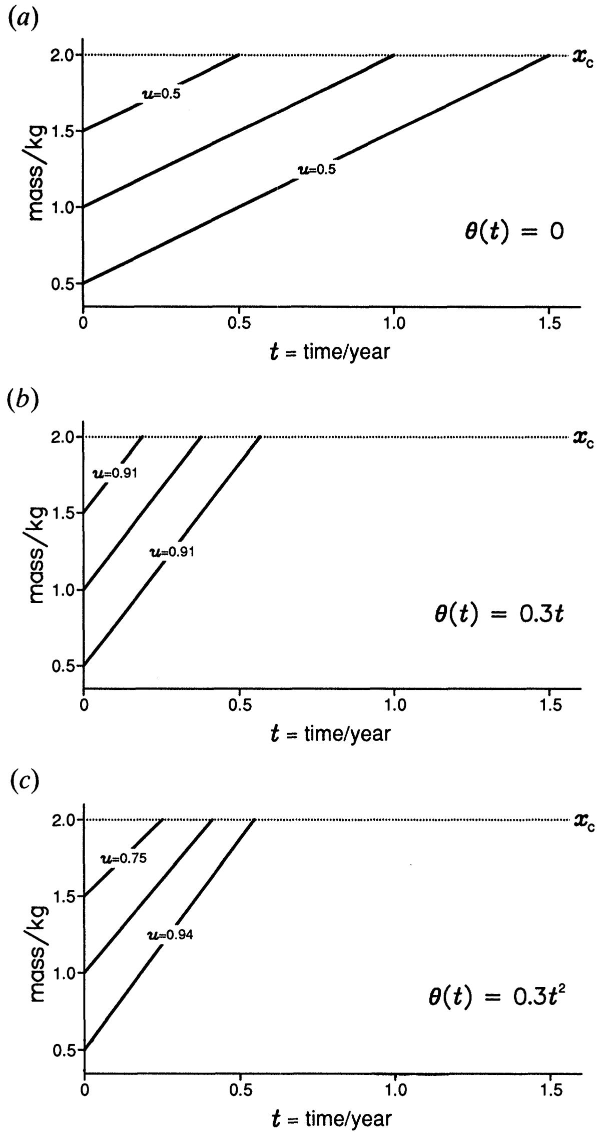

Figure 3. Growth to a fixed size under three different time penalties. This might illustrate a mammal after weaning which must grow to 2 kg before it can reproduce. For each time penalty we consider three different sizes at weaning. (*a*) No time penalty; (*b*) $\mathrm{Rep}(\tau) = \mathrm{Rep}(0)\exp(-0.3t)$; (*c*) $\mathrm{Rep}(\tau) = \mathrm{Rep}(0)\exp(-0.3t^2)$. $M(u,x) = 0.8u^2\ \mathrm{yr}^{-1}$. $\gamma(u,x) = (4u-1)\ \mathrm{kg\ yr}^{-1}$.

(*d*) *The M/γ rule in a stochastic context*

Gilliam (1982) derived the M/γ rule under the assumption that the environment was deterministic. Options were characterized by their predation rate M and gain rate γ. In this section we introduce stochasticity into the food supply, and suppose that an animal has a range of options which differ in M, mean gain rate γ, and variance in gain per unit time σ^2.

Table 1. *The minimization of mortality per unit gain when the environment is stochastic and the gain rate is* $\gamma = 1$

(For each value of mortality M and variance σ^2 the table gives k' as defined in equation (7), s the probability of surviving over an increase of h in the state variable and γ_0 the gain rate which is certainty equivalent to $\gamma = 1$. By certainty equivalent we mean that the value of k' when the gain rate is γ_0 and the variance is 0 is the same as when the gain rate is 1 and the variance is σ^2.)

	$\sigma^2 =$	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
(i)	$M = 0.05$											
	k'	0.0500	0.0500	0.0500	0.0499	0.0498	0.0497	0.0496	0.0494	0.0492	0.0490	0.0489
	$s(h=10)$	0.6065	0.6066	0.6068	0.6072	0.6077	0.6084	0.6092	0.6102	0.6113	0.6125	0.6138
	γ_0	1.0000	1.000	1.001	1.002	1.004	1.006	1.009	1.012	1.016	1.020	1.024
(ii)	$M = 0.25$											
	k'	0.2500	0.2497	0.2488	0.2472	0.2452	0.2426	0.2397	0.2363	0.2327	0.2288	0.2247
	$s(h=10)$	0.08208	0.0823	0.0831	0.0844	0.0861	0.0884	0.0910	0.0941	0.0976	0.1015	0.1056
	γ_0	1.0000	1.001	1.005	1.011	1.020	1.030	1.043	1.058	1.074	1.093	1.112
(ii)	$M = 1$											
	k'	1.0000	0.995	0.981	0.959	0.931	0.899	0.865	0.831	0.797	0.764	0.732
	$s(h=2.5)$	0.0821	0.0831	0.0861	0.0910	0.0976	0.1056	0.1150	0.1253	0.1364	0.1482	0.1604
	γ_0	1.0000	1.005	1.020	1.043	1.074	1.112	1.156	1.204	1.255	1.309	1.366

We model the change in the animal's state as a diffusion process with upward drift γ and variance per unit time σ^2. Then, in the absence of any state-dependent effects, it is shown in Appendix 1 that the usual criterion based on minimization of

$$k = M/\gamma,$$

must be replaced by one based on the minimization of

$$k' = (\sqrt{(\gamma^2 + 2M\sigma^2)} - \gamma)/\sigma^2. \qquad (7)$$

We expect that this criterion will perform quite well even if there are state-dependent effects.

k' decreases with σ^2 for fixed M and γ, so that, given the choice between options with the same predation rate M and gain rate γ, the most variable option should be chosen. For small $M\sigma^2$, we have

$$k' \cong (M/\gamma)(1 - (M\sigma^2/2\gamma^2)).$$

Some idea of the magnitude of the stochastic effects can be seen from table 1.

When M, γ and σ^2 do not depend on state, k' does not depend on state, and an animal following the optimal strategy will not change its choice of options over time. But the derivation of k' was based on the approximation that starvation due to adverse fluctuation in the food supply could be ignored (Appendix 1). Once starvation becomes important, optimal behaviour can depend on state and hence time. McNamara *et al.* (1991) show that it can be optimal to switch from a feeding option with low variance to one with high variance as reserves increase.

We have not formulated the choice of options in terms of a choice of u. Had we done so we would have found that u^* is constant over time when option parameters do not depend on state. This is in contrast to the results on a fixed time to reproduce given below, in which u^* usually decreases with time when we introduce stochasticity, even in the absence of state dependence.

An alternative approach to modelling environmental variability is given by Houston & McNamara 1990. They assumed that each environment is characterized by a probability distribution of the parameter that determines an animal's growth. The probability distribution specifies the possible growth trajectories for the environment. In any particular growing season, only one of these will occur and unlike the preceding model, growth is deterministic with growth rate at a given size proportional to the growth parameter. Before an environment is chosen, the particular growth trajectory is unknown. Houston & McNamara show that if the means of the growth parameter are all equal, survival to a critical size is maximized by maximizing the variance of the growth parameter when mortality is high and minimizing the variance of the growth parameter when mortality is low.

4. FIXED TIME

In this section we are concerned with an animal's behaviour over some period of its life $[0, T]$. The animal starts in state $x(0)$ at time 0. If an animal is alive at time T and is in state x, then its expected reproductive success after time T is given by a terminal reward $R(x)$ (McNamara & Houston 1986). $R(x)$ can be thought of a state-dependent generalization of Fisher's reproductive value. We seek behaviour over the time period that maximizes expected future reproductive success, i.e. that maximizes the probability that the animal survives to T multiplied by the expected reward given that the animal survives.

There are a variety of biological contexts in which a well-defined period $[0, T]$ can be identified. For example, a small bird in winter can only forage during the daylight hours. We can take foraging to start at $t = 0$ (dawn) and end at the time $t = T$ (dusk) when the bird roosts for the night. $R(x)$ is then the long-term survival probability as a function of reserves at T (e.g. see McNamara & Houston 1982, 1986, 1992*b*). For a foraging wading bird, the tidal cycle may determine $[0, T]$. In a species which grows until the end of summer, T would be the end of the growing period and R would specify subsequent reproductive success as a function of size when growth stopped.

Our results are divided into two parts. We begin by assuming that $M(u,x)$, $a(x)$ and $b(x)$ are independent of x. For a small bird foraging between dawn and dusk, this amounts to ignoring mass-dependent metabolism and predation. We believe the model is likely to be a reasonable first approximation in this case. For a growing animal, it is often possible to choose the state variable in such a way that $\gamma(u,x)$ does not depend on x. This procedure is described in detail in Appendix 2 and illustrated below. In this case our results apply provided that mortality is independent of body mass.

The case with no mass-dependence will not always be realistic, but acts as a null model against which mass-dependent effects can be compared. The effect of mass dependence in mortality, in the rate of food gain $a(x)$, and in the rate of metabolic loss $b(x)$ are analysed after we have analysed the mass-independent case in detail.

5. FIXED TIME: NO EFFECT OF STATE

We start by looking at the simplest possible case in which the terminal reward is a step function, there is no refuge, no premature termination of foraging and no stochasticity in the food supply. We then relax these simplifying assumptions one at a time.

(*a*) *Baseline case*

Our assumptions are as follows:

1. The terminal reward function R is a step function

$$R(x) = \begin{cases} 1 & \text{if} \quad x \geqslant x_c \\ 0 & \text{if} \quad x < x_c. \end{cases} \tag{8}$$

What this means is that the animal has a fitness of zero if its state at time T is less than the critical value x_c, but for all states at or above x_c fitness is constant. This sort of function has been used to model the relationship between the reserves of a bird at dusk and its probability of surviving the night (e.g. Stephens 1981; Houston & McNamara 1985). (A more realistic function is described in the next section.) A step function is also likely to be appropriate for an animal that must build up its reserves to a critical level before migrating at a fixed time.

The optimal policy maximizes survival over the period $[0,T]$ subject to the condition that $x(T) \geqslant x_c$. Because $x(T)$ can be increased only by an increase in u and hence an increase in predation, it is obvious that the best value of x at T is x_c.

2. The foraging process is not subject to possible interruptions or terminations before T. We summarize this assumption by saying that there is no premature termination.

3. The food supply is not stochastic.

Given these assumptions, the optimal policies in two circumstances are as follows.

