

Life history and the fitness consequences of imperfect information

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Summary

The acquisition of information incurs costs in time, energy, exposure to predation, and/or lost opportunity. Without information, however, animals will be unable to assess the costs and benefits of decisions. Obtaining perfect information may be impossible, but how close to perfect do animals need assessments of ecological factors, such as predation risk, before estimation errors affect fitness? A recent article suggested that animals should be tolerant to imperfect information about predation risk, possibly relying on simple rules of thumb. Using a dynamic state variable approach, we examine some of the assumptions underlying this work, and show that tolerance towards imperfect information is dependent on life-history strategy. By changing the relationship between energy and fitness, assumptions about life-history strategies can be modified. Calculations show that tolerance to imperfect information is sensitive to these assumptions with some life histories leading to overestimation, while other life histories result in underestimation. One consistent effect across life histories is that animals with a higher rate of increase in fitness with respect to energy should show greater tolerance to imperfect information.

Keywords: dynamic optimization; estimation errors; foraging behaviour; imperfect information; life history; predation risk

Introduction

In most environments, animals need information to make decisions that maximize fitness. Early models in behavioural ecology assumed that animals had perfect information about their environment (Stephens and Krebs, 1986). This is obviously not true, and many researchers have begun to investigate how animals acquire and use information (e.g. Stephens, 1987; Valone and Brown, 1989; Mangel, 1990; Roitberg, 1990; Valone, 1991, 1992; Templeton and Giraldeau, 1995). If information is free, we expect animals to acquire enough information for perfect assessments (Chavas and Pope, 1984; Templeton and Franklin, 1992); however, we expect some cost to be associated with the acquisition of information. Even if information is free, an environment may be too variable for animals to acquire perfect assessments. Given that perfect information is desirable, but its acquisition is costly, we are left with the question: How tolerant should animals be to imperfect information?

Roitberg (1990) used a dynamic state variable approach to determine whether fruit flies should be optimistic (errors biased towards overestimation) or pessimistic (errors biased towards underestimation) about the value of foraging patches. Roitberg's model predicted – and his field data supported the prediction – that fruit flies should be optimistic in their assessment of patch quality. More recently, Bouskila and Blumstein (1992) asked if animals should be tolerant to imperfect information about predation risk. Using a similar dynamic state variable approach, they modelled

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the effect of error in the estimation of predation risk on the fitness of a forager. Their analysis showed that, in general, tolerance to imperfect information was predicted to be skewed towards overestimation of predation risk, and that tolerance to imperfect information would be relatively large. This led Bouskila and Blumstein (1992) to conclude that, when there is a cost to reducing error, animals should be using simple rules of thumb leading to overestimation of predation risk.

Abrams (1994), using a deterministic model, showed that either under- or overestimation of predation risk could be expected. Abrams' model predicted that the advantage to any given bias in the estimation of predation risk would depend on the costs and benefits of foraging (i.e. on the relationship between fitness and foraging gains). This would suggest that tolerance to imperfect information should be influenced by the life history of the forager. Life history refers to those traits of an organism's life cycle that contribute to its reproductive success (Stearns, 1992). Hence, the life history of an organism would determine how foraging gains contribute to fitness (Abrams, 1983, 1991). Obviously, this is only one aspect of an organism's life history.

Newman (1991) demonstrated that, by changing the relationship between energy gains and the probability of survival, the patch-residence times of modelled foragers could be significantly lengthened. Using Bouskila and Blumstein's (1992) model, we investigate how assumptions about life history influence predicted tolerance to imperfect information through modifications to the model's terminal fitness function (the fitness–foraging relationship).

The model

The model used by Bouskila and Blumstein (1992) is a modified version of the patch choice model described by Mangel and Clark (1988). A forager chooses between two patches based upon parameter values of the probability of finding food (λ), which is determined by the rate of encounter with food (r), the energy obtained with each successful discovery (Y), the energetic cost of a decision (α) and the probability of death by predation (β) (see Table 1 for a summary). This decision is repeated for each time step, t , during a foraging period of T time steps. A forager avoids starvation by keeping its energy reserves at each time period, $X(t)$, above a critical level, x_c .

