



A Lifetime Perspective on Foraging and Mortality

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Food intake carries many potential risks which may impair an animal's reproductive success not only in the current breeding cycle, but also for the rest of its lifetime. We examine the lifetime trade-off between the costs and benefits of food intake by presenting a simple animal foraging model, where each unit of food eaten carries with it a risk of mortality. We show that the optimal food intake rate over an animal's lifetime, for both semelparous and iteroparous animals, is not maximal. Instead, animals are required to strike a balance between the immediate reproductive benefits of gathering food and the future reproductive costs incurred by the food's mortality risk. This balance depends upon the lifespan of the animal as well as the nature of the risk. Different mortality risks are compared and it is shown that a mortality risk per unit time spent foraging is not, in general, equivalent to a mortality risk per unit of food consumed. The results suggest that a mortality risk per unit of food consumed, such as that presented by the presence of a toxin or of a parasite in the diet, has important consequences for feeding behaviour and is a possible factor involved in food intake regulation.

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Introduction

For all animals, the consumption of food provides the raw materials for growth, survival and reproduction and is, therefore, a major determinant of an animal's fitness. Evolutionary theory tells us that a behaviour will persist in a population if it tends to maximize fitness over an animal's lifetime. This clearly implies that it is the lifetime feeding behaviour of an animal

which should be of evolutionary importance, despite the fact that food intake is commonly thought of on the much shorter time-scale of hours or days (Stephens & Krebs, 1986). In the past, the majority of theoretical studies on food intake behaviour considered only the short, behavioural time-scale (e.g. Gilliam & Fraser, 1987; Johnson *et al.*, 1995). In this paper we consider a model of optimal food intake strategy which combines both the short, behavioural and the long, life history time-scales. We assume that foraging carries an evolutionary cost, and compare the effects of a cost per unit time spent foraging (e.g. predation) against a cost per unit

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food consumed (e.g. toxins or metabolic costs). In such a model food intake is generally optimal rather than maximal. This optimum applies on the time-scale of one breeding cycle, implying that short-term intake may fluctuate to a certain extent, but ultimately it must be regulated in accordance with the optimum. Including a mortality cost of food intake is therefore important to consider, because it offers the possibility that food intake is not maximal. If mortality costs of food can be shown to play a rôle in the regulation of intake, any research field concerned with food intake (e.g. human health and animal production systems) will be presented with a new direction for research, which will see food intake much more as an adaptive behaviour. Studying the mortality cost of food offers the possibility of improving our understanding of feeding behaviour and the factors underlying food intake.

At present there are two popular hypotheses for short-term food intake regulation: food intake is maximized subject to unavoidable constraints, such as digestion capacity, cognitive ability, or detoxification capacity (Stephens & Krebs, 1986; Allen, 1996) and food intake is sufficient to satisfy an animal's requirements, also subject to constraints (Emmans, 1989, 1997; Ward, 1992). Under both of these hypotheses there need be no distinction between a short-term regulation strategy and a lifetime strategy, because neither hypothesis requires food intake to be costly, implying that a short-term strategy holds no long-term detriment for an animal. Farm animals, such as cows, hens and pigs, are generally observed to eat sufficient for their requirements and no more (Emmans, 1989, 1997; Whitmore *et al.*, 2001), although such feeding behaviour may reflect a response to artificial selection. In these intensive agricultural systems requirement models of food intake work well, but their extension to food intake regulation in more natural environments holds many challenges (Yearsley *et al.*, 2001). Observational support for short-term intake maximization also exists (Illius *et al.*, 1999), and constraints have been shown to be important (Weeks, 1996). However, there is also evidence to suggest that food intake rate need not always be the maximum permitted by some constraint. For

example, studies have shown that animals are capable of increasing their intake rate in response to decreases in available feeding time or increases in energetic demands (Kyriazakis & Emmans, 1991; Owen-Smith, 1994; Friggens *et al.*, 1999; Iason *et al.*, 1999), and others have shown that animals do not always feed up to their maximum capacity (Schmid-Hempel *et al.*, 1985; López-Calleja *et al.*, 1997; Josens *et al.*, 1998).

A further possible intake rate regulation hypothesis, is that food intake itself carries a fitness cost. When an animal's feeding behaviour incurs an evolutionary cost as well as a benefit, the short-term optimal strategy need no longer be the same as the long-term, lifetime optimal strategy. This is true even if an animal is thought of as using a short-term "rule of thumb", since the consequences of the "rule of thumb" can approximate a long-term optimal strategy. When food intake is viewed over an animal's lifetime, the immediate benefit of increasing food intake can be offset by a cost which may only manifest itself sometime later in the animal's life. Foraging in the wild commonly carries a risk of predation (Lima, 1998), and each morsel of food may carry a risk of parasitic infection (Lozano, 1991; Lafferty, 1992; Hutchings *et al.*, 1999, 2000), a toxin load (Duncan & Gordon, 1999; Stapley *et al.*, 2000; Sherman & Flaxman, 2001) or a risk of injury. A broad range of evidence for various food intake costs exists in the literature: energy expenditure, either through foraging activity or food digestion, carries fitness costs (Deerenberg & Overkamp, 1999), food storage can also be costly (Witter & Cuthill, 1993), reproductive effort carries its own fitness costs (Bell, 1980; Partridge, 1987; Deerenberg *et al.*, 1997), the ingestion or production of free-radicals can have a highly damaging effect upon the body (Finkel & Holbrook, 2000) and reducing food intake has been shown to have fitness benefits (Masoro, 1995; Sohal & Weindruch, 1996). The fact that animals balance these costs against lifetime reproductive benefits is supported by studies on a range of animals, such as birds (Ghalambor & Martin, 2000, 2001) and insects (Scrimgeour & Culp, 1994; Stoks & Johansson, 2000). These and other costs can be classified as either a cost per unit time spent