(i) *A discrete set of options*

Assume that the animal has the choice of a series of habitats. Each habitat has a characteristic predation rate M and gain rate γ, independent of the animal's state. Gilliam & Fraser (1987) present a technique for finding the best allocation of time between the possible habitats. Let there be n habitats with the predation rate in habitat i being M_i and the gain rate being γ_i $(i=1, \ldots, n)$. Then by plotting the habitats in a space with axes of gain rate and mortality, the optimum allocation can be found graphically: see figure 1*d*. (The solution minimizes mortality over the whole period.) As Gilliam & Fraser point out, the optimal solution is either to spend all the time in one habitat or to spend time in at most two habitats. When two habitats i and j are used, all patterns of exploitation that result in the same proportion of time in habitat i have equal fitness, and it does not matter in which order the habitats are exploited.

(ii) *M is a convex function of u and there is no refuge*

The basic result for this case is what we call the 'Risk-spreading Theorem'.

Suppose that it is possible to get from state $x(0)$ at time 0 to state x_c at time T. Then the optimal strategy for doing so (i.e. the policy that minimizes the probability of death from predation) is to use a constant value of u. We call this result the 'Risk-spreading Theorem', because the risk of predation is thus spread evenly over T. The constant value of u satisfies

$$(au-b)\,T = x_c - x(0).$$

This result and a formula for the cost of deviation from constant u are derived in Appendix 3. Sibly *et al.* (1985) derived the Risk-spreading Theorem using Pontryagin's Maximum Principle. The theorem is illustrated in figure 4*a* by an example of a small bird that must attain sufficient reserves by dusk if it is to survive the night.

(*b*) *R is log-concave*

The step function used in the previous section means that all states that are below x_c at T are equally bad, and all states that are above x_c at T are equally good. In many circumstances it is more realistic to assume that R is a smoothly increasing function of x. Models of the long-term survival of a small bird in a stochastic environment suggest that log $R(x)$ is concave (e.g. McNamara & Houston 1982, 1986). In this section we assume that R has this property. This is always true when R is increasing and concave, but it can also be true when R is sigmoidal, i.e. convex for small x and concave for large x. If we define $r(x) = \log R(x)$, our assumptions are $r'(x) > 0$ and $r''(x) < 0$.

To find the optimal policy, we start by finding the best way to get from state $x(0)$ at $t=0$ to a particular state x_T at $t=T$. By the Risk-spreading Theorem, it is best to adopt a constant value of u that can be found from the equation

$$x_T - x(0) = (au-b)\,T.$$

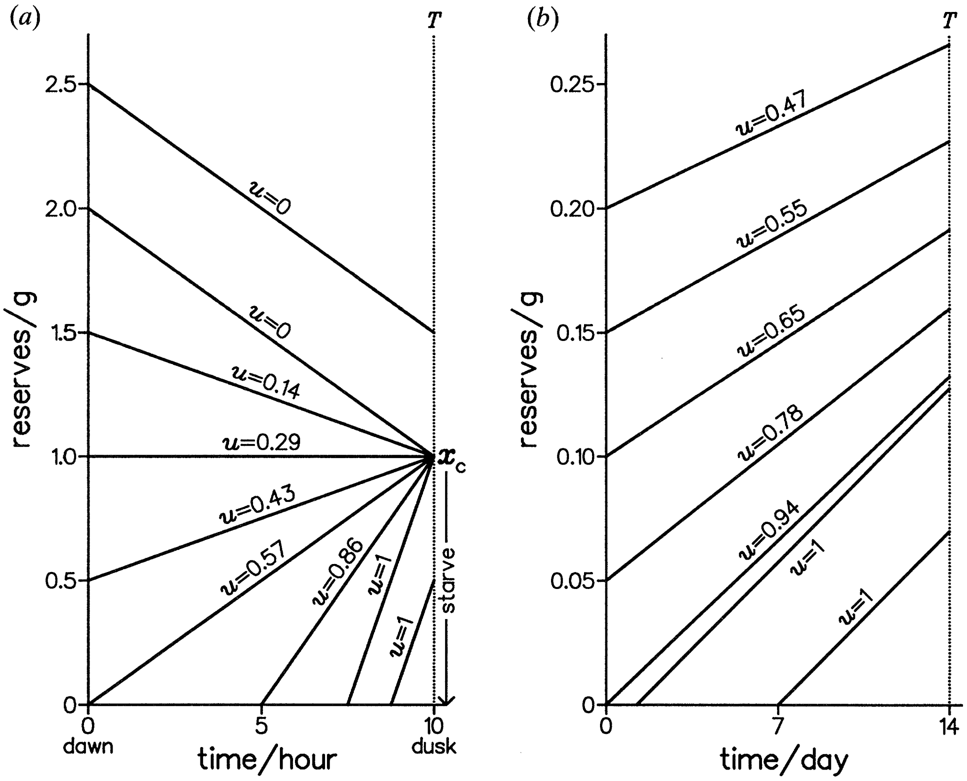

Figure 4. Risk spreading with (*a*) a step-function terminal reward and (*b*) a linear terminal reward. (*a*) is based on a bird of 15 g lean mass which has 10 h of daylight to forage and requires 1 g of energy reserves at dusk if it is to survive the night. u could be the proportion of time feeding as opposed to being vigilant. $M(u,x)$ can be any convex function of u. $\gamma(u,x) = (0.35u - 0.1)$ g h^{-1}. u is constant and depends on the reserves when foraging starts. (*b*) is based on a large ($\simeq 0.5$ g) spider with a fortnight to go before winter. The number of eggs in the clutch laid at the end of the fortnight is proportional to the reserves accumulated by then. $M(u,x) = 0.04u^2$ day^{-1}. $\gamma(u,x) = 0.01u$ g day^{-1}.

The probability that the animal survives the period $[0, T]$ is $\exp(-M(u)\,T)$, and so the animal's expected future reproductive success is

$$W(x_T) = \exp(-M(u)\,T) R(x_T).$$

Thus if we define $w(x_T) = \log W(x_T)$ it follows that

$$w(x_T) = r(x_T) - M(u)\,T.$$

The best choice $x_T{}^*$ of x_T maximizes $W(x_T)$, and hence also $w(x_T)$. By differentiation

$$ar'(x_T{}^*) = M'(u^*),$$

where

$$x_T{}^* - x(0) = (au^* - b)\,T.$$

(i) *Example*

Suppose that fitness at final time T is proportional to state; i.e. $R(x) = R_0 x$ for some constant R_0. Take $M(u) = mu^2$, and suppose for ease of presentation that $b = 0$ and $T = 1$. The above equations then reduce to

$$a/x_T{}^* = 2mu^*, \quad x_T{}^* = x(0) + au^*.$$

Eliminating $x_T{}^*$ from these equations gives

$$2u^* = (x(0)^2/a^2 + 2/m)^{1/2} - x(0)/a,$$

and hence

$$2x_T{}^* = (x(0)^2 + 2a^2/m)^{1/2} + x(0).$$

It is then easy to verify the following:

1. u^* increases as a increases. That is, the better the food the harder the animal works and the greater the predation risk it incurs.
2. u^* and $x_T{}^*$ decrease with increasing m. That is, as the predator attack rate increases, an animal should take less risks and hence end up in a lower state at final time T.
3. u^* decreases with increasing $x(0)$, while x^* increases with increasing $x(0)$. If the initial state is higher an animal has more to lose in expected future reproductive success by being killed by a predator. It should thus take less risk. The decrease in u^* means that $x^* - x(0)$ decreases, but this decrease is not enough to compensate for the increase in $x(0)$ and the state at final time increases. This effect is illustrated in figure 4*b* by an example of a spider accumulating reserves to convert into eggs.

(*c*) *The effect of a refuge*

We start by assuming that the terminal reward is a step function, as given by equation (8), and that the animal can stop foraging and go to a refuge where it is completely safe from predators. When the animal is foraging (outside the refuge), the predation rate is $M(u)$, where $M(0) > 0$ and M is increasing and strictly convex. When it is outside the refuge, the animal's

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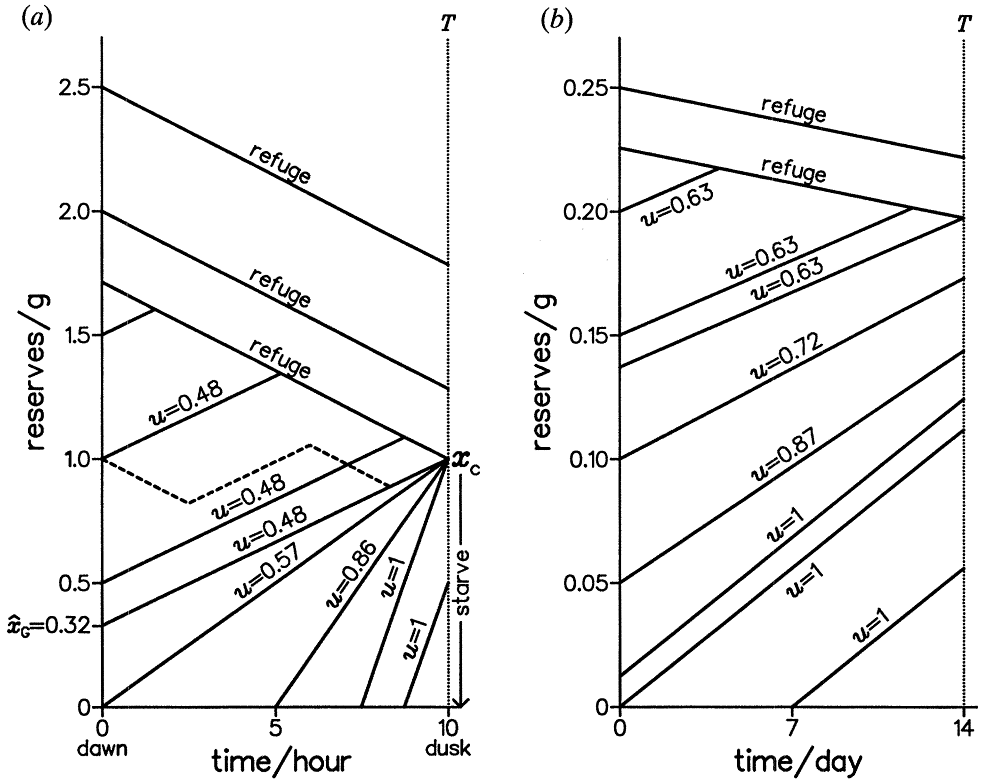

Figure 5. The same scenario as for figure 4 but with the option of a refuge included. (*a*) $M(u,x)$ proportional to $(0.15+u^2)$ h^{-1}, but in the refuge there is no predation. $\gamma(u,x)=(0.35u-0.1)$ g h^{-1}, but in the refuge $\gamma=-0.071$ g h^{-1} due to metabolic expenditure. The dashed line gives an alternative optimal routine in which some time is spent in the refuge at the beginning of the day. (*b*) $M(u,x)=(0.02+0.04u^2)$ day^{-1}, but in the refuge predation = 0.004 day^{-1}. $\gamma(u,x)=(0.01u-0.002)$ g day^{-1}. Metabolic expenditure in the refuge is the same as while foraging so that $\gamma=-0.002$ g day^{-1}.

rate of energy expenditure is b, whereas inside the refuge it is b_r (figure 1*c*).