During each time period, the forager's energy reserves change depending on the patch chosen and foraging success in that patch. If a forager chooses patch i and finds food, its new energy reserves will be:

$$x'_i = x - \alpha_i + Y_i \quad (1)$$

where x represents current energy reserves. If the forager is unsuccessful, its new energy reserves will be:

$$x''_i = x - \alpha_i \quad (2)$$

The range of possible energy reserve levels is bound by an upper maximum capacity, x_{cap} , and a minimum critical level, x_c .

The probability of finding food at each time step in patch i will be determined by the rate of encounter with food in patch i :

$$\lambda_i = 1 - e^{-r_i} \quad (3)$$

The forager's expected fitness from time t to the time horizon, T , given energy reserves x , is defined by the equation:

$$F(x, t, T) = (1 - \beta_i)[\lambda_i F(x'_i, t + 1, T) + (1 - \lambda_i)F(x''_i, t + 1, T)] \quad (4)$$

Table 1. Parameters, parameter values and descriptions of parameters used in the basic model^a

Parameter	Value(s)	Description
T	25	The final time step (time horizon)
t	–	The current time step for all $t < T$
α_i	1, 1	Energetic cost of a decision per t
r_i	0.16, 1.61	Rate of encounter with food per t
λ_i	0.15, 0.8	Probability of finding food per t
Y_i	1, 2	Units of energy obtained per successful discovery
β_i	0.0001, 0.04	Probability of death by predation per t
$X(t)$	–	State variable (energy reserves) at time t
x	–	Current level of energy reserves
x_c	3	Critical level of energy reserves
x_{cap}	15	Maximum capacity of energy reserves
x_{sat}	10	Saturation point, or x required for maximum fitness

^aWhen two parameter values are reported, they correspond to patch 1 and patch 2 respectively. Patch 1 is the safe but food-poor patch, while patch 2 is the risky but food-rich patch. Parameter values correspond to those used by Bouskila and Blumstein (1992).

where x'_i , x''_i and λ_i are defined by Equations (1), (2) and (3). The forager chooses the patch, i , at each time step to maximize $F(x, t, T)$. For a complete description of the dynamic state variable approach and stochastic dynamic programming (SDP), see Mangel and Clark (1988).

In the model described by Bouskila and Blumstein (1992), the forager makes decisions with error in one of the parameter values (e.g. estimation of the probability of death by predation in patch 2, β_2). Fitness is calculated based upon the true parameter value, allowing calculation of the effect that estimation error has on the fitness of the modelled forager. The true parameter values used in the basic model are reported in Table 1. Estimation errors were calculated as:

$$\% \text{ Error} = \frac{100(R - E)}{R} \quad (5)$$

where R is the real parameter value and E is the forager's erroneous estimate of the parameter value. Negative errors represent overestimation and positive errors represent underestimation. Calculations in our version of the model were run at 5% error intervals.

At the end of the time period, fitness is calculated based upon the forager's energy reserves, and the terminal fitness function (TFF). The TFF relates the terminal value of the state variable $X(t = T)$ (i.e. energy reserves) to fitness (Mangel and Clark, 1988). As stated earlier, one aspect of the life history of an animal determines how foraging gains contribute to fitness. The TFF determines the relationship between fitness and foraging gains (energy reserves), and hence is an assumption about the life history of the modelled forager.

Bouskila and Blumstein (1992) used a step function (Fig. 1a) as their TFF. The step function defines terminal fitness as:

$$F(x, T, T) = \begin{cases} 1 & \text{if } x > x_c \\ 0 & \text{if } x \leq x_c \end{cases} \quad (6)$$

An animal with this type of life history receives zero fitness if its energy reserves fall below the critical level, x_c . However, if the forager keeps its energy reserves above x_c , it can expect to receive maximum fitness. The step function, as a TFF, probably represents a situation where the forager is avoiding starvation over a non-breeding interval, so the terminal condition is either survival (fitness = 1) or starvation (fitness = 0) (Mangel and Clark, 1988).