foraging, or a cost per unit of food consumed. We shall call these two classes of cost the “background mortality risk whilst foraging” and the “mortality risk of consumption”, respectively. In addition, there can be a third mortality risk whilst the animal is not foraging. For example, there may be a predation risk whilst an animal is resting, or a risk of injury due to territorial defence. We will call this risk the “background mortality risk whilst not foraging”. The mortality risk of consumption should be particularly relevant to foraging theory. Such a mortality does not depend upon the time spent foraging, but rather the amount of food consumed. Possible examples being the ingestion of parasites, toxins or free-radicals.

The effect of predation risk upon foraging behaviour has been extensively studied (Lima, 1998), and the mortality risk of consumption has been investigated in relation to free-radical production (Ketelaars & Tolkamp, 1992a,b; Tolkamp & Ketelaars, 1992; Emmans & Kyriazakis, 1995), but despite the relevance of lifetime fitness to the question of foraging behaviour, the majority of theoretical studies have not explicitly investigated foraging behaviour over a lifetime, concentrating instead upon more or less instantaneous effects, lifetime averages (e.g. Abrams, 1991) or a daily, seasonal or yearly routine, such as the over-winter survival strategy of birds (Bednekoff & Houston, 1994). There has also been an emphasis upon the background mortality risk whilst foraging and the regulation of time spent foraging (Lima, 1998), as opposed to the mortality risk of consumption and the regulation of food intake rate whilst foraging. The exception are models which incorporate an animal’s state, which have looked at more general mortality risks (Houston & McNamara, 1999).

In this paper, we describe a simple model which considers an animal’s food intake over its entire lifetime. We explicitly consider different mortality risks by including a mortality risk of consumption, a background mortality risk whilst foraging and a background mortality risk whilst not foraging, and show that changes in these mortality risks lead to different responses in the optimal food intake. Finally, we consider how optimal food intake is predicted to change as an

animal ages and approaches the end of its reproductive life.

Methods

In order to concentrate on the evolutionary aspects of foraging, we develop a simple, abstract model animal. We assume that evolutionary forces have adapted an animal’s foraging behaviour to maximize its fitness. We consider a large population of identical animals whose feeding behaviour is not limited by the availability of resources. If the population density is stable and regulated through changes in lifetime offspring production then an evolutionary stable strategy maximizes an animal’s lifetime reproductive effort (Mylius & Dickmann, 1995). We therefore take as a measure of fitness an animal’s lifetime reproductive effort, which is the total energy invested in reproduction during its lifetime (Metz *et al.*, 1992; Kozłowski, 1999). If population size were regulated through some other mechanism then lifetime reproductive effort may no longer be a valid measure of fitness.

We examine two cases, semelpary and iteropary. An animal has a breeding cycle with a fixed length of one time unit, where the choice of time unit depends upon the animal under study. For example, the breeding cycle could refer to an animal which reproduces yearly, monthly or daily, or even an animal which reproduces immediately after each gestation period. The average feeding rate of an animal whilst feeding is denoted by i , measured in units of an animal’s maintenance costs, and the proportion of time spent feeding during one breeding cycle is denoted by p . The probability that an animal survives from the start until the end of one breeding cycle is $P(i)$. It is assumed that the available energy gathered over one breeding cycle (the energy gathered minus the maintenance costs for one breeding cycle) is “converted” into offspring at the end of that cycle. Therefore, at the end of one breeding cycle, the average energy available for reproduction, per individual in the population, $g(i)$, is given by the function

$$g(i) = (ip - 1)P(i), \quad (1)$$

where all quantities are in dimensionless units.

The mortality risks are described by dividing each breeding cycle into N periods, of which n_f are times when the animal is feeding, and the rest are times when the animal is not feeding. One way to describe the survival probability, $P(i)$, is as the polynomial,

$$P(i) = \left(1 - p \frac{ir + \alpha}{n_f}\right)^{n_f} \times \left(1 - (1 - p) \frac{\beta}{N - n_f}\right)^{N - n_f}, \quad (2)$$

where r is the mortality risk of consumption per unit food consumed (which in the model's units is equal to the mortality risk associated with eating to maintain live weight), α and β are the background mortality risks per unit time whilst feeding and not feeding, respectively. The functional form of eqn (2) was chosen for simplicity and because it encompasses both the linear case ($n_f = 1$) and the case when survival is a Poisson process ($n_f = \infty$). If survival is a Poisson process then an increase in food intake causes a decrease in survival which is independent of the current food intake [i.e. $P(i_1 + i_2) = P(i_1)P(i_2)$]. This type of mortality risk could represent the case when a prey's chances of escaping predation remain unaffected by the number of times it has been attacked or when the probability of surviving a parasitic infection is strictly proportional to the number of parasites in the host. If $0 < n_f < \infty$ in eqn (2), which includes the linear case $n_f = 1$, then the risks from food intake are not independent, so that the survival probability is decreased if there have been preceding risks due to food intake [i.e. $P(i_1 + i_2) < P(i_1)P(i_2)$]. For example, this type of mortality risk could represent the case when a prey's chances of escaping from a predator are decreased by continued predation, or when the deleterious effects of a toxin are only felt above a critical threshold. The robustness of our conclusions to the form of eqn (2) will be discussed later.