Let $\hat{u}_G$ be the value of u that minimizes $M(u)/(au-b+b_r)$, and let $\hat{x}_G$ be the state at time 0 such that, when the control variable is maintained at the value $\hat{u}_G$, the state at time T is x_c (i.e. $\hat{x}_G+\gamma(\hat{u}_G)T=x_c$). Then, as shown in Appendix 4 and illustrated in figure 5*a*, the optimal policy has one of two forms depending on the starting value $x(0)$.

1. If $x(0)<\hat{x}_G$, then u^* is constant and greater than $\hat{u}_G$.
2. If $x(0)\geqslant\hat{x}_G$, then $u^*=\hat{u}_G$ for the time required to get to x_c by time T. The remaining time is spent in the refuge.

In the second case it does not matter whether the animal starts by foraging and then rests until T (figure 5), or starts by resting and then forages until T, or alternates between the two throughout the period (c.f. our remarks on Gilliam & Fraser (1987) above). However, once stochasticity or premature termination is introduced into the model, it does matter in which order foraging and resting are performed (see below).

Figure 5*b* illustrates the effect of a refuge when $R(x)$ is log-concave rather than a step function.

(*d*) *Premature termination and a refuge*

In the earlier section in which reproduction occurred in a fixed state, we considered premature terminations–interruptions after which foraging could not recommence. In that case the animal had zero reproductive success after a premature termination; but when reproduction occurs at a fixed time, the animal may already have attained a sufficient state to survive after an interruption until the end of the time period. For the moment, we assume that after termination the animal enters a refuge until time T. In the refuge there is no predation risk and the metabolic expenditure is b_r. The animal may also choose to enter the refuge before termination. Premature termination occurs at rate q, and thus food is available to the animal for an exponential time with mean q^{-1}. These assumptions might apply to a diurnally active animal whose foraging can be interrupted until dusk by bad weather. At the end of this section we develop an example based on the early onset of winter for a hibernating animal.

Consider first the case when R is a step function. An animal whose state x at time t satisfies $x-b_r(T-t)<x_c$ will receive a terminal reward of zero if its foraging is terminated at this time. Thus premature termination acts as an extra source of mortality. Since termination occurs at rate q, the effective mortality is $q+M(u)$. Once $x-b_r(T-t)\geqslant x_c$, the animal will survive premature termination and should enter the refuge whether interrupted or not. The results derived for the refuge when there is no premature termination can thus be modified as follows. Let $\hat{u}_G$ be the value of u that minimizes $(q+M(u))/(au-b+b_r)$ and let $\hat{x}_G$ be, as

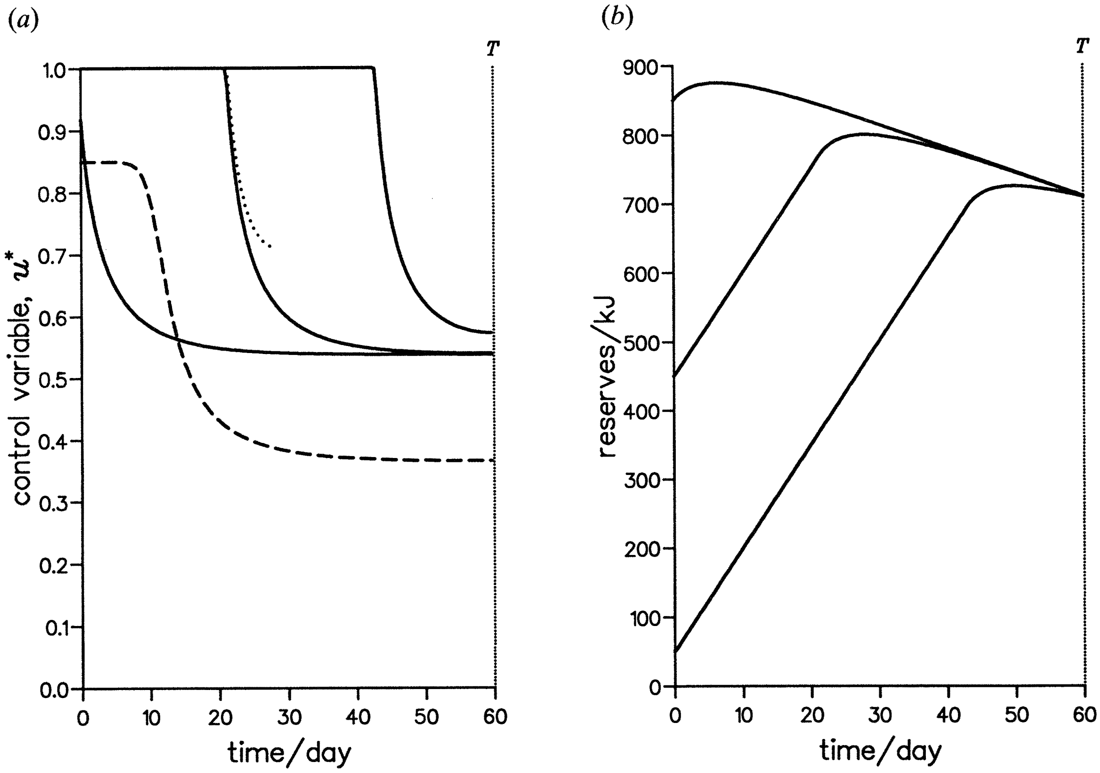

Figure 6. Premature termination with an S-shaped terminal reward. The sets of three solid lines are based on the dormouse example described in the text, and each corresponds to a different level of energy reserves at $t=0$. $M(u,x)=(0.0005+0.0015u^{1.5})$ day^{-1}; in the refuge $M=0.0015$ day^{-1}. $\gamma(u,x)=(40u-25)$ kJ day^{-1}; in the refuge $\gamma=-3.5$ kJ day^{-1}. Interruption rate, $q=0.015$ day^{-1}. The terminal reward is given by $R(x)=x^{20}/(x^{20}+c)$ where c is a constant that ensures the point of inflexion is at $x=500$ kJ. For these parameters the animal does not go into the refuge voluntarily, but it does if we reduce the predation rate in the refuge; the dotted line corresponds to predation in the refuge $=0.00088$ day^{-1} and $x(0)=450$ kJ. If the probability of interruption and metabolic costs are lowered, the initial plateau can be lower than $u^*=1$; for the dashed line $q=0.00015$ day^{-1}, $\gamma(u,x)=(40u-15)$ kJ day^{-1}, $x(0)=450$ kJ. All curves show quantities conditional on termination not having occurred. The control variable is shown in (*a*) and the reserves are shown in (*b*).

before, the state at time 0 such that $\hat{x}_G+\gamma(\hat{u}_G)T=x_c$. As with the refuge, if $x(0)<\hat{x}_G$, then u^* is constant and greater than $\hat{u}_G$; while if $\hat{x}(0)\geqslant x_G$, then $u^*=\hat{u}_G$ when the animal is not in the refuge (figure 5*a*). In contrast to the case of a refuge alone, it does matter in which order the animal forages and rests in the refuge. Resting before its state is sufficiently high incurs a mortality risk of q. It is thus optimal to forage first and then rest.

The effect of increasing the termination rate q is to increase $\hat{u}_G$ and hence increase the optimal value of u.

When R is not a step function, premature termination reduces an animal's reproductive success at time T but may not reduce it to zero. Typically, an animal with low reserves behaves as if termination of foraging is equivalent to death, and uses the constant control $u^*=\hat{u}_G$ if the time to go till T is sufficiently large. As reserves increase, the loss in reproductive success as a result of an interruption decreases until it is approximately optimal to ignore interruptions altogether. The control variable u^* is then again constant (by the Risk-spreading Theorem) and can be found by the analysis given above. Figure 6 illustrates the double plateau in u^*.

In figure 6 we consider a small mammal such as a dormouse which must build up its reserves during the autumn in order to survive its period of hibernation. We consider a two-month period ending at time T in late autumn. When winter ends varies from year to year and thus the terminal reward is a sigmoidal function of energy reserves at T. The onset of winter is also stochastic and terminates the animal's foraging at a constant rate q before time T. The animal hibernates after termination, but it can also choose to enter this refuge earlier. During hibernation metabolic costs are lower, but here we do not assume that the refuge has zero predation, and predation may be higher than when active. u describes how much of the night is spent active. If u is low, dangerous times are avoided and so predation risk is a convex function of u. Using metabolic rates based on Gebczynski *et al.* (1972) and plausible values for other parameters, the optimal strategy is to initially feed all night and then switch to feeding for around half the night (figure 6). This pattern of behaviour is in agreement with that observed by Walhovd (1971).

(*e*) *Stochasticity*

In the last example (on dormice) environmental stochasticity manifested itself in two ways. Premature termination occurred because of variation in when winter started. Variation in the length and severity of winter was modelled by the sigmoidal terminal-reward function. This section considers a third form of stochasticity, variation in the energy expenditure or gain while the animal is foraging. For instance the energy required to capture a prey item, the number of prey items caught, and their sizes, are all stochastic.

To model this, $\gamma(u,x)$ is now taken to be the mean change in x per unit time. The variation about this mean is modelled as independent of u. This is most appropriate when variability is in energy expenditure; in earlier work (e.g. McNamara *et al.* 1987) similar results were obtained when variation was in capture success. We assume a step-function terminal reward given by equation (8).

Results have been obtained numerically using dynamic programming. As usual the optimal policy is a deterministic function of x and t, $u_{\mathrm{OPT}}(x,t)$. But the state $x^*(t)$ and control variable $u^*(t)$ of an animal following this policy are now non-deterministic functions of t. Initially we present results in terms of the mean value of $u^*(t)$, $E(u^*(t))$.

In the absence of stochasticity, $E(u^*(t))$ would be constant by the Risk-spreading Theorem. When stochasticity is high, $E(u^*(t))$ starts at a higher value than this and tends to decrease with time, possibly to a lower value than in the deterministic case (figure 7). Policies are geared towards a run of bad luck, and when this does not come about animals have a high enough x^* to afford a lower u^*. When variance in gain is independent of u, many animals attain the critical value x_c well before T, and at T $E(x^*(T)) > x_c$.