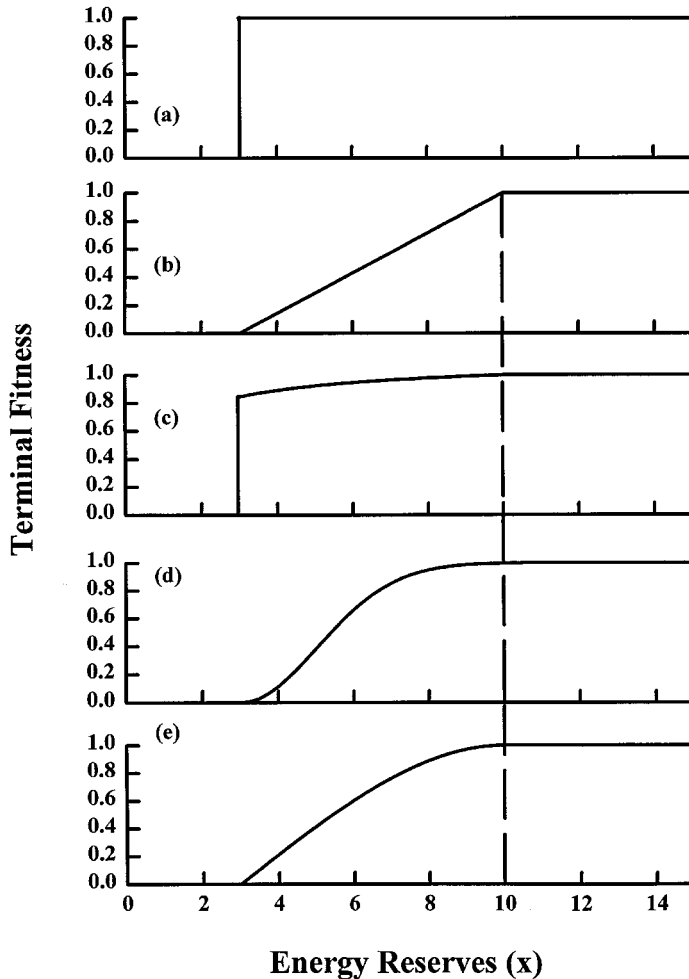


Figure 1. The five terminal fitness functions (TFFs) used in our dynamic state variable model representing possible life histories: (a) the step function used by Bouskila and Blumstein (1992); (b) a straight line function; (c) a saturation curve; (d) a sigmoid curve; (e) Abrams' equation. The dashed reference line represents the saturation point, x_{sat} , where maximum fitness is obtained in the basic model.

We define four alternative TFFs related to possible life histories. All are defined so fitness ranges between zero and 1 (see Table 2 for the values of constants) for comparability of our results to those reported by Bouskila and Blumstein (1992). The first alternative TFF is a straight line function (Fig. 1b). Fitness increases linearly with increasing energy reserves up to some maximum:

$$F(x, T, T) = \begin{cases} 1 & \text{if } x \geq x_{\text{sat}} \\ a + bx & \text{if } x_c < x < x_{\text{sat}} \\ 0 & \text{if } x \leq x_c \end{cases} \quad (7)$$

where x_{sat} , the saturation point, is the level of energy reserves where maximum fitness is attained. A straight line TFF could describe the life history of an animal whose fitness is limited by the time available to gain access to resources other than food. For example, the reproductive success of a

Table 2. Constants used to define the alternative TFFs in the basic model^a

TFF	<i>a</i>	<i>b</i>	<i>c</i>
Straight line	-0.429	0.143	N.A.
Saturation curve	1.000	0.906	-0.604
Sigmoid curve	1.000	0.120	N.A.
Abrams' equation	1.500	$(x - x_c)/(x_{sat} - x_c)$	N.A.

^a All calculations performed with double precision; however, for clarity of presentation, the constants have been rounded to the third decimal place. N.A., not applicable.

male guppy, *Poecilia reticulata*, may be limited by the time available to court females (Baerends *et al.*, 1955; Farr, 1980). In such cases, higher energy reserves would provide more time for non-foraging activities.

If fitness increases in a curvilinear fashion with increasing energy reserves, the TFF may be described by a saturation curve (Fig. 1c):

$$F(x, T, T) = \begin{cases} 1 & \text{if } x \geq x_{sat} \\ \frac{a(x-c)}{1+ab(x-c)} & \text{if } x > x_c \\ 0 & \text{if } x \leq x_c \end{cases} \tag{8}$$

A saturation TFF represents a life history where initial increases in fitness with increasing energy reserves are quick, followed by a decreasing rate of fitness gains, requiring more energy per unit of fitness (e.g. animals investing in the quality of offspring). For example, Lemon and Barth (1992) measured reproductive success in four populations of zebra finches, *Taeniopygia guttata*, where feeding rate was manipulated. Reproductive success, as measured by offspring fledged per female, increased with increased feeding rate in a curvilinear manner similar to a saturation curve.