When the survival probability is a linear function of the food intake rate ($n_f = 1$), then eqn (2) simplifies down to

$$P(i) = (1 - ipr - \alpha p)B, \quad (3)$$

where $B = [1 - (1 - p)\beta/(N - 1)]^{N-1}$ is the survival probability whilst not feeding. If an animal breeds for a maximum of N_c breeding cycles, the lifetime reproductive effort, LRE , is the sum of the expected number of offspring from each breeding cycle

$$LRE = \sum_{y=1}^{N_c} g(i_y) P(i_y)^{y-1}, \quad (4)$$

where i_y is the feeding rate during breeding cycle y . The optimal feeding rate over each breeding cycle, \hat{i}_y , is found by maximizing the lifetime reproductive effort with respect to the feeding rate. The maximum lifetime reproductive effort can be analytically calculated in two extreme cases; when the survival probability is a linear function of food intake rate ($n_f = 1$), and when survival probability is a Poisson process ($n_f = \infty$). In the rest of this paper we shall concentrate upon the former case where $n_f = 1$, which implies that mortality risk is proportional to the amount of food eaten during one breeding cycle. The case of a Poisson survival process, where each feeding bout's mortality risk is independent, is presented in Appendix A since the results are qualitatively very similar to $n_f = 1$. Realistic survival functions are likely to lie somewhere between these two extremes. The behaviour of the model to values of n_f between these two extremes is intermediate.

SEMELPARY

A semelparous animal has one breeding cycle in its lifetime ($N_c = 1$). In this case, the lifetime reproductive effort is simply the energy available for reproduction at the end of one breeding cycle

$$LRE = g(i). \quad (5)$$

Optimal food intake is found by maximizing eqn (5).

ITEROPARY

An iteroparous animal can reproduce for an indeterminate number of breeding cycles ($N_c > 1$). In this case, the lifetime reproductive effort is the sum of the expected number of offspring from all breeding cycles. If we assume

that the feeding rate is independent of the breeding cycle (an assumption which will be relaxed in the following section), then the lifetime reproductive effort can be written as

$$\begin{aligned} LRE &= \sum_{y=1}^{\infty} g(i) P(i)^{y-1} \\ &= \frac{g(i)}{1 - P(i)}. \end{aligned} \quad (6)$$

Optimal food intake is found by maximizing eqn (6).

THE PROPORTION OF A BREEDING CYCLE SPENT FEEDING

In our simple model, there are two time-scales over which food intake can be measured: the intermediate time-scale corresponding to intake over one breeding cycle, and the short time-scale corresponding to intake whilst foraging. If the proportion of spent time foraging in each breeding cycle (p) is assumed to be constant, then these two measures of food intake are equivalent. Whenever this is the case for our results, the optimal food intake over one breeding cycle will be presented. However, p may itself be the result of adaptive behaviour, in which case our model can be used to determine the optimal proportion of time spent feeding, \hat{p} . In this case the two measures of food intake are not equivalent. If \hat{p} is close to zero then short-term food intake may be constrained even if the food intake over a breeding cycle is optimized.

To investigate an adaptive feeding time we maximized the lifetime reproductive output of a semelparous animal [eqn (5)] and an iteroparous animal [eqn (6)] with respect to p , assuming that the food intake over the breeding cycle (ip) was already at its optimal value. Since the optimal value of p was found to depend upon the functional form of the survival probability whilst not feeding (B), we present results for the simple case where B is a linear function of p , such that $B = 1 - \beta(1 - p)$ (i.e. $N - n_f = 1$). Simulations where B took a variety of functional forms (i.e. $N - n_f > 1$) gave qualitatively similar results.

CHANGES IN FOOD INTAKE THROUGHOUT AN ANIMAL'S LIFETIME

There is no reason to expect an animal's feeding behaviour to remain constant throughout its lifetime. Instead, it is expected that adaptive behaviour early on in the life cycle will be influenced by future reproductive possibilities (Engen & Stenseth, 1989). Analytical solutions to life history strategies of optimal foraging have been studied by Abrams (1991) and Engen & Stenseth (1989), with the conclusion that older individuals are more likely to pursue dangerous food types.

Using the techniques of dynamic programming (Mangel & Clark, 1988; Houston & McNamara, 1999), optimal intake rate can be calculated as a function of an animal's breeding cycle. If the future reproductive success of an animal is denoted by V , then the optimal food intake during a breeding cycle, given the possibility of this future reproductive success, can be calculated to be

$$\hat{ip} = \frac{1}{2} \left[1 - V + \frac{1}{r}(1 - \alpha p) \right], \quad (7)$$

where we have used the linear survival probability [eqn (3)]. If the future reproductive success is zero ($V = 0$), then eqn (7) reduces to the result for a semelparous animal [eqn (8)]. However as the probability of future reproductive success increases the optimal food intake for the current breeding cycle decreases.

Equation (7) can be used to calculate how optimal food intake should vary throughout an animal's lifetime. If an animal has a maximum number of breeding cycles in its lifetime, after which its reproductive life ceases (in reality fecundity is most likely to gradually decrease over a number of breeding cycles, making the above scenario a rather extreme example, but one which nevertheless conveys the basic idea), then for this final breeding cycle we can set $V = 0$, and calculate the optimal food intake. It is then possible to use this result to calculate the future reproductive success for the previous breeding cycle. By working backwards through an animal's lifetime it is possible to calculate its optimal food intake as a function of age.

