Info-Gap Robust-Satisficing Model of Foraging Behavior:
Do Foragers Optimize or Satisfice?

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Abstract

In this paper we compare two mathematical models of foraging that reflect two competing theories of animal behavior: optimizing and robust-satisficing. The optimal foraging model is based on the marginal value theorem (MVT). The robust-satisficing model developed here is an application of info-gap decision theory. The info-gap robust-satisficing model relates to the same circumstances described by the MVT. We show how these two alternatives translate into specific predictions that at some points are quite disparate. We test these alternative predictions against available data, collected in numerous field studies with a large number of species from diverse taxonomic groups. We show that a large majority of studies appear to support the robust-satisficing model and to reject the optimal-foraging model.

Keywords: optimal foraging, satisficing, robustness, Knightian uncertainty, info-gaps.

1   Introduction

The concept of optimal foraging is central to the fields of behavioral ecology in general and foraging behavior in particular. The literature on optimal foraging reveals that data supporting its quantitative predictions are scarcer than data contradicting such predictions. For example, Nonacs (2001) surveyed numerous studies that evaluated a specific behavioral feature of foraging animals, namely, patch residence time (PRT). Nonacs compared observed values of PRT to the value predicted by the marginal value theorem (MVT), one of the most influential concepts in optimal foraging theory (Charnov, 1976). From among the studies reviewed by Nonacs (2001), more than 75% contradicted the predictions of the MVT.

Ward (1992) views the concept of optimal foraging as an "exemplar" (Kuhn 1974), a term similar to Kuhn's earlier definition of "paradigm" (Kuhn 1962). In accord with Kuhn's (1962) description of scientists' reactions when confronting findings that contradict a prevailing paradigm, some authors of those studies, as well as Nonacs himself, suggested that additional factors need to be accounted for. These authors showed that when one or another factor is added to the model, predictions do agree with the data. The need for ad hoc modifications suggests the usefulness of considering alternative paradigms. However, such alternatives have rarely been considered. In this paper we present a quantitative model of foraging based on robust-satisficing rather than optimization.

Myers (1983) and Ward (1992, 1993) proposed that the concept of satisficing, developed by Simon (1955) and used frequently by psychologists (Plous, 1993) and economists (Conlisk, 1996), may serve as an alternative working hypothesis to optimal foraging. However, in spite of Ward's detailed account of satisficing as an alternative to optimal foraging more than a decade ago (Ward 1992, 1993), this hypothesis was not translated into a specific mathematical model capable of yielding testable predictions. A major argument against satisficing as an explanation of animal behavior has been that it does not yield testable predictions (Stephens and Krebs 1986, Nonacs and Dill 1993).

This paper will develop a testable model of satisficing and will compare this model against field evidence.

Information-gap decision theory (Ben-Haim 2001) combines Simon's concept of satisficing: satisfying minimal requirements (Simon 1955) with Knight's (1921) concept of non-probabilistic uncertainty as opposed to probabilistic risk. The info-gap concept underlies mathematical models in many areas of technology (Ben-Haim 1996, 2005), economics (Ben-Haim and Jeske 2003), project management (Ben-Haim and Laufer 1998), conservation biology (Regan *et al* 2005) and so on. Here we define and construct an info-gap decision strategy as an alternative to a specific optimal foraging model. This is described in detail in section 3.

In this paper we follow Ward and compare two mathematical models of foraging that reflect two competing theories of animal behavior: optimizing and robust-satisficing. The optimal foraging model is based on the well-known marginal value theorem (Charnov 1976). While many distinct realizations of the MVT have been studied, we use one specific model as a proto-typical illustration of the widely observed phenomenon that measured PRTs are longer than predicted by optimizing theories. The info-gap robust-satisficing (IGRS) model developed here is an application of info-gap decision theory (Ben-Haim 2001). The IGRS model relates to the same circumstances described by the MVT. We test these alternative predictions against available data, collected in numerous field studies. We ask if, given the available data, there is a difference in plausibility of these two models (Hilborn and Mangel 1997, pp.7–8).

2   Optimal Foraging with the Marginal Value Theorem

The specific optimal-foraging model upon which we focus employs the 'giving up time' version of the MVT, which is a deterministic rate-maximization model (Charnov 1976). This concept was discussed by Stephens and Krebs (1986) among others, and is described briefly here. A major decision made by a foraging animal is whether to continue foraging in the current patch or to leave, looking for a more profitable patch. The decision is not to quit foraging in favor of another activity, but rather to move to a different foraging area. The gain from a patch per unit time may decrease with time since the animal exploits it (possibly together with other animals). This gives rise to the need to evaluate current gain against expected gain in other patches. We will consider situations in which the remaining foraging time is large compared to the transit time from one patch to another.

The marginal value theorem asserts that in order to maximize its gain, the animal needs to leave the patch once the following condition is met:

$$g_0 t < g_1 t - c \tag{1}$$

where t is the time left for foraging (which is large compared to travel time), g_0 is the current rate of gain, g_1 is the average expected rate of gain in other patches, and c is the estimated energy cost of travel to the next patch. The MVT predicts that an animal is expected to leave at that particular moment. Earlier or later departure would result in sub-optimal exploitation of resources.

Our aim is not to survey optimal foraging models, or to suggest that eq.(1) is superior to other optimal foraging models. Rather, this realization of the MVT is characteristic of the vast array of optimal foraging models in that its predictions of PRTs generally fall short of observed PRTs. The aim of this paper is to develop an alternative concept for foraging models, which is introduced in the next section. The performance of this new foraging model is compared with evidence and discussed in sections 4 and 5.