Alternatively, fitness could increase exponentially with increasing energy reserves, then plateau at some maximum, as described by a sigmoid curve (Fig. 1d):

$$F(x, T, T) = \begin{cases} a(1 - e^{-b(x-x_c)^2}) & \text{if } x > x_c \\ 0 & \text{if } x \leq x_c \end{cases} \tag{9}$$

A sigmoid TFF may represent the life history of female fish. Growth efficiency increases with increasing food, but decreases again at high levels of food rations (Ricker, 1979). Fecundity, however, increases exponentially with the size of female fish (Bagenal, 1978). If we consider these two relationships together, the result would be initial fitness increasing exponentially with increasing energy reserves, then, due to reduced growth efficiency, fitness would plateau at high levels of energy reserves, producing a sigmoid TFF. This simplified view ignores the effects of food availability and population density (for a review, see Bagenal, 1978), and temperature and oxygen availability (Ricker, 1979), on fecundity and growth.

In an attempt to compare our results and the predictions of Abrams' (1994) model, we also include a TFF using an equation given by Abrams that, according to his model, shows underestimation of predation risk. We have slightly modified Abrams' equation to fit the dynamic state variable model:

$$F(x, T, T) = \begin{cases} 1 & \text{if } x \geq x_{sat} \\ 1 - a[2/3 - b + \frac{b^3}{3}] & \text{if } x_c < x < x_{sat} \\ 0 & \text{if } x \leq x_c \end{cases} \tag{10}$$

Abrams' equation looks like a saturation curve when plotted in the range used in our calculations (Fig. 1e) and would represent a similar life history.

These calculations allow us to investigate the influence that a range of life-history characters have on tolerance to imperfect information. We do this by numerically solving the dynamic programming equation (Equation 4), employing backward iterations, while changing the TFF. While these alternative TFFs may not accurately represent a particular organism, they do represent a reasonable range of naturally occurring life-history characters.

Results

The results of our calculations can be presented by plotting the fitness consequences of estimation error against the percent error (Fig. 2) to demonstrate tolerance to imperfect information. We define fitness consequences as the effect of estimation error on fitness compared to a state of perfect information:

$$\text{fitness consequences} = \frac{(\text{fitness with perfect information}) - (\text{fitness with erroneous information})}{(\text{fitness with perfect information})} \quad (11)$$

Thus, the fitness consequences range between zero and 1, and zero percent estimation error (perfect information) has a fitness consequence of 0.000. As the fitness consequences increase, the experienced fitness decreases. The flat region around perfect information in Fig. 2 is defined as the tolerance zone. This is the region with little influence of imperfect information on the expected fitness of the modelled forager. Choosing a fitness consequence of 0.001 as our criterion for tolerance, while consistent with Bouskila and Blumstein (1992), is arbitrary. Within the tolerance