Results

SEMELPARY

The food intake rate which maximizes this lifetime reproductive effort, \hat{i} , can be calculated from eqn (5) as

$$\hat{i}p = \frac{n_f}{1 + n_f} \left[1 + \frac{1}{r} \left(1 - \frac{\alpha p}{n_f} \right) \right]. \quad (8)$$

This equation states that if there is a mortality risk of consumption then maximization of intake rate does not maximize fitness. Instead, fitness is maximized when the food intake rate over a breeding cycle has a finite value of \hat{i} . The optimal food intake rate for a semelparous animal over its breeding cycle, as a function of both the consumption mortality risk and the background mortality risk whilst feeding (which is called the mortality risk whilst feeding and can be written as $\hat{i}pr + \alpha p$), is shown as the dotted line in Fig. 1(a). Increases in the consumption mortality risk (r) and the background mortality risk whilst feeding (α), both have the effect of increasing the probability of mortality whilst feeding, which reduces the optimal feeding rate [Fig. 1(a)]. However, the background mortality risk whilst not feeding (β) does not appear in eqn (8), and has no effect upon an animal's optimal food intake rate.

ITEROPARY

For an iteroparous animal, the optimal food intake rate which maximizes the lifetime reproductive success can then be calculated by substituting eqn (3) into eqn (6), giving the optimal food intake rate as

$$\hat{i}p = \frac{1}{Br} \left(\sqrt{1 + B(r + \alpha p - 1)} + B - 1 - \alpha p B \right), \quad (9)$$

where $B = (1 - (1 - p)\beta/(N - 1))^{N-1}$, is the probability of surviving whilst not feeding. Equation (9) gives the feeding rate which maximizes the lifetime reproductive success of an iteroparous animal. As for the semelparous result of eqn (8), maximizing the lifetime reproductive effort does not lead to maximal food intake rate.

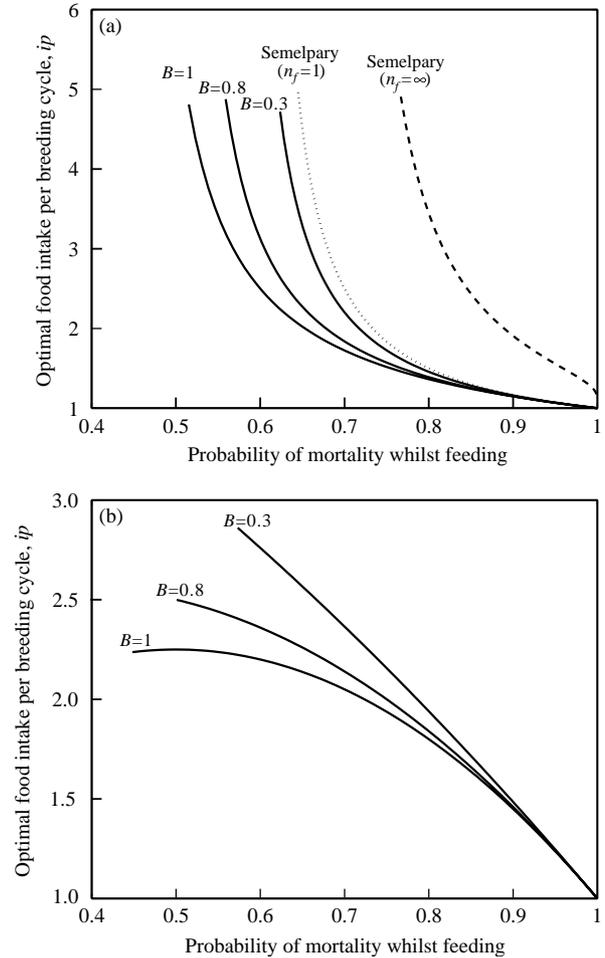


FIG. 1. The optimal food intake rate over one breeding cycle, $\hat{i}p$, in units of maintenance requirements. (a) (····) and (—) show results for semelpary, and iteropary, respectively, with a linear survival function ($n_f = 1$) whilst the (---) line shows the result for semelpary with survival a Poisson process ($n_f = \infty$). α is held constant at 0.2. (b) Results are only for $n_f = 1$, and r is held constant at 0.2. The probability of mortality whilst feeding incorporates both the mortality risk of consumption and the background mortality risk whilst feeding, and is given by $\hat{i}pr + \alpha p$ ($n_f = 1$), or $1 - \exp(-\hat{i}pr - \alpha p)$ ($n_f = \infty$). The background mortality risk whilst feeding is α . The background mortality risk whilst not feeding is $1 - B$ where $B = [1 - (1 - p)\beta/(N - 1)]^{N-1}$ ($n_f = 1$) or $\exp(-\beta)$ ($n_f = \infty$), where β and N are constants. These results assume that intake rate is constant throughout an animal's lifetime.

The optimal food intake rate as a function of mortality risk whilst feeding is shown in Fig. 1(a). As the mortality risk increases ($\hat{i}pr + \alpha p \rightarrow 1$), then the optimal food intake rate given by eqn (9) approaches the result for semelpary [eqn (8)] with $n_f = 1$. As survival approaches a Poisson process [Fig. 1(a) and

Appendix A] the optimal food intake rate increases for both semelpary and iteropary. The survival function given by eqn (2) predicts the largest food intake rate for a Poisson process ($N = n_f = \infty$) because it has the property that changes in food intake rate have the smallest effect upon mortality.