Stochasticity has already been shown to generate a decline in $E(u^*(t))$ in a model of feeding routines of birds (J. M. McNamara, A. I. Houston & S. L. Lima, unpublished results) and in a model of the dawn and dusk choruses (McNamara *et al.* 1987). These examples use energy reserves as the state variable x. We now present an example in which an animal must migrate a critical distance x_c and the state variable x is the distance travelled towards this goal. The animal must finish its migration within a set time, perhaps because of the onset of winter, or in order to find an unpaired mate. Sources of stochasticity might be bad weather, the direction and strength of winds or currents and errors in navigation. For instance Cochran (1975) observed a peregrine falcon on migration that, depending on the weather, spent 37% to 69% of the day circling in thermals; in following winds it attained 47 km h^{-1}, but only 16 km h^{-1} in cross winds. Figure 7 is motivated by this example, with the most appropriate stochasticity being perhaps $\sigma = 59$ km day^{-1}. We know of no data on birds that shows a decline in migration rate (c.f. Dorst 1962); a decline in migration rate has been reported in the Monarch butterfly (Baker 1978) but there are other potential explanations, such as fatigue or a changing environment. Two assumptions of our model may not be appropriate to many migrating animals: in our model the migrant knows the precise value of x, and the value of u chosen does not depend on how favourable that day is for travelling.

It can just be seen in figure 7 that in two cases $E(u^*(t))$ increases for some of the time. But it should be noted that this does not imply that a majority of animals following the policy will be observed to increase u^*. In the more extreme example in figure 8 most of the increase in $E(u^*(t))$ is generated by a minority of birds who have been unlucky and have consequently dramatically increased their u^*. Figure 8 also shows that $u^* = 0$ for many animals near the end of the time period. In observational studies these animals, having ceased foraging (and perhaps moved elsewhere), may not be included in the sample. Consequently observations on $E(u^*(t))$ may be biased (J. M. McNamara, A. I. Houston & S. L. Lima, unpublished results).

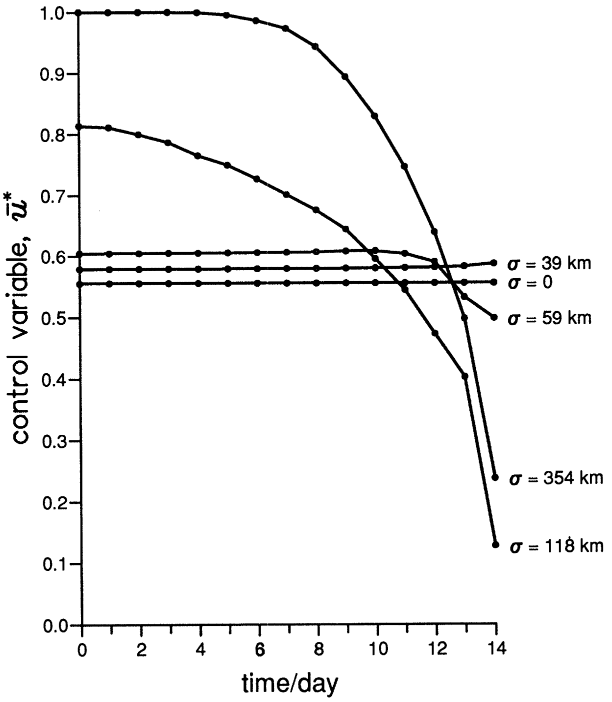

Figure 7. Effect of stochasticity for an example based on a bird migration lasting 15 days, in which the environment varies from day to day. $x_c = 2500$ km. $M(u,x) = 0.001u^{1.5}$ day^{-1}. $\gamma(u,x) = 300u$ km day^{-1}. For each curve, σ the per-day standard deviation in distance covered, is given. For illustrative purposes we show extreme values of σ, as well as more realistic ones.

6. FIXED TIME: STATE-DEPENDENT EFFECTS

When first setting up our model we discussed how an animal's state (reserves, size, log(size), etc.) might affect mortality rate and its food supply. We now analyse such state-dependent effects when the animal controls its behaviour over a fixed time interval $[0,T]$, and relate our conclusions to those obtained when reproductive success was assessed at a fixed state x_c.

Our starting point is the baseline case of the previous section. This null case assumed no state dependence, stochasticity or premature termination. We will introduce state dependence in turn on energy gain and then predation. Conclusions hold provided $M(u,x)$ is either a linear, strictly convex or piecewise

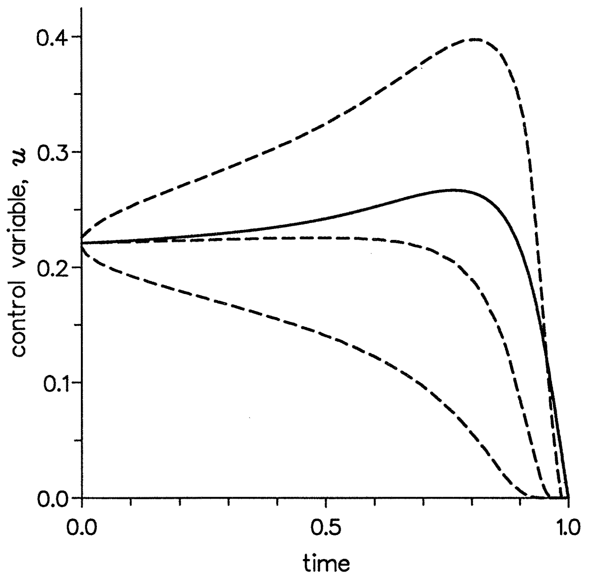

Figure 8. An abstract example in which stochasticity causes $E(u^*(t))$ to increase over the first half of the time period. The solid line shows the mean $E(u^*(t))$. The dashed lines show the median and both quartiles of u^*. $T=1$. $x_c=1$. $x(0)=0$. $M(u,x)=xu^{1.5}$. $\gamma(u,x)=8u$. Standard deviation in gain $\sigma=1$.

linear and convex function of u for each x (figure 1*a*,*b* and *d*).

(*a*) *Gain dependent on state, predation independent of state*

We first allow γ to depend on x, but assume that M does not depend on x, i.e. $\gamma(u,x)=a(x)u-b(x)$ and $M(u,x)=M(u)$. It is shown in Appendix 5 that, whatever the terminal reward function: (i) if $b(x)/a(x)$ is an increasing function of x, then $u^*(t)$ increases with t; and (ii) if $b(x)/a(x)$ is a decreasing function of x, then $u^*(t)$ decreases with t.

In the special case $b=0$, u^* is constant. (This also follows from rescaling x and applying the Risk-spreading Theorem.) The general pattern agrees with that derived from Gilliam's rule in Example 1, where fitness is assessed at a fixed state. As an example in which $b(x)/a(x)$ increases with x, consider a small bird in winter. We take x to be energy reserves, u to be the proportion of time feeding as opposed to being vigilant and $[0,T]$ to be a daylight period ending at dusk. For the sake of illustration, we suppose, perhaps unrealistically, that predation risk does not depend on energy reserves. $a(x)$ is then the energy gained per unit time feeding and $b(x)$ is the rate of metabolic expenditure.

In this scenario it is reasonable to assume that $a(x)$ is either constant or decreases with x, because a heavier bird has fewer feeding options available. Metabolic expenditure, especially of flight, will increase with reserves. Thus $b(x)/a(x)$ increases with x and hence $u^*(t)$ increases with t; i.e. according to this simple model the bird should become less vigilant as dusk approaches. Figure 9 illustrates $u^*(t)$ and $x^*(t)$ when $a(x)$ is constant, $b(x)$ increases linearly with x and $M(u)=mu^2$. It is shown in Appendix 5 that $u^*(t)$ is proportional to $\exp(b_1t)$ where $b_1=b'(x)$ in this case.

(*b*) *The form of state-dependent predation*

In the last example it was perhaps unrealistic to assume predation was independent of state. Once we introduce state dependence on predation risk we must specify not only how $M(u,x)$ changes with x for fixed u, but also how this relationship changes when behaviour, u, changes. As we show below, this interaction between x and u is crucial. We consider two cases in detail: a multiplicative and then an additive interaction.

To isolate the effect of state dependence in predation from that in energy gain, we will assume that $a(x)$ and $b(x)$ are constant. In fact the case in which $b(x)/a(x)$ is constant can always be reduced to this case by rescaling x (Appendix 2).

(*c*) *Gain independent of state, multiplicative state-dependent predation*

Assume that $a(x)=a$ and $b(x)=b$ are constants and that M can be written multiplicatively as

$$M(u,x)=N(u)\alpha(x),$$

where N is some function of u and α is some function of x. This form of mortality might apply to vigilance behaviour. Suppose that an animal which detects a predatory attack escapes; if it fails to detect the attack it sometimes escapes. Therefore

$$\begin{array}{l}\text{mortality}\\ \text{rate}\end{array} = \begin{array}{l}\text{attack}\\ \text{rate}\end{array} \times \begin{array}{l}\text{Probability fails}\\ \text{to detect}\end{array} \times \begin{array}{l}\text{Probability}\\ \text{to escape}\end{array}$$

Typically, the probability that it fails to detect is a function of the proportion of time spent vigilant, $1-u$, and hence of u. If escape is hampered by excess fat reserves, the probability it fails to escape is a function of x.

We begin with a general result valid for any terminal reward function. As before, u_G is the value of u which minimizes M/γ. Because

$$M(u,x)/\gamma(u,x)=(N(u)/(au-b))\alpha(x),$$

u_G does not depend on x. Results can then be expressed in terms of how predation depends on state and the value of u^* compared with u_G. In Appendix 6 it is shown that either $u^*(t)\leqslant u_G$ for all t between 0 and T or $u^*(t)\geqslant u_G$ for all t between 0 and T. If $\alpha(x)$ is increasing in x, $u^*(t)$ increases in t if $u^*(t)\leqslant u_G$ and decreases in t if $u^*(t)\geqslant u_G$. Conversely if $\alpha(x)$ is decreasing in x, $u^*(t)$ decreases if $u^*(t)\leqslant u_G$ and increases if $u^*(t)\geqslant u_G$. These results are summarized in table 2*a*(i) and illustrated in figures 10*a* and 11*a*.