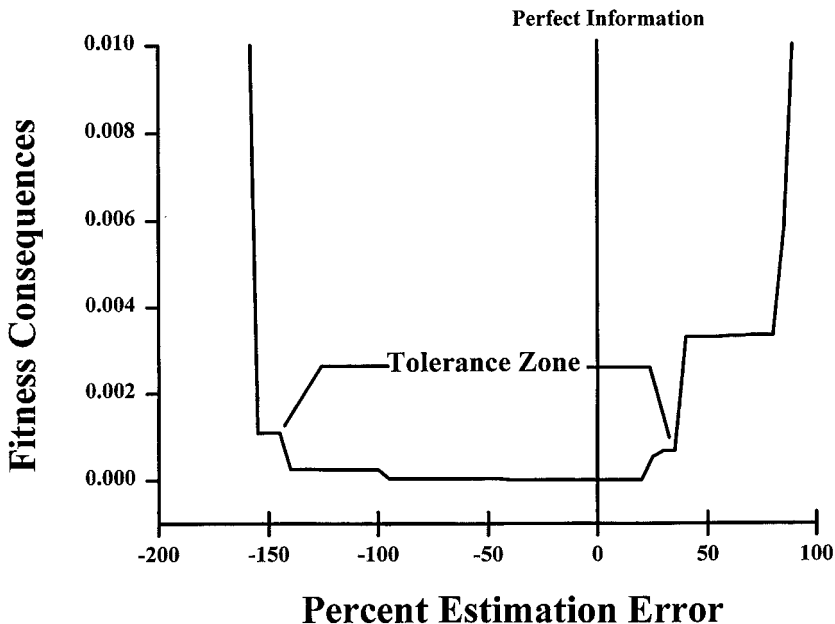


Figure 2. Fitness consequences of imperfect information plotted against estimation error in the probability of death by predation in the risky patch (β_2). Note that these fitness consequences refer to how much fitness is reduced by the use of imperfect information. The terminal fitness function in this case is the step function (Fig. 1a) used by Bouskila and Blumstein (1992). All parameter values as reported in Table 1; expected fitness taken at $X(t = 0) = 13$.

zone, imperfect information has a fitness consequence less than 0.1% of the fitness with perfect information. For example, in Fig. 2, the tolerance zone ranges from -145% to $+40\%$ error, and the size of the tolerance zone is 185% error. Our results, however, are fairly robust to changes in this criterion. While selection will act on any fitness consequence greater than zero, we believe that this level of fitness consequence is low enough for selection to be weak.

TFFs, tolerance and predation risk

Modifications to the model's TFF had a marked influence on predicted tolerance to imperfect information. When comparing tolerance to imperfect information about predation risk (β_2), the size of the tolerance zone decreases from 185% error (range -145% to $+40\%$) when the TFF is a step function to 30% error (range -10% to $+20\%$) when the TFF is a saturation curve (Fig. 3). Bouskila and Blumstein (1992) concluded that tolerance to imperfect information should be relatively large and biased towards overestimation of predation risk, based on results from the step TFF (Fig. 3). All four alternative TFFs result in reduced tolerance to imperfect information

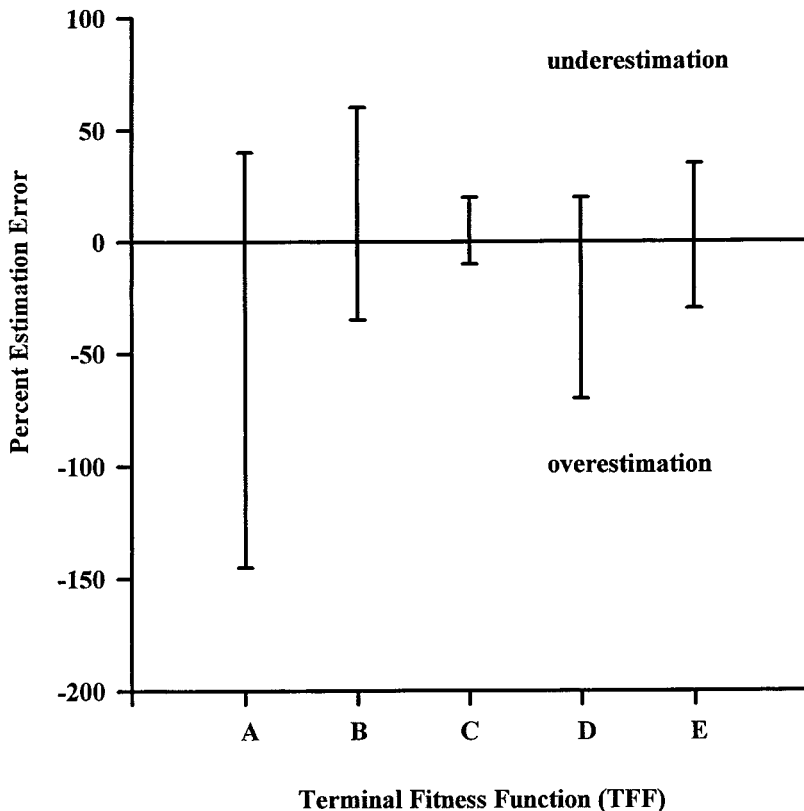


Figure 3. Percent estimation error in predation risk in the risky patch (β_2) showing the range of the tolerance zone for each terminal fitness function (TFF). A, the step function; B, the straight line function; C, the saturation curve; D, the sigmoid curve; E, Abrams' equation. The solid reference line shows perfect information. Below the line is overestimation, above the line is underestimation. All calculations were performed with the parameter values reported in Table 1; data calculated based on expected fitness at $X(t=0) = 13$.

compared to tolerance predicted with the step TFF. Furthermore, the straight line function, the saturation curve and Abrams' equation all show zones of tolerance biased towards underestimation of predation risk.