It is important to realize that the background mortality whilst feeding (α) is not equivalent to the consumption mortality risk (r). Firstly, a background mortality risk alone would have always predicted food intake rate maximization. Secondly, increases in the consumption mortality risks always lead to decreases in optimal food intake rate, whilst increases in background mortality (both α and $1 - B$) can result in either increasing or decreasing optimal food intake rate [Figs. 1(b) and 2]. As the survival function approaches Poisson ($n_f = \infty$), the background mortality risk predominantly increases optimal food intake rate [eqn A.5].

THE PROPORTION OF A BREEDING CYCLE SPENT FEEDING

The results presented above consider the optimal food intake averaged over a breeding cycle ($\hat{i}p$), and assume that the proportion of time spent feeding per breeding cycle is constant. If instead it is assumed that the proportion of time spent feeding per breeding cycle (p) is adaptive, then we can calculate the optimal value of p . For a semelparous animal the optimal proportion of time spent foraging can be calculated explicitly to be

$$\hat{p} = \frac{2}{3} \left(1 - \frac{1}{\beta} \right) + \frac{1-r}{3\alpha}, \tag{10}$$

where realistic values for \hat{p} must lie in the range from zero to one. If the value of \hat{p} calculated from eqn (10) lies outside this range then \hat{p} is set to the value of the nearest bound. The optimal value of p for an iteroparous animal, which does not have a simple analytical solution, was calculated numerically and is shown in Fig. 3 along with the results of eqn (10).

In general, Fig. 3 shows that optimal food intake on the short-term (\hat{i}) as well as the intermediate-term ($\hat{i}\hat{p}$) need not be maximal. Our results are intuitively obvious, in that the

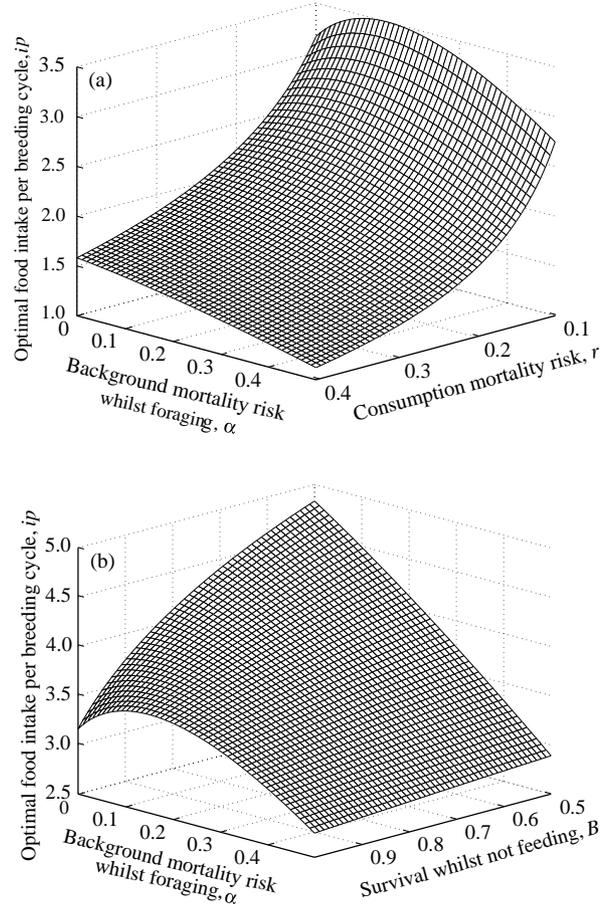


FIG. 2. The optimal food intake rate over one breeding cycle, $\hat{i}p$, in units of maintenance requirements, given by eqn (9), showing the general dependence of the solution on the parameters r , α , and B . (a) B is held constant at 1. (b) r is held constant at 0.1. The background mortality risk whilst feeding is α , the background mortality risk whilst not feeding is $1 - B$, where $B = [1 - (1 - p)\beta / (N - 1)]^{N-1}$, and β and N are constants. These results assume that intake rate is constant throughout an animal's lifetime.

optimal feeding time is predicted to decrease as the mortality risk from feeding increases relative to the mortality risk from not feeding. Therefore, at low consumption mortality risks it is optimal to spend all the available time feeding ($\hat{p} = 1$), implying time maximization and non-maximal short-term intake rate. At high consumption mortality risks it is optimal to spend as little time feeding as possible ($\hat{p} = 0$), implying time minimization and short-term intake maximization. The transition from $\hat{p} = 1$ to 0 causes the short-term food intake (\hat{i}) to increase, despite the decrease in food intake over a breeding cycle [Fig. 3(b)]. Short-term food intake will,