(i) *Step-function terminal reward*

When the terminal reward is given by equation (8) and N is such that $N(0)=0$, the results given in table 2*a*(i) can be rephrased in terms of the initial state $x(0)$. Let x_G be the state at time 0 such that, when the control variable is maintained at the value u_G, the state at time T is x_c (i.e. $x_G+\gamma(u_G)T=x_c$). Our results are derived in Appendix 6, summarized in table 2*b*(i) and illustrated in figures 10 and 11. When the starting value $x(0)$ equals x_G, u^* is constant over the time

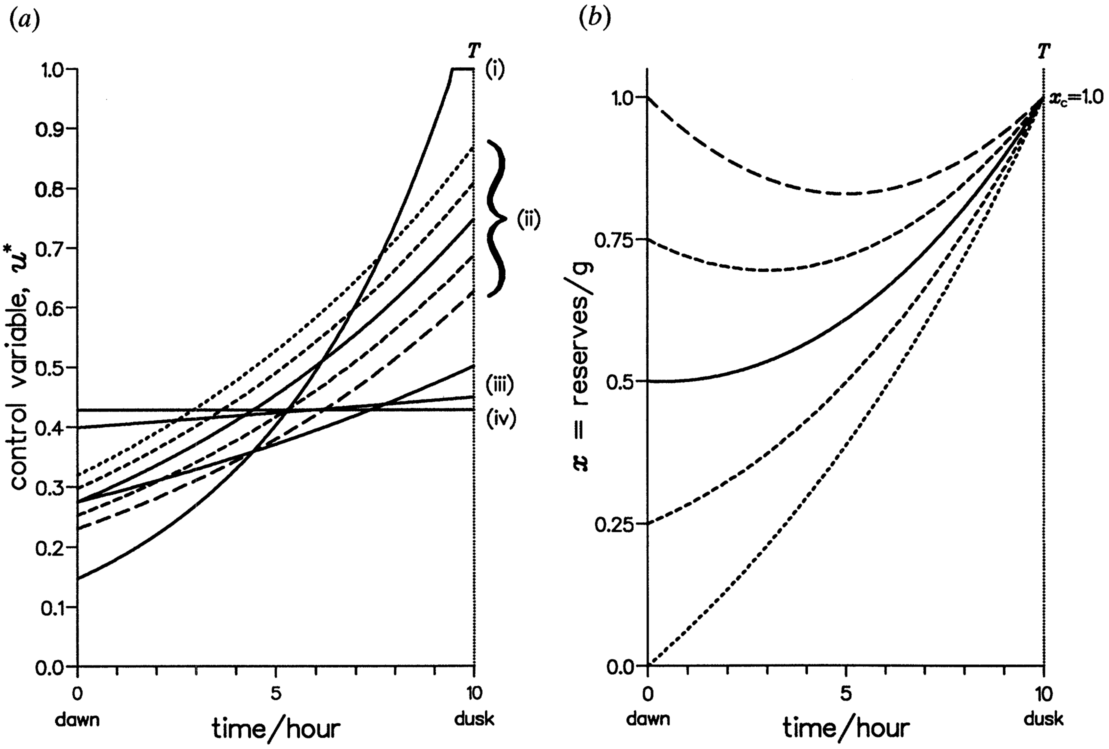

Figure 9. The effect of mass-dependent metabolism on a small bird. The parameters are the same as in figure 4*a* except that metabolic cost $b(x) = b_0 + b_1(x - 0.5)$ g h^{-1}. b_0 is always 0.1 g h^{-1}, so that metabolic cost at $x = 0.5$ g is the same in all cases. (*a*) Control variable u^* as a function of time. (i) $b_1 = 0.2$ h^{-1}; (ii) $b_1 = 0.1$ h^{-1}; (iii) $b_1 = 0.02$ h^{-1}; (iv) $b_1 = 0$. In all the solid lines the start value was 0.5 g. The dashed lines are for a range of start values in case (ii); corresponding trajectories of reserves are shown in (*b*).

interval $[0, T]$ and equal to u_G. So for this special case the optimal trajectory is the same as that when fitness is assessed at a fixed state. For other starting values u^* is not constant; whether u^* increases or decreases with time can now be specified in terms of whether α is increasing with x and whether $x(0)$ is greater than x_G.

(ii) *Ludwig & Rowe (1990)*

We now show how the results in table 2*a*(i) can be used to rederive a result of Ludwig & Rowe (1990). They consider an animal which has a choice between two habitats. Habitat 2 has a higher rate of food gain than Habitat 1 but also has a higher predation risk. They analyse in detail a case in which the rate of change of weight w is

$dw/dt = \lambda_i l(w)$ in Habitat i,

and the predation risk is

$s_i m(w)$ in Habitat i.

(Here we have used the symbol s_i rather than Ludwig & Rowe's γ_i to avoid confusion with our $\gamma(u,x)$.)

To re-express their model in terms of our current model we define a new state variable x by $dx/dw = l(w)^{-1}$. Then (Appendix 2)

$dx/dt = \lambda_i$ in Habitat i.

Defining a function α by $\alpha(x) = m(w(x))$, the predation risk in Habitat i becomes $s_i\alpha(x)$. Now let u be the proportion of time in Habitat 2. Then it is easily shown that the rate of gain is

$\gamma(u,x) = (\lambda_2 - \lambda_1)u + \lambda_1$,

and the predation risk is $M(u,x) = N(u)\alpha(x)$, where α is defined above and

$N(u) = s_1 + (s_2 - s_1)u$.

Thus gain is independent of state, x, and M is multiplicative.

Consider the case in which $s_2/\lambda_2 < s_1/\lambda_1$. Then an animal minimizing its predation risk per unit increase in state should spend all its time in Habitat 2; i.e. $u_G = 1$. It follows that $u^*(t) \leqslant u_G$ for all t. We now apply the results shown in table 2*a*(i). They show that when $\alpha(x)$ (and hence $m(w)$) is increasing, $u^*(t)$ is increasing. Thus any switch of habitat that occurs must be from Habitat 1 to Habitat 2. Conversely if α is decreasing any switch must be from Habitat 2 to Habitat 1.

Analysis of the case $s_1/\lambda_1 < s_2/\lambda_2$ is similar. In this case $u_G = 0$. Table 2*a*(i) then shows that when α is increasing, any switch is from Habitat 2 to Habitat 1, and when α is decreasing any switch is from Habitat 1 to Habitat 2.

Ludwig & Rowe (1990) implicitly assume that $m(w)$ (and hence $\alpha(x)$) is a decreasing function, and our results agree with their results for this case. We have also just shown that assuming $m(w)$ increasing gives opposite predictions.

(*d*) *Gain independent of state, additive state-dependent predation*

As in the previous model we assume that $a(x) = a$

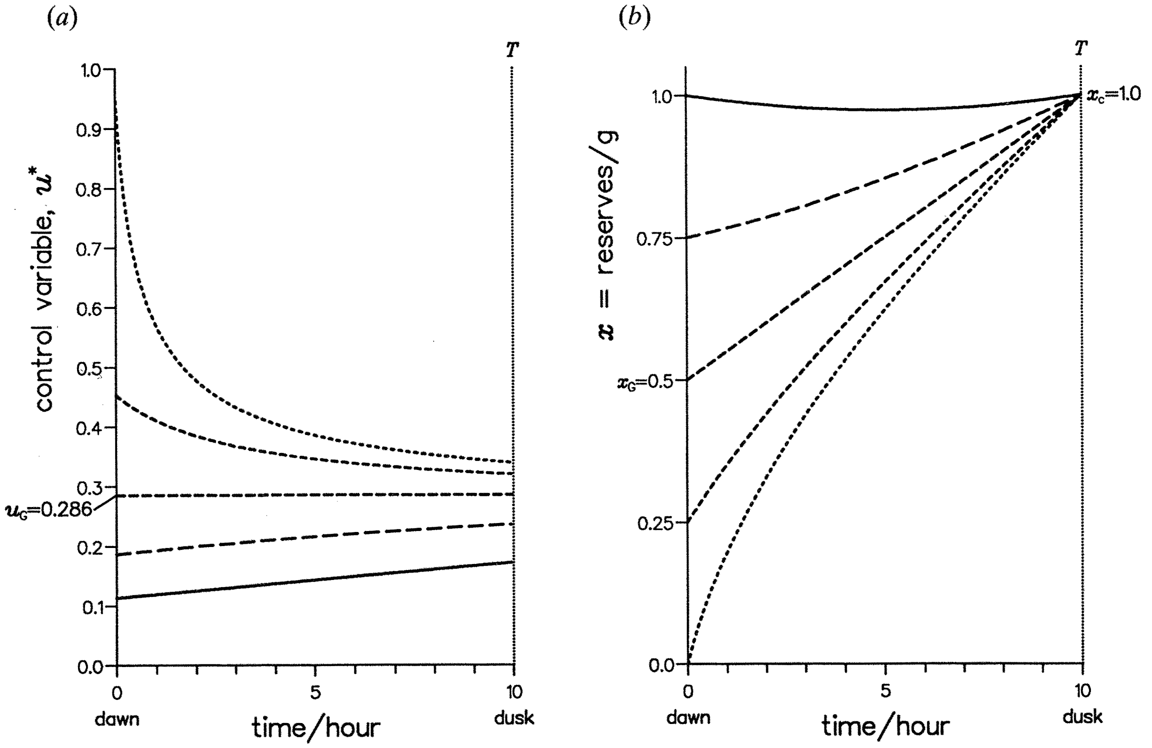

Figure 10. Multiplicative mass-dependent predation with predation increasing with mass. The example is again of the small bird of figures 4*a* and 9 except metabolic cost $b(x) = 0.5$ g h^{-1} and $M(u,x) = k\,u^2\,(1+\sqrt{(2x)})^2$ (so that, as in (ii) of figure 9, reserves of 1.0 are twice as 'expensive' as reserves of 0.5). (*a*) Control variable u^* as a function of time for different starting values $x(0)$. The corresponding trajectories of reserves are shown in (*b*).