TFFs, tolerance and patch profitability

To investigate the effect of error in a forager's estimate of patch profitability, we ran the model with error in the rate of encounter in the food-rich patch (r_2). The size of the tolerance zone was calculated 20 times with each TFF, allowing r_2 to range from 0.25 to 5.00 at intervals of 0.25. We found that, for all the TFFs, except the step function, the size of the tolerance zone follows a U-shaped curve as encounter rate increases (Fig. 4). This is not a surprising result if we consider the effect erroneous information about patch profitability has on fitness. At low encounter rates, erroneous estimates of r_2 have little influence on fitness, since the probability of starvation is high. At high encounter rates, fitness consequences for alternative TFFs (i.e. all TFFs except the step function) would be small due to plateaus (see Fig. 1) and the small effect of variation in energy reserves on expected fitness. As for the step function, Bouskila *et al.* (1995) showed that foragers minimize their visits to the risky patch (their Fig. 1). Since there is no benefit to high energy reserves, erroneous estimates of patch profitability can have drastic effects on fitness if energy reserves fall below the critical level leading to relatively narrow tolerance zones.

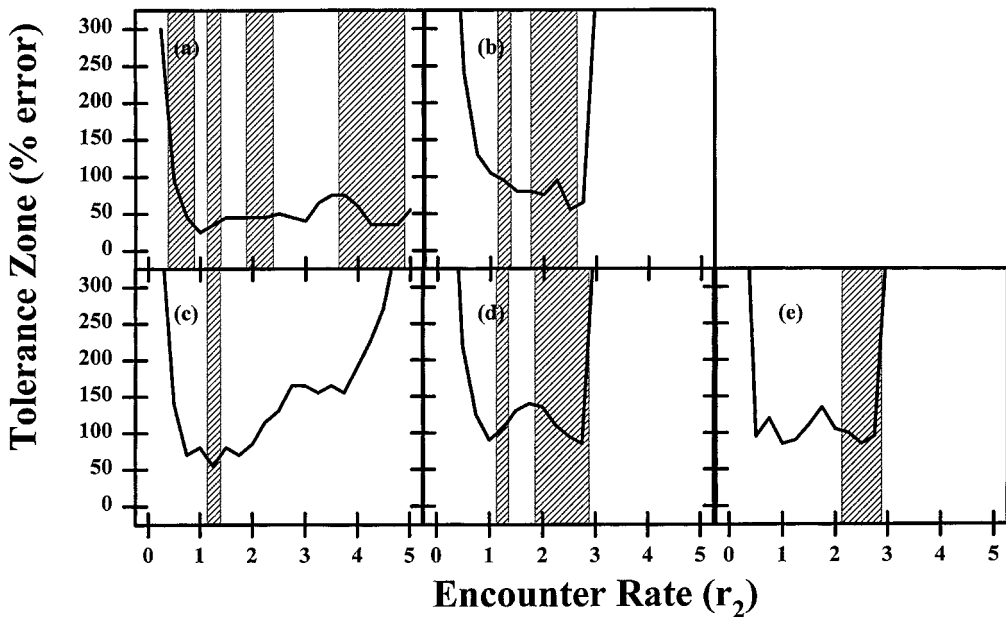


Figure 4. Size of the tolerance zone (measured in % error in encounter rate, r_2) over a large range of encounter rates in the food-rich patch (r_2). Hatched areas represent conditions where the tolerance zone is biased towards underestimation of encounter rate, and the clear areas represent conditions where the tolerance zone is biased towards overestimation of encounter rate. These results are from the dynamic state variable model when the terminal fitness function is: (a) a step function; (b) a straight line function; (c) a saturation curve; (d) a sigmoid curve; and (e) Abrams' equation. All other parameter values as reported in Table 1; data calculated based on expected fitness at $X(t = 0) = 13$.

From Fig. 4 we can see that there are intermediate encounter rates at which foragers are predicted to have low tolerance to imperfect information about patch profitability. Over most of the range of encounter rates investigated, tolerance zones are biased towards overestimation of patch profitability, the exception mostly occurring when tolerance is relatively low. However, both the range of low tolerance and the ranges of underestimation of encounter rate are influenced by assumptions about the TFF (Fig. 4).