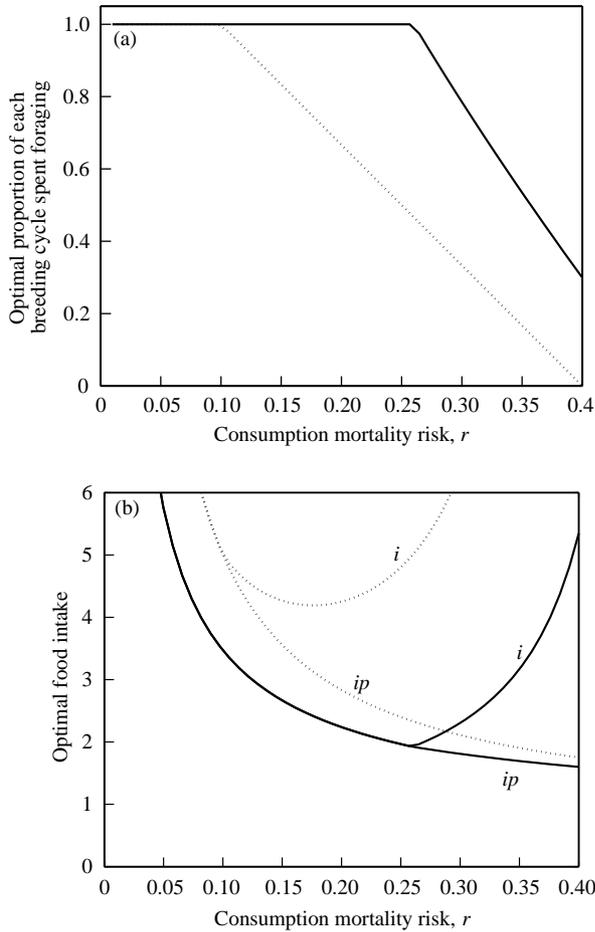


FIG. 3. (a) The optimal proportion of a breeding cycle spent feeding, \hat{p} , and (b) the corresponding optimal food intake per breeding cycle, \hat{ip} as a function of the consumption mortality risk (r). The (\cdots) are for an Semelparous animal, the (—) lines are for a iteroparous animal [eqn (8) and (10)]. Lines marked with i show the optimal food intake rate whilst foraging, lines marked with ip show the optimal food intake over one breeding cycle. The survival probability is given by eqn (3) with $N = 2$ and $n_f = 1$. Other parameters are $\alpha = 0.1$ and $\beta = 0.25$.

therefore, be at its lowest for intermediate mortality risks.

CHANGES IN FOOD INTAKE THROUGHOUT AN ANIMAL'S LIFETIME

For an animal with a maximum of ten breeding cycles, and no background mortality risk ($\alpha = \beta = 0$), the optimal food intake predicted with dynamic programming is presented in Fig. 4. This shows that an animal's optimal intake rate monotonically increases as the animal ages. For young animals food intake is

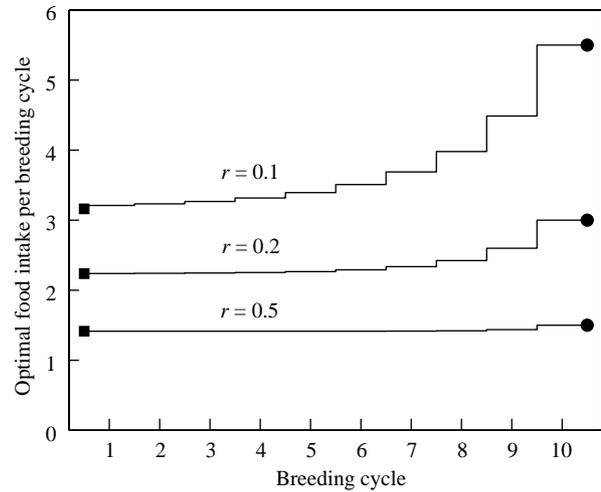


FIG. 4. The optimal food intake rate over each breeding cycle, \hat{ip} , in units of maintenance requirements for an animal that stops reproducing after ten breeding cycles. The three lines corresponding to $r = 0.1, 0.2$ and 0.5 are shown, where r is the consumption mortality risk when an animal's food intake rate just covers maintenance requirements. In each run r is held constant. All results assume no background mortality risk ($\alpha = \beta = 0$). The (■ ■ ■) and (● ● ●) show the optimal food intake rate over one breeding cycle for an iteroparous animal with no maximum number of breeding cycles and a semelparous animal, respectively.

close to the optimal intake rate for an iteroparous animal and as an animal ages intake rate approaches the result for a semelparous animal. An animal's feeding strategy is therefore leading to an increase in the mortality rate with age. After ten breeding cycles it is certain that the animal will never reproduce again, and so the strategy for an animal in its final breeding cycle is identical to the strategy of a semelparous animal. The predicted food intake rate decreases towards the food intake rate prediction for an iteroparous animal [eqn (9), and represented by the solid squares in Fig. 4], as the number of possible future breeding cycles increases. If either background mortality risk, or mortality risk of consumption or maintenance costs increase, relative to an animal's intake rate, then the rate of change of the optimal food intake rate decreases. Figure 4 shows that increasing consumption mortality risk (r), causes a decrease in the average gradient of optimal food intake rate against age. Therefore, the feeding strategy of animals with either many breeding cycles, or high maintenance costs or a high mortality risks,

will be well approximated by eqn (9), which assumes a constant intake rate throughout an animal's reproductive life.

Discussion

It has long been realized that mortality risk is an important evolutionary force. Mortality has often been associated with a risk of predation, and the trade-off between increasing food intake and the increasing risk of predation through prolonged foraging has been extensively studied in relation to patch use and prey choice (reviewed in Lima & Dill 1990; Lima, 1998). These studies have tended to concentrate upon a relatively short time-scale (e.g. a series of foraging bouts or survival over one winter). Models which include an animal's state (e.g. its levels of energy reserves) have started to look at feeding behaviour over an extended period (e.g. daily or seasonal routines) (Houston & McNamara, 1999). Feeding behaviour over an animal's lifetime, which must combine a behavioural time-scale with a longer, life history time-scale, has received far less attention (Abrams, 1991; Engen & Stenseth, 1989), perhaps because the long-term consequences of predation are unclear (Lima, 1998). Abrams (1991) explored the average foraging life history strategy which maximizes a population's growth rate and looked at how food availability influences the optimal foraging effort. Abrams found optimal foraging effort could increase or decrease with increasing food availability depending upon an animal's life history. Engen & Stenseth (1989) also explored lifetime foraging behaviour and in particular optimal diets in relation to a food item's nutritional value and its mortality risk. Neither model distinguishes between the different mortality risks associated with foraging, nor specifically addresses the issues of food intake regulation.