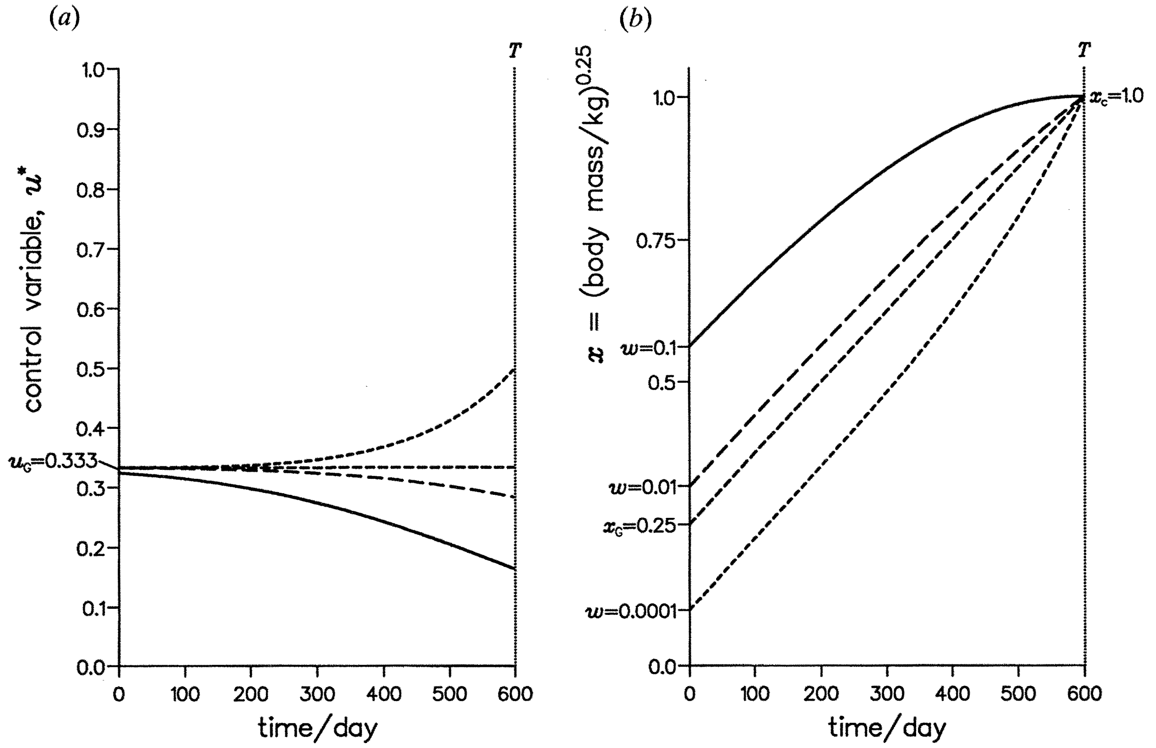

Figure 11. Multiplicative mass-dependent predation with predation decreasing with mass. The example is based on the hypothetical fish of figure 2, which now must attain a mass of 1 kg within 600 days. Let w = body mass/kg. We assume $\mathrm{d}w/\mathrm{d}t = (0.03u - 0.005)w^{0.75}$ day^{-1}. To remove the mass dependence on gain, we define a new state variable $x = w^{0.25}$, so that $\mathrm{d}x/\mathrm{d}t = 0.0075u - 0.00125$ day^{-1}. Predation is inversely proportional to mass (Type III survivorship curve): $M(u,x) = ku^2/x^4$. (*a*) control variable u^* as a function of time for different starting values $x(0)$. The corresponding trajectories of reserves are shown in (*b*).

Table 2. *The dependence of* u^* *on time when mortality depends on state*

(Gains independent of state, fixed final time.)

(*a*) $M(u,x) = N(u)\alpha(x)$		
(i) classification in terms of $u^*(t)$		
	$u^*(t) \leqslant u_G$	$u^*(t) \geqslant u_G$
$\alpha'(x) > 0$	$du^*/dt \geqslant 0$	$du^*/dt \leqslant 0$
$\alpha'(x) < 0$	$du^*/dt \leqslant 0$	$du^*/dt \geqslant 0$
(ii) classification in terms of $x(0)$ when R is a step function and $N(0) = 0$		
	$x(0) \leqslant x_G$	$x(0) \geqslant x_G$
$\alpha'(x) > 0$	$du^*/dt \leqslant 0$	$du^*/dt \geqslant 0$
$\alpha'(x) < 0$	$du^*/dt \geqslant 0$	$du^*/dt \leqslant 0$
(*b*) $M(u,x) = N(u) + \alpha(x)$		
$\alpha'(x) > 0$	$du^*/dt \geqslant 0$	
$\alpha'(x) < 0$	$du^*/dt \leqslant 0$	

and $b(x) = b$ are constants, but now assume that predation risk can be expressed additively as

$$M(u,x) = N(u) + \alpha(x).$$

This form of M would arise if there were two independent sources of mortality, one source dependent on behaviour alone and the other source dependent on state alone.

It is shown in Appendix 7 that u^* increases with time if and only if $\alpha'(x) > 0$. This result is included in table 2.

Sibly et al. (1985)

These authors investigate a model of optimal growth that can be transformed so that gain is independent of state. In our terms, x is the logarithm of size, and $dx/dt = u$ (see Appendix 2). They reach the conclusion that $u^*(t)$ is increasing if and only if $\alpha'(x) > 0$. We have seen that this result holds for additive mortality but not for multiplicative mortality. Sibly *et al.* specify how mortality depends on x for fixed u and on u for fixed x, but do not discuss how x and u interact. Their conclusion is based on a graphical argument, which rests on the implicit assumption that mortality as a function of u does not change over time. But mortality depends on u and x and so as x changes, the mortality function will change. When $M(u,x) = N(u) + \alpha(x)$, the effect of increasing x is to shift the function upwards without changing its shape. In this case the argument of Sibly *et al.* applies. When $M(u,x) = N(u)\alpha(x)$, then as x increases, the shape of the function changes and the argument of Sibly *et al.* is invalid.

7. DISCUSSION

In this paper we have established some general analytic results concerning the trade-off between gaining energy and avoiding predation. We have also carried out numerical investigations of cases that we have not solved analytically. Our results are relevant to a variety of biological contexts, including foraging, choice of habitat and growth. We now discuss these topics, bringing out the implications of our results and comparing them with those of other people.

(*a*) *Foraging and satiation*

When foraging is being studied, u has a clear interpretation in terms of foraging intensity, with the animal's rate of energetic gain being given by $\gamma(x,u) = a(x)u - b(x)$. When x is the animal's level of energy reserves, $b(x)$ can be thought of as mass-dependent metabolism, so $a(x)u$ is the gross rate of gain. Rate maximization corresponds to $u = 1$.

The Risk-spreading Theorem tells us that if there is no premature termination of the foraging process and no refuge, if $a(x)$ and $b(x)$ are constants a and b and if energetic gain is deterministic rather than stochastic, then it is optimal to keep u constant over the foraging period. To get satiation effects, one or more of these conditions must be violated.

It is often observed that intake rate declines over a foraging bout (e.g. Bousfield 1933; McCleery 1977). We refer to this as satiation. This term does not necessarily imply physiological constraints such as filling of the gut and indeed our model assumes no such constraints. The models of satiation suggested by Sibly & McFarland (1976) and Heller & Milinski (1979) involve a cost that is additive in state and behaviour. It is not clear, however, what aspects of the animal's biology these costs are meant to represent (but see Sibly & Calow 1986). Our results establish a variety of conditions in which the optimal value of u decreases with time. In the absence of state-dependent effects, stochasticity or premature termination can result in such a trend. In our model, if an animal's foraging is terminated before final time, the animal's reserves decrease until final time. Houston & McNamara (1989) modelled premature termination in a slightly different way, but they also found satiation effects.

In the absence of stochasticity or premature termination, state-dependent effects can produce satiation. When predation is independent of x, if $a(x)/b(x)$ is a decreasing function of x then it is optimal for u to decrease over time. When $a(x)$ and $b(x)$ do not depend on x, then state-dependent predation can result in satiation. When the effects of state and behaviour are additive, so that $M(x,u) = \alpha(x) + N(u)$, then the optimal behaviour involves satiation if $\alpha'(x) < 0$. But unless birds with low reserves are too weak to avoid predation, it seems unlikely that an increase in reserves will reduce predation risk. When the effects of state and behaviour are multiplicative, i.e. $M(x,u) = \alpha(x)N(u)$, an increase in predation with reserves can under some circumstances result in satiation. The relevant results are summarized in table 2.

(*b*) *Group size*

Mangel (1990) considers two sorts of model of optimal flock size. In the one that is directly relevant to this paper, flocks form before food is found. The flock size n in which a bird forages determines the mean and variance of the bird's energetic gain and the probability that it is killed by a predator. Mangel assumes that the mean gain and the danger of predation both decrease as n increases. Metabolic expenditure increases with increasing energy reserves.

To put Mangel's model into our terms, we can regard flock size n as being parameterized by u, such that u decreases as n increases. If we ignore the fact that u influences variance, then our results indicate that in the absence of stochasticity and mass-dependent effects, flock size should be constant over the foraging period. If either stochasticity or mass-dependent metabolism are present, they will tend to make u^* decrease with time, which means that the optimal flock size should increase.

Mangel computed optimal flock size as a function of reserves and time when $R(x) = x/(x+0.1)$. He found that optimal flock size increased with t for fixed x. It does not follow, however, that flock size will increase with time. As Mangel points out, to find expected behaviour it is necessary to follow the policy forward in time. In our terms, optimal flock size is related to $u_{\mathrm{OPT}}(x,t)$. To determine u^* it is necessary to find not only u_{OPT}, but also how x changes over time when the optimal policy is followed.

(*c*) *Growth*

When an animal's growth is not constrained to occur within a fixed time interval, Gilliam's μ/g criterion provides a simple way to combine the disadvantages of predation and the advantages of growth. It has been used to analyse growth and habitat choice in fish and amphibians (e.g. Werner *et al.* 1983; Werner & Gilliam 1984; Werner 1986; Werner & Hall 1988). As Ludwig & Rowe (1990) point out, the criterion will not necessarily result in optimal behaviour when there are time constraints. In this paper we have shown that a time penalty is equivalent to an extra source of mortality, θ_0, that is independent of the animal's choice of action. The effect of such an additional mortality is to increase the optimal rate of growth above the Gilliam rate u_G.

If there are no time constraints, we can use the μ/g criterion to explore the effect of an increase in predation pressure. The prediction depends on how the effect of predation pressure, α, and the effect of behaviour, N, jointly determine mortality. If mortality is the sum, $\alpha + N$, of these terms so that there is no interaction between the sources of mortality, then Gilliam's criterion predicts an increase in growth rate with increasing predation pressure. If mortality is the product, αN, of these terms, then Gilliam's criterion predicts that predation pressure should have no effect on growth rate. If, however, mortality rate is $\alpha N + \theta_0$ where θ_0 is a source of mortality (or a time penalty) which is independent of predation pressure, then Gilliam's criterion predicts a decrease of growth with increasing predation pressure.

The predation pressure α may be increased in two different ways. First, $\alpha = \alpha(x)$ is a function of size x, and there may be a range of sizes for which the predation risk is especially high. Should the animal hurry through this size range? The above discussion shows that this is not necessarily advantageous; the optimal behaviour depends on specific details.

Secondly, even two animals of the same size may be exposed to different levels of predation because they are in different localities or because predation pressure may vary from year to year. If an animal can detect such variation, should an increase in predation pressure decrease growth rate? Such a decrease has been observed (e.g. Skelly & Werner 1990; Werner 1991; Fraser & Gilliam 1992). The above analysis suggests reasons for this. There is, however, another explanation. Animals may interpret an increase in predation pressure as temporary and play safe by adopting a low growth rate while waiting for the danger to decrease.