TFF details

Assumptions about the TFF can be modified by changing the details without changing the TFF's overall shape. In the basic model, all alternative TFFs have a saturation point set at $x_{\text{sat}} = 10$. Thus, fitness increases with increasing energy reserves between 3 (x_c) and 10 (x_{sat}). Any forager at the end of the time period with $X(T) \geq 10$ received maximum fitness, $F(x, T, T) = 1$. However, this characteristic of the TFF can also be modified, so the saturation point can occur as soon as $x = 4$ (as for the step TFF), or as late as $x = 15$ or later, in which case no forager in this model could obtain maximum fitness. The more a TFF resembles a step function (i.e. the lower the saturation point and the higher the rate of increase in fitness with respect to energy reserves), the larger the zone of tolerance (see Table 3).

Discussion

The model considered here predicts that the aspect of life history described by the relationship between energy and fitness is important in determining tolerance to imperfect information, and this is true when discussing information about predation risk or patch profitability. Therefore, it is not possible to make general predictions about whether estimation of predation risk will be biased towards overestimation (e.g. Bouskila and Blumstein, 1992; Bouskila *et al.*, 1995) or underestimation. This is similar to the conclusion Abrams (1994) drew from his deterministic model.

The influence of life history on tolerance to imperfect information is not too surprising in light of the aspect of life history considered (i.e. the mapping of energy on to fitness). Imperfect infor-

Table 3. The effect of the saturation point (x_{sat}) in defining the TFF on the size (and range) of the tolerance zone (in % error) when the straight line function, saturation curve, sigmoid curves and Abrams' equation were used as the model's TFF^a

x_{sat}	Straight line	Saturation curve	Sigmoid curve	Abrams' equation
5	110% (-40%, +70%)	215% (-170%, +45%)	145% (-110%, +35%)	165% (-150%, +15%)
10	95% (-35%, +60%)	30% (-10%, +20%)	90% (-70%, +20%)	65% (-30%, +35%)
15	115% (-40%, +75%)	30% (-5%, +25%)	50% (-25%, +25%)	75% (-40%, +35%)
20	115% (-40%, +75%)	80% (-55%, +25%)	60% (-25%, +35%)	130% (-115%, +15%)
25	115% (-40%, +75%)	75% (-50%, +25%)	55% (-30%, +25%)	95% (-15%, +80%)

^a Error occurs in estimation of the probability of death by predation in the risky patch (β_2). For comparison, the size of the tolerance zone for the step function is 185% error (range -145% to +40%). $X(t = 0) = 13$; all other parameter values as reported in Table 1.

mation about both predation risk and patch profitability will affect the state variable – that is, energy reserves. Underestimating predation risk or overestimating patch profitability leads to a forager spending more time in the dangerous patch than would be optimal, thus reducing fitness through increased predation risk. Overestimating predation risk or underestimating patch profitability leads to underexploitation of the most profitable patch, and reduced fitness through diminished energy reserves. Thus, we can see why using the step function as the TFF leads to the prediction that animals should be overestimating predation risk. With the step function, fitness does not decrease as energy reserves decrease until energy reserves fall below the critical level, x_c .

Not only did we show that the shape of the food–fitness relationship (TFF) changes tolerance to imperfect information, but the details of the relationship are also important (Table 3). Regardless of the general shape of the relationship, as the TFF looks more like a step function (smaller x_{sat}), the tolerance to imperfect information increases. This suggests that, when it is easier to attain maximum fitness (i.e. a higher rate of increase in fitness gain per unit of energy gain), tolerance to imperfect information should be greater. Specifically, the relatively large tolerance to imperfect information Bouskila and Blumstein (1992) observed was due to the extreme discontinuity of their terminal fitness function. Furthermore, additional calculations by Bouskila (1993) employed TFFs that lead to conclusions similar to Bouskila and Blumstein's (1992) conclusions about tolerance to imperfect information being biased towards overestimation of predation risk, although the zone of tolerance was smaller.