The model presented here considers an animal's lifetime food intake regulation, and the effects of different foraging mortality risks, assuming that animals have evolved to maximize their lifetime reproductive effort. The model predicts an optimal intake rate that balances the immediate benefits of food intake against the immediate, and future costs, associated with a

mortality risk. For example, the model could account for the foraging behaviour of an adult bird who must provision itself and its clutch of young. Whilst foraging the bird runs a predation risk (which we have termed a background mortality risk whilst foraging) and a risk of injury during the handling of each prey item (which we have called the mortality risk of consumption). In this case, the model predicts how the bird should balance its needs and the needs of its young against the costs to itself and the possible loss of future breeding opportunities. A second example would be a browsing herbivore such as a deer, or an antelope, where once again there is a predation risk for each second spent foraging, and where the mortality risk of consumption could be the toxic effect of a plant's secondary compounds, or the metabolic costs of digesting the plant. For these and other scenarios the model makes two general conclusions. Firstly, a mortality risk of consumption is qualitatively different from a background mortality risk whilst feeding. Previously, only the second of these two concepts has been generally included in foraging models (Lima & Dill, 1990; Lima, 1998). An increasing mortality risk of consumption always has the effect of reducing optimal food intake, whilst the effect of an increase in the background mortality risk whilst foraging has no generic effect, and can lead to an increasing or decreasing optimal food intake depending upon factors such as the magnitude of the mortality risk. This implies that if food intake is optimal then these two mortalities cannot be used interchangeably. Secondly, even if food intake is generally optimal, there will still be regions of the parameter space where intake is expected to be maximal, subject to constraints. When mortality risk is low, or the proportion of time spent foraging is low, the optimal food intake rate predicted by the model can be unrealistically high, at more than 5 times the cost of maintaining live weight (Kirkwood, 1983). In these cases it is reasonable to assume that intake rate would be determined by some other regulation mechanism. Since the largest optimal food intake rate is predicted for semelpary, the results of the model suggest that semelparous animals are more likely to be intake rate maximizers. Data from insects

and birds clearly show that species whose probability of surviving for more than one breeding cycle is low have a relatively high reproductive effort and a low sensitivity to predation risk (Stoks & Johansson, 2000; Ghalambor & Martin, 2001). In contrast, for higher mortality risks, the model predicts optimal food intake rates that equate to a reproductive production of up to two times the cost of maintaining live weight, which is consistent with allometric studies where mean metabolic rate in free-living organisms are generally of the order of 1.5–4 times maintenance costs, with a maximum of five times maintenance costs (Kirkwood, 1983). In this situation it is realistic to envisage an animal as an intake rate optimizer.

Although our model explores mortality risk, the results could be generalized to any risk which results in a reduced fecundity or survival. This could include costs, such as reduced fertility, somatic damage by free-radicals, reduced probability of mating or reduced offspring survival. Although we have chosen a specific functional form for survival, given by eqn (2), and we have presented only two cases, where $n_f = 1$ and $n_f = N = \infty$, the general conclusions of the model are robust not only to changes in n_f and N but also to more general changes in the survival function. In particular, consumption mortality risk need not be a linear function of intake rate. If consumption mortality is described by an increasing polynomial of food intake rate, such that high intake rates are disproportionately more risky, then optimal food intake rate is reduced, whilst the qualitative behaviour of the model is maintained. In the case where low intake rates are disproportionately more risky, there may be no optimal intake rate. In general, therefore, increasing consumption mortality is predicted to reduce the optimal food intake rate, and increasing background mortality is predicted to cause increases in optimal intake rate at low mortalities and decreases towards higher mortalities.

The extension of the model to investigate the variation of food intake over an animal's lifetime suggests that, for the majority of an animal's lifetime, food intake is close to the predictions for iteropary and only towards the end of an animal's lifetime is food intake predicted to

significantly increase as the future reproductive effort decreases towards the terminal horizon of the animal's lifespan. This result not only agrees with previous theoretical work (Engen & Stenseth, 1989), but is consistent with several feeding behaviour studies: female mosquitoes (*Aedes aegypti*) are observed to take larger blood meals, at a greater risk to themselves, as they get older (Xue *et al.*, 1995), and studies on rats show a decreasing ability to regulate food intake as they age (Scarpace *et al.*, 2000; Mooradian *et al.*, 2000).

By proposing a general mechanism where food intake rate can be optimized, and thus avoiding the necessity of invoking constraints as factors limiting food intake, this work proposes that it is evolution that determines the majority of constraints seen in nature and not vice versa. The model shows that optimal food intake may be expected to show adaptive changes during an animal's lifetime as the balances between the costs and benefits of food intake changes. The model further highlights that not all mortality risks result in the same conclusions. In particular, a mortality risk of consumption, such as parasitism and toxicity, which have previously been largely overlooked in foraging studies, may have important implications for an animal's lifetime feeding behaviour. Food intake costs may play a role in interpreting observed variations in food intake, such as infection-induced anorexia (Exton, 1997; Kyriazakis *et al.*, 1998) or food related parasite avoidance (Hutchings *et al.*, 1999, 2000). Recent work suggests that animals are aware of the costs of food intake and can alter their feeding behaviour to reduce the intake of parasites (Hutchings *et al.*, 2000). In fact, the effects of the costs of food intake may be more far-reaching than suggested by our simple model, since our results assume that mortality acts immediately, and the effects are not delayed until future breeding cycles. With the incorporation of risks such as parasitism, it is possible that a mortality risk in one breeding cycle could have a continuing effect in later breeding cycles, or not be felt until much later on in the animal's lifetime. The importance of these time-delay effects could be studied using dynamic programming, but is still to be studied.