(*d*) *Flexibility in both final state and final time*

Our paper has dealt with the increase of the state variable to a fixed state or decision making within a fixed time. Although these scenarios are sometimes appropriate, very often the animal decides both its final state and its final time, there being a trade-off between the advantages of a high final state and the disadvantages of a late final time. For instance a male spider deciding how large to grow before moulting into an adult, should trade-off the advantages of larger size (e.g. in terms of mate choice) with the disadvantage of finding fewer unmated females if he moults later. Rowe & Ludwig (1991) analyse this sort of trade-off with reference to life-history decisions such as metamorphosis.

Our models do not deal directly with the case in which both final state and time are flexible. Nevertheless, our results do yield insights into this situation. Suppose there is no stochasticity and that the final state under an optimal policy is x_F and the final time is t_F. Our results will not predict x_F or t_F. But whatever their values, the optimal trajectory will coincide with the optimal trajectory for a fixed-time problem with final time $T = t_F$ and a step-function terminal reward with $x_c = x_F$. Thus if the qualitative form of the trajectory predicted by our fixed time analysis does not depend on x_F or t_F, we can predict the form of the optimal trajectory when final state and time are flexible. For example, in the absence of complicating factores such as interruptions and mass dependence, the Risk-spreading Theorem will still predict that a constant value of u is optimal whatever the trade-off between final state and time. Similarly, if we now make metabolic expenditure increase more rapidly with state than food intake ($b(x)/a(x)$ increases with x) then we still predict that $u^*(t)$ will increase with time t.

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APPENDIX 1. MODIFICATION TO GILLIAM'S (1982) RULE WHEN THERE IS STOCHASTICITY

We assume an animal has a choice of options, where each option is characterized by a mortality rate M, a mean net gain per unit time γ and a variance in gain per unit time σ^2. Reserves are in the range $(-\infty, x_c)$ and we seek the strategy which maximizes the animal's probability of reaching x_c.

Let $x < y < x_c$. Then it can be seen that the optimal policy for reaching x_c from x must maximize the probability of reaching y from x. It follows that the optimal action to choose in state $x (x < x_c)$ does not depend on x. We can therefore restrict attention to policies which always choose the same option, and seek the best policy in this class.

We model the change of reserves under the policy of choosing a fixed option with parameters M, γ and σ^2 as a diffusion process with killing rate M, drift γ and diffusion coefficient σ^2. Let $f(x)$ be the probability of reaching x_c starting from x under the policy. Then f satisfies the backward equation

$$\tfrac{1}{2}\sigma^2 f''(x) + \gamma f'(x) - Mf(x) = 0, \qquad \text{(A1.1)}$$

and boundary condition

$$f(x_c) = 1. \qquad \text{(A1.2)}$$

It can be verified that equations (A1.1) and (A1.2) have solution

$$f(x) = \exp\{-k'(x_c - x)\} \qquad x \leqslant x_c, \qquad \text{(A1.3)}$$

where k' is the positive root of the equation

$$\tfrac{1}{2}\sigma^2 k'^2 + \gamma k' - M = 0. \qquad \text{(A1.4)}$$

Thus k' is given by equation (7).

Since, for each $x, f(x)$ is maximized by minimizing k' we conclude that the optimal policy is to always choose the fixed option which minimizes k'.

Finally, we note the analogy between k' and the performance criterion $k = M/\gamma$ of Gilliam (1982). When there is no stochasticity the probability of reaching x_c under a fixed option with parameters M and γ is

$$g(x) = \exp\{-k(x_c - x)\}. \qquad \text{(A1.5)}$$

Thus, by comparing equations (A1.3) and (A1.5) we see that k' plays the same role in a stochastic setting as M/γ plays in a deterministic one.

APPENDIX 2. TRANSFORMATION OF THE STATE VARIABLE

The rate of increase of the state variable x is given by

$$\mathrm{d}x/\mathrm{d}t = \gamma(u,x). \qquad \text{(A2.1)}$$

Assume $\gamma(u,x) = a(x)u - b(x)$. Define the new state variable $y = y(x)$ by

$$y(x) = \int_{x_0}^{x} \frac{\mathrm{d}v}{a(v)},$$

where x_0 is some fixed reference state. Then $\mathrm{d}y/\mathrm{d}x = 1/a(x)$ and hence by equation (A2.1)

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \gamma(u,x)/a(x) = u - (b(x)/a(x)),$$

so that the term multiplying u does not depend on state. If $b(x)$ and $a(x)$ scale the same as each other, the ratio $b(x)/a(x)$ does not depend on x. Calling the ratio B we can then write

$$\mathrm{d}y/\mathrm{d}t = u - B$$

so that, in the new state variable y, rate of increase of state is independent of state.

APPENDIX 3. THE RISK-SPREADING THEOREM

Assume $\gamma(u,x) = au - b$ where a and b are constants, and that $M(u,x) = M(u)$ is a convex function of u alone. Let states x_0 and x_T be given. Let u^* be the constant value of the control u such that if $x(0) = x_0$ then $x(T) = x_T$; i.e.

$$(au^* - b)T = x_T - x_0. \tag{A3.1}$$

Here we consider all controls $\underline{u} = \{u(t): 0 \leqslant t \leqslant T\}$ during $[0,T]$ such that if $x(0) = x_0$ then $x(T) = x_T$, and show that the control minimizing predation risk within this class is given by $u(t) = u^*$ for all $t \in [0,T]$.

Let $\underline{u}$ be a control such that if $x(0) = x_0$ then $x(T) = x_T$. Then

$$\int_0^T \gamma(u(t))\mathrm{d}t = x_T - x_0, \tag{A3.2}$$

so that by equations (A3.1) and (A3.2) and the definition of γ

$$\frac{1}{T}\int_0^T u(t)\mathrm{d}t = u^*. \tag{A3.3}$$

The probability of surviving until time T under this control is

$$\exp\left\{-\int_0^T M(u(t))\mathrm{d}t\right\},$$

and is minimized by minimizing

$$f(\underline{u}) = \frac{1}{T}\int_0^T M(u(t))\mathrm{d}t. \tag{A3.4}$$

Now let W be a random variable which has a uniform distribution on the interval $[0,T]$ and define the random variable U by $U = u(W)$. Then equation (A3.3) can be written as

$$\mathbb{E}(U) = u^* \tag{A3.5}$$

and equation (A3.4) can be written as

$$f(\underline{u}) = \mathbb{E}\{M(U)\}. \tag{A3.6}$$

Our problem then becomes one of choosing a random variable U taking values in $[0,1]$ which minimizes $\mathbb{E}\{M(U)\}$ subject to the constraint that $\mathbb{E}(U) = u^*$. Since M is convex, Jensen's inequality tells us that this can be done by choosing U equal to a constant u^*; i.e. the optimal policy has $u(t) = u^*$ for all $t \in [0,T]$.

An approximate formula for the cost of deviating from u^* can be found by expanding $M(u)$ in a Taylor series about $u = u^*$. This expansion gives

$$\mathbb{E}\{M(U)\} \simeq M(u^*) + \tfrac{1}{2}M''(u^*)\mathrm{Var}\{U\}. \tag{A3.7}$$

Thus the cost increases with the degree of convexity of M and the variance of U. For $M(u) = mu^2$ formula (A3.7) is exact and reduces to

$$\mathbb{E}\{M(u)\} = mu^{*2} + m\mathrm{Var}\{U\}. \tag{A3.8}$$

APPENDIX 4. OPTIMAL POLICY WHEN THERE IS A REFUGE

We assume that $\gamma(u) = au - b$ where a and b are constant, and assume $M(u)$ is a convex increasing function of u which satisfies $M(0) > 0$. Inside the refuge there is no predation and $\gamma = -b_\mathrm{r}$. The terminal reward function is given by equation (8).

If $x(0) \geqslant x_\mathrm{c} + b_\mathrm{r}T$ the animal can survive by entering the refuge for the whole time period. We thus henceforth restrict attention to the case

$$x(0) < x_\mathrm{c} + b_\mathrm{r}T. \tag{A4.1}$$

By the Risk-spreading Theorem the optimal policy involves the use of the same control u whenever the animal is not in the refuge. Thus the optimal policy must be of the form: spend time t out of the refuge using fixed control u and spend time $T - t$ in the refuge. Clearly t must satisfy $0 \leqslant t \leqslant T$. It can also be seen that it cannot be optimal to use a value for u for which $au + b_\mathrm{r} - b \leqslant 0$; for then it would be better in terms of both energy gain and predation risk to enter the refuge. Thus if we define u_min by

$$u_\mathrm{min} = \max\{0,(b - b_\mathrm{r})/a\} \tag{A4.2}$$

an optimal u must satisfy

$$u_\mathrm{min} < u \leqslant 1. \tag{A4.3}$$

Finally, note that since an optimal policy must result in $x(T) = x_\mathrm{c}$, u and t must be related by the constraint

$$x(0) + (au - b)t - (T - t)b_\mathrm{r} = x_\mathrm{c},$$

and hence

$$t = \frac{x_\mathrm{c} - x(0) + b_\mathrm{r}T}{au + b_\mathrm{r} - b}. \tag{A4.4}$$

By equation (A4.1) $t > 0$ provided u satisfies equation (A4.3).

The predation risk under the policy of employing control u for time t is $1 - \exp\{-M(u)t\}$ and is minimized by minimizing $M(u)t$. Thus, by equation (A4.4) the optimal control u minimizes

$$f(u) = \frac{M(u)}{au + b_\mathrm{r} - b} \tag{A4.5}$$

subject to the constraint (A4.3) and the constraint $t \leqslant T$.

We now look at the behaviour of $f(u)$ in the range $u_\mathrm{min} < u \leqslant 1$. Differentiation gives

$$f'(u) = (au + b_\mathrm{r} - b)^{-2}[M'(u)(au + b_\mathrm{r} - b) - aM(u)].$$

Thus $f'(u) < 0$ for u sufficiently close to u_min. We also have

$$\frac{\mathrm{d}}{\mathrm{d}u}[M'(u)(au + b_\mathrm{r} - b) - aM(u)] = (au + b_\mathrm{r} - b)M''(u),$$

which is positive for $u > u_\mathrm{min}$ as M is convex. Thus there exists $\hat{u}_G \in (u_{\min},1)$ such that $f'(u) < 0$ for $u \in (u_{\min},\hat{u}_G)$ and $f'(u) > 0$ for $u \in (\hat{u}_G,1)$. f is thus unimodal on the interval $(u_{\min},1)$ with a minimum at $\hat{u}_G$. Now define $\hat{x}_G$ so that

$$\hat{x}_G + (a\hat{u}_G - b)T = x_c. \qquad \text{(A4.6)}$$

Consider the case $x(0) \geqslant \hat{x}_G$. Then if control $u = \hat{u}_G$ is used, the time t must satisfy $t \leqslant T$ by equation (A4.6) and (A4.4). Thus $f(u)$ is minimized subject to constraints (A4.3) and $t \leqslant T$ by setting $u = \hat{u}_G$. If, however, $x(0) < \hat{x}_G$, the constraint $t \leqslant T$ implies $u \in (\hat{u}_G,1)$. Since $f(u)$ is monotonic increasing for u in this range $f(u)$ is minimized subject to the constraint $t \leqslant T$ by choosing u as small as possible subject to this constraint. This value of u can be seen to result in $t = T$.