Value of information

Stephens (1989) defines the value of information as the difference in pay-off between being informed and being uninformed. The tolerance zone observed in our results can be considered the zone over which the value of information is low. There is very little difference in fitness pay-off between acting with perfect information versus acting with an erroneous estimate, as long as that estimate falls within the tolerance zone. The fitness consequences plotted in Fig. 2 can be viewed as the value of information (Stephens, 1989), or the maximum fitness cost a forager should willingly incur to obtain perfect information. In the present model, there is no cost to acquiring information. In fact, the modelled foragers did not acquire information at all as an erroneous estimate was assigned from the start. However, if we wish to consider the circumstances in which information should be valued, this model may lend some insight. We know that information is valued only when having information leads to different decisions (Gould, 1974; Chavas and Pope, 1984; Stephens, 1989). If increasing the accuracy of the estimate from 25% to 10% error does not lead to a decision with any appreciable increase in fitness, the value of information would be low. Thus, this model shows that assumptions about the food–fitness relationship of the animal considered can have an influence on the value of information. This means that two animals in exactly the same situation, but with different life histories, may value information differently. Other life-history traits, such as age of maturity, size at maturity, size of offspring, clutch size, and so on, should be investigated for an impact on the value of information.

Predation risk

Bouskila and Blumstein (1992) used this dynamic state variable approach to conclude that foragers should overestimate predation risk. This conclusion is based upon the assumption that the relationship between foraging gains and fitness (the TFF) is a step function. Abrams (1994) objected and used a deterministic model to show that both over- and underestimation of predation risk can be expected. Bouskila *et al.* (1995) claimed that Abrams' deterministic model was not comparable

to their model, and that Bouskila (1993) had used alternative TFFs to show that overestimation of predation risk was still predicted. Abrams (1995) claimed that underestimation was still possible, and that none of the TFFs used by Bouskila (1993) conformed to the conditions that his model claimed led to underestimation of predation risk. The alternative TFFs used by Bouskila (1993) were similar to the sigmoid curve TFF we used, and his results are similar to ours for this TFF.

We included Abrams' (1994) equation in our calculations because Abrams' model predicts that, with this equation, tolerance should be biased towards underestimation of predation risk. In the basic run of the model with Abrams' equation as a TFF, our results show tolerance biased to underestimation of predation risk (Fig. 3). However, when the saturation point is changed from $x_{\text{sat}} = 10$, we observe a bias towards overestimation of predation risk (Table 3). This does not mean that underestimation will be uncommon, but rather that Abrams' (1994) model does not necessarily make the same predictions as Bouskila and Blumstein's (1992) model concerning the underestimation of predation risk. Both models, however, do predict that some foragers will underestimate predation risk.

Patch profitability

The only comparable work on erroneous estimates of patch profitability is Roitberg's (1990) model of fruit flies. Our results show that life history should influence tolerance to imperfect information about patch profitability. Comparing Roitberg's results with our results may not be valid, since his model does not use an explicitly stated TFF. Instead, as fruit flies search for food items in patches, they increase fitness by laying an egg as they find an appropriate item. There is no carryover from day to day, and no benefit in failing to lay all 10 eggs available in a given day. This type of life history would be most similar to our condition of a straight line TFF. Under these conditions, we find that our results lead to the prediction that foragers should be optimistic about, or overestimate, patch profitability (Fig. 4b). Roitberg's (1990) data on giving-up times are significantly shifted towards an over-representation of optimistic fruit flies, as expected from Roitberg's (1990) model and our results. Valone (1993) shows that, without the use of public information, social foragers pay a cost of foraging in groups by leaving patches too soon; that is, social foragers underestimate patch quality compared to solitary foragers. If, however, social foragers use rules biased towards overestimation of patch profitability, then underestimation by social foragers without public information would be minimized or countered.

Conclusions

Our model results demonstrate that tolerance to imperfect information is sensitive enough to assumptions about life history that no general conclusions can be drawn concerning an expected observation of over- versus underestimation of predation risk. Furthermore, the size of the tolerance zone can be manipulated through the details of life history. From this model, we conclude that animals will show tolerance to imperfect information, but the extent of this tolerance may change from one situation to the next. Therefore, animals may use rules of thumb; however, to avoid decreases in fitness from a lack of information, the rules of thumb should either be flexible to local ecological conditions or lead to erroneous estimates that fall within the boundaries of the narrowest tolerance zones. We may still expect organisms to use rules of thumb, but they may not be as simple as expected from Bouskila and Blumstein's (1992) analysis. The one general prediction we can draw from our results is that the greater the rate of increase in fitness with respect to increasing energy reserves (i.e. the lower x_{sat} and the steeper the TFF), the more tolerant an animal should be to imperfect information.

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