It is obvious that the issues raised by this work can only be developed by fully quantifying the costs of food intake over an animal's lifetime. To date no work has been able to provide such data, due perhaps to the considerable difficulties in working on a life history time-scale. Future studies, which look at food intake over an animal's lifetime and provide a comprehensive evaluation of the mortality risks associated with foraging, will undoubtedly progress our understanding of food intake regulation and the factors underlying an animal's foraging behaviour. Success is most likely with studies on animals such as insects and laboratory mammals, whose lifetime performance and mortality risks can be evaluated on the time-scale of months.

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Appendix A

Solutions When Mortality is a Poisson Process

Analytical solutions to our model can be obtained when $n_f = 1$ and in the limit as $n_f = \infty$ (corresponding to linear and exponential survival probabilities). Solutions for $n_f = 1$ are presented in the main body of the paper. The case when $n_f = \infty$ corresponds to a mortality

risk which is a Poisson process, implying that the contribution of additional food intake to the mortality risk is independent of the current level of food intake. Whilst the solutions for $n_f = \infty$ are qualitatively similar to those for $n_f = 1$, we included the details here because realistic scenarios are likely to lie somewhere between these two cases.

When mortality is described by a Poisson process the survival probability can be written

as

$$P_\infty(i) = e^{-i p r - (1-p)b}, \tag{A.1}$$

where $b = \alpha + \beta$ is the overall background risk of mortality. This is the limit of eqn (2) as $n_f \rightarrow \infty$.

SEMELPARY

Using eqs (1) and (A.1) gives the lifetime reproductive effort for a semelparous animal as,

$$LRE = (i p - 1) e^{-i p r - (1-p)b}. \tag{A.2}$$

The maximum lifetime reproductive effort occurs when the food intake rate over the breeding cycle is

$$\hat{i}p = 1 + \frac{1}{r}. \tag{A.3}$$

A more intuitive method of obtaining this result [eqn (A.3)] is simply to regard foraging as a form of gambling. An animal must gain enough food units to meet maintenance requirements ($\hat{i}p > 1$) as a prerequisite for reproduction. Once this has been achieved and an animal has accumulated x units of food over and above maintenance requirements ($x = \hat{i}p - 1$), its expected loss of “disposable” energy due to a risk of mortality (i.e. energy available for reproduction) per unit “disposable” food foraged is xr . The animal should stop foraging when its expected loss due to the risk of mortality exceeds the gain (i.e. when $xr > 1$), at which point $x = 1/r$.

The optimal food intake rate, \hat{i} , given by eqn (A.3) is the maximum of all possible optimal food intakes [eqn (8)]. As shown by the dashed line in Fig. 1(a), the optimal food intake rate for a semelparous animal with survival described by $n_f = \infty$ is always greater than the corresponding predictions when survival is described by $n_f = 1$. Reducing the number of feeding bouts in a breeding season or introducing more than one breeding cycle both reduce the optimal food intake rate.

ITEROPARY

When an animal is iteroparous, the lifetime reproductive effort is given by substituting

eqn (A.1) into eqn (6) to give

$$LRE = \frac{i p - 1}{e^{i p r + (1-p)b} - 1}. \tag{A.4}$$

Equation (A.4) is equivalent to a result obtained by Houston & McNamara (1986) for an animal foraging in a patchy environment, but here the environment is the animal’s lifetime and each patch is a breeding cycle.

The feeding rate, \hat{i} , which maximize the lifetime reproductive effort is given by

$$\hat{i}p = 1 + \frac{1}{r} (1 + W_0[-\exp(-K)]) \tag{A.5}$$

where $K = 1 + r + (1 - p)b$, and $W_0[x]$ is the principle branch of the Lambert W function (Corless *et al.*, 1996) evaluated at x . The Lambert W function has a minimum of -1 when $K = 1$ and a maximum of 0 when $K = \infty$. So the minimum optimal food intake rate is just sufficient to meet maintenance requirements, $\hat{i} = 1$, whilst the maximum optimal food intake rate is the same as the result for semelpary [eqn (A.3)]. The optimal food intake rate given by eqn (A.5) is a continuously decreasing function of consumption mortality risk, r , and an increasing function of background mortality risk, $b = \alpha + \beta$. This is in contrast to the result for $n_f = 1$ [eqn (9)], where it was found that optimal food intake could increase with increasing background mortality risk, α , if α was sufficiently small, B sufficiently close to unity and consumption mortality risk was low, $r \ll 1$ [Figs 1(b) and 2].

Unlike the result for semelpary [eqn (A.3)], the background mortality risk now affects the optimal intake rate. When mortality risk is high, be it due to the background risk or the consumption risk, the optimal feeding rate under iteropary approaches the optimal feeding rate for semelpary. This is because the animal’s first breeding cycle dominates the lifetime reproductive effort at high mortality risks. As for semelpary, the optimal food intake given by eqn (A.5) is always greater than the optimal food intake rate when survival is a linear function [eqn (9)]. This implies that intake rate is more likely to be maximized, subject to constraints, if survival is described by a Poisson process.