APPENDIX 5. GAIN DEPENDENT ON STATE, PREDATION INDEPENDENT OF STATE

We assume that

$$\mathrm{d}x/\mathrm{d}t = a(x)u - b(x). \qquad \text{(A5.1)}$$

No assumptions are made about the form of the terminal reward R. Let the initial state $x(0)$ be given, and let x_T denote the state at time T under an optimal policy. Then *a fortiori* the optimal policy minimizes the probability of death from predation among all those controls for which $x(T) = x_T$. We thus seek a control $\underline{u} = \{u(t): 0 \leqslant t \leqslant T\}$ which minimizes

$$\int_0^T M(u(t))\,\mathrm{d}t$$

(cf. Appendix 3) subject to the constraint that

$$x(T) = x_T.$$

We use the Pontryagin Maximum Principle (PMP) (Lee & Markus 1967). As in the text let $x^*(t)$ and $u^*(t)$ be respectively the optimal trajectory and the optimal control along this trajectory. Then the costate variable $p(t)$ satisfies

$$p'(t) = p(t)\,[a'(x^*(t))u^*(t) - b'(x^*(t))], \qquad \text{(A5.2)}$$

and the optimal control maximizes the Hamiltonian

$$H(x,u,p) = p[a(x)u - b] - M(u).$$

We have

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}[p(t)a(x^*(t))] &= p'a + pa'\frac{\mathrm{d}}{\mathrm{d}t}(x^*(t))\\ &= p[ab' - a'b] \qquad \text{(A5.4)}\end{aligned}$$

by equations (A5.1) and (A5.2). Here all functions are evaluated along the optimal trajectory. Manipulating equation (A5.4) then gives

$$\frac{\mathrm{d}}{\mathrm{d}t}\{\log(pa)\} = b\frac{\mathrm{d}}{\mathrm{d}x}\left\{\log\left(\frac{b}{a}\right)\right\}\bigg|_{x = x^*(t)}$$

Thus

$p(t)a(x^*(t))$ increases with $t \Leftrightarrow b(x)/a(x)$ increases with x at $x = x^*(t)$.

By equation (A5.3) the optimal choice of u maximizes

$$f(u) = pau - M(u). \qquad \text{(A5.5)}$$

But then $f'(u) = pa - M'(u)$, which increases with pa for fixed u. It follows that the value u^* maximizing $f(u)$ is a non-decreasing function of pa. Thus

$u^*(t)$ increases with $t \Leftrightarrow p(t)a(x^*(t))$ increases with t

$\Leftrightarrow b(x)/a(x)$ increases with x at $x = x^*(t)$.

In special case $a(x) = a = \text{const}$, $b(x) = b_0 + b_1x$ and $M(u) = mu^2$, equation (A5.2) gives $p'(t) = b_1p(t)$, so that $p(t) = A\mathrm{e}^{b_1t}$. Equation (A5.5) than becomes

$$f(u) = aA\mathrm{e}^{b_1t}u - mu^2,$$

and hence $f'(u^*) = 0$ implies

$$2mu^*(t) = aA\mathrm{e}^{b_1t}.$$

Thus $u^*(t)$ increases exponentially with t provided $u^* \leqslant 1$.

APPENDIX 6. GAIN INDEPENDENT OF STATE, PREDATION MULTIPLICATIVE

We assume $\gamma(u,x) = au - b$ where a and b are constants and that $M(u,x) = N(u)\alpha(x)$ where $N(u)$ is increasing and either linear or convex. Initially we make no assumptions about R.

Proceeding as in Appendix 5 we deduce that the optimal control maximizes

$$H(x,u,p) = p(t)\,[au - b] - \alpha(x)N(u) \qquad \text{(A6.1)}$$

as a function of u, where the costate p satisfies

$$p'(t) = \alpha'(x)N(u). \qquad \text{(A6.2)}$$

To apply these equations we investigate the properties of the function f defined by

$$f(u,t) = p(t)au - \alpha(x^*(t))N(u). \qquad \text{(A6.3)}$$

From equation (A6.1), for each $t \in [0,T]$ $u^*(t)$ maximizes $f(u,t)$ as a function of u. Since

$$\frac{\partial^2 f}{\partial u^2} = -\alpha(x^*(t))N''(u) \leqslant 0$$

f is either linear or concave. It follows that if

$$\frac{\partial^2 f}{\partial t\partial u}(u^*(t),t) \geqslant 0$$

we must have $u^*(t)$ increasing in t, and if

$$\frac{\partial^2 f}{\partial t\partial u}(u^*(t),t) \leqslant 0$$

we must have $u^*(t)$ decreasing. Thus we can find the form of u by finding the sign of

$$\frac{\partial^2 f}{\partial t\partial u}.$$

From equation (A6.3)

$$\frac{\partial^2 f}{\partial t\partial u} = ap'(t) - \alpha'(x^*(t))N'(u)\frac{\mathrm{d}}{\mathrm{d}t}(x^*(t)).$$

Now

$$\frac{\mathrm{d}}{\mathrm{d}t}(x^*(t)) = au^*(t) - b,$$

thus by equation (A6.2) the above equation gives

$$\frac{\partial^2 f}{\partial t \partial u} = \alpha'(x^*(t))\,[aN(u) - (aN(u) - (au-b)N'(u)]. \tag{A6.4}$$

Define the function h by

$$h(u) = aN(u) - (au-b)N'(u).$$

Then $h(u) > 0$ for $u < b/a$. For $u \geqslant b/a$

$$h'(u) = -(au-b)N''(u) \leqslant 0.$$

Define u_G by $h(u_G) = 0$ if $h(1) < 0$, else set $u_G = 1$.

Then

$$h(u) \geqslant 0 \quad \text{for} \quad 0 \leqslant u \leqslant u_G,$$

$$h(u) \leqslant 0 \quad \text{for} \quad u_G \leqslant u \leqslant 1.$$

We note that since

$$\frac{\mathrm{d}}{\mathrm{d}u}\left[\frac{N(u)}{au-b}\right] = -(au-b)^{-2}b(u),$$

u_G minimizes

$$\frac{N(u)}{au-b}$$

among those u for which $au - b > 0$. Thus u_G is in fact the Gilliam rate defined in the main text.

Returning to equation (A6.4) we see that if α is an increasing function of x then

$$0 \leqslant u \leqslant u_G \Rightarrow \frac{\partial^2 f}{\partial t \partial u} \geqslant 0,$$

and

$$u_G \leqslant u \leqslant 1 \Rightarrow \frac{\partial^2 f}{\partial t \partial u} \leqslant 0.$$

Thus

$$0 \leqslant u^*(t) \leqslant u_G \Rightarrow \frac{\mathrm{d}}{\mathrm{d}t}(u^*(t)) \geqslant 0,$$

and

$$u_G \leqslant u^*(t) \leqslant 1 \Rightarrow \frac{\mathrm{d}}{\mathrm{d}t}(u^*(t)) \leqslant 0.$$

It follows that if $0 \leqslant u^*(0) \leqslant u_G$, then $0 \leqslant u^*(t) \leqslant u_G$ for all $t \in [0,T]$ and $u^*(t)$ is increasing on $[0,T]$. Conversely if $u_G \leqslant u^*(0) \leqslant 1$, then $u_G \leqslant u^*(t) \leqslant 1$ for all $t \in [0,T]$ and $u^*(t)$ is decreasing on $[0,T]$.

When α is a decreasing function of x a similar analysis shows that either $u^*(t) \leqslant u_G$ for all t and $u^*(t)$ is decreasing or $u^*(t) \geqslant u_G$ for all t and $u^*(t)$ is increasing.

Now assume that R is given be equation (8) and that $N(0) = 0$. If $x(0)$ is such that $x(0) - b > x_c$ then $u^*(t) = 0$ for all t. If $x(0)$ is such that $x(0) + a - b < x_c$ then all controls give zero payoff. We thus restrict attention to the case $x_c + b - a < x(0) < x_c + b$. In this case it is possible to be in state x_c at time T, and it can thus be seen that $x^*(T) = x_c$ under an optimal policy.

Let x_G be such that $x_G + (au_G - b)T = x_c$. Then since $x^*(T) = x_c$ and $u^*(t) - u_G$ does not change sign on $[0,T]$, we have $x(0) > x_G \Rightarrow u^*(0) \leqslant u_G$ and $x(0) < x_G \Rightarrow u^*(0) > u_G$. Thus when α is increasing

$$x(0) > x_G \Rightarrow u^*(t) \text{ increasing on } [0,T],$$

$$x(0) < x_G \Rightarrow u^*(t) \text{ decreasing on } [0,T].$$

The analysis of the case where α is a decreasing function of state is similar and reveals

$$x(0) > x_G \Rightarrow u^*(t) \text{ decreasing on } [0,T],$$

$$x(0) < x_G \Rightarrow u^*(t) \text{ increasing on } [0,T].$$

APPENDIX 7. GAIN INDEPENDENT OF STATE, PREDATION ADDITIVE

As in Appendix 6 we assume a and b are constants, but now assume that $M(u,x) = \alpha(x) + N(u)$.

Applying PMP the optimal control maximizes

$$H(x,u,p) = p(t)\,[au - b] - \alpha(x) - N(u) \tag{A7.1}$$

as a function of u, where the costate p satisfies

$$p'(t) = \alpha'(x^*(t)). \tag{A7.2}$$

Let

$$f(u,t) = p(t)au - N(u). \tag{A7.3}$$

Then f is linear or convex and, for each $t \in [0,T]$, $u^*(t)$ maximizes f as a function of u. By equation (A7.2)

$$\frac{\partial^2 f}{\partial t \partial u} = a\alpha'(x^*(t)).$$

Thus,

$$\alpha \text{ increasing} \Rightarrow \frac{\partial^2 f}{\partial t \partial u} \geqslant 0 \Rightarrow u^* \text{ increasing},$$

$$\alpha \text{ decreasing} \Rightarrow \frac{\partial^2 f}{\partial t \partial u} \leqslant 0 \Rightarrow u^* \text{ decreasing}.$$