3   Info-gap Robust-Satisficing

Info-gap theory provides a quantification of severe Knightian uncertainty, as well as a concept of robustness to this uncertainty. We will describe these concepts in detail, and explain the info-gap

robust-satisficing strategy for patch residence time. We will compare this to the foraging strategy based on the MVT.

Performance function. Consider an animal foraging in patch 0 and contemplating moving to patch 1. More precisely, the animal must decide either to remain for t minutes in the current patch, or move to another patch for t minutes, where the move itself costs c Joules ($c > 0$). We assume that the time remaining for foraging is far greater than the travel time to the next patch. Let g_i denote the rate of gain if the animal is in patch i, in Joules/minute. Let s be the decision parameter, so $s = 0$ means 'stay in patch 0' while $s = 1$ means 'move to patch 1'. The total gain for decision s is:

$$G(s, g) = g_0 t(1 - s) + (g_1 t - c)s \tag{2}$$

Maximizing behavior. The total gain, $G(s, g)$ is maximized by $s = 1$ (moving to the new patch) if and only if relation (1) holds, which is the strategy recommended by the marginal value theorem.

Satisficing behavior. Maximal gain may be desirable, but need not be mandatory. The lowest acceptable gain, the minimum required for survival, will be denoted $G_{\min}$. A 'satisficing' strategy is one which yields no less than the minimum required gain:

$$G(s, g) \geq G_{\min} \tag{3}$$

If $G_{\min}$ is less than the maximum possible gain, then more than one strategy may satisfy the gain requirement in eq.(3). When this is the case, then additional considerations can be brought to bear on the choice of a strategy. Specifically, the strategy can be selected to enhance robustness to uncertainty or, equivalently, to enhance reliability or confidence in extracting the needed nourishment from an uncertain world.

Info-gap uncertainty. Now suppose the animal has estimates of the rates of energy gain in each patch. That is, g_i is estimated to be $\widetilde{g}_i$. Specifically, $\widetilde{g}_0$ is the current rate of gain in the patch where the animal is located, and $\widetilde{g}_1$ is the animal's guess based on experience (both ontogenetic and phylogenetic experience) of the rate of gain in other patches. Both of these numbers are uncertain. $\widetilde{g}_0$ is uncertain because the future rate of gain here depends on the future supply here, on future competition here, etc. $\widetilde{g}_1$ is uncertain because it is an historical average which may not match future reality. Specifically, $\widetilde{g}_i$ is the best available estimate of g_i, but the error of this estimate is unknown. That is, the animal has incomplete knowledge of the variability of g_i and limited capability for evaluating strategy options. The uncertainty in the estimated gain rates undermines the confidence in attaining the critical gain $G_{\min}$.

An info-gap model for unknown fractional error in the estimated rates of gain is:

$$\mathcal{U}(\alpha, \widetilde{g}) = \left\{ g = (g_1, g_2) : \left| \frac{g_i - \widetilde{g}_i}{\widetilde{g}_i} \right| \leq \alpha, \ i = 0, 1 \right\}, \quad \alpha \geq 0 \tag{4}$$

$\mathcal{U}(\alpha, \widetilde{g})$ is the set of all rates of gain g_i which deviate from the estimates $\widetilde{g}_i$ by no more than a fraction α. The magnitude of this fractional error is unknown, (the animal does not know how wrong $\widetilde{g}_i$ is), so the horizon of uncertainty α is unbounded. Thus the info-gap model, $\mathcal{U}(\alpha, \widetilde{g})$, $\alpha \geq 0$, is not a single set of gain rates g_i but rather an unbounded family of nested sets of possible gain-rates. The info-gap model is 'unbounded' in the sense that there is no largest set and there is no worst case. The set $\mathcal{U}(\alpha, \widetilde{g})$ of gain rates becomes more inclusive as the horizon of uncertainty α increases. 'Nesting' of the uncertainty sets means that $\mathcal{U}(\alpha, \widetilde{g})$ is contained in $\mathcal{U}(\alpha', \widetilde{g})$ if $\alpha < \alpha'$. The info-gap model is a quantification of non-probabilistic uncertainty.

Robust satisficing behavior. The robustness, $\widehat{\alpha}(s, G_{\min})$, of decision s is defined here as the greatest horizon of uncertainty α up to which the actual gain is no less than the critical value $G_{\min}$ for all realizations of the gain-rates g:

$$\widehat{\alpha}(s, G_{\min}) = \max \left\{ \alpha : \left(\min_{g \in \mathcal{U}(\alpha, \widetilde{g})} G(s, g) \right) \geq G_{\min} \right\} \tag{5}$$

3

We can "read" this relation from left to right as follows. The robustness $\widehat{\alpha}$ of decision s with minimal foraging requirement $G_{\min}$ is the maximum horizon of uncertainty α up to which the minimal gain $G(s, g)$, for all gain rates g available at uncertainty α (namely, those in $\mathcal{U}(\alpha, \widetilde{g})$), is no less than the critical value $G_{\min}$.

Robustness to uncertainty implies confidence in attaining the critical foraging requirement. A central idea which we will develop in subsequent discussion is that more robustness is preferred to less robustness, at the same critical gain $G_{\min}$. That is, robustness has fitness value. Choice s is preferred over s' if the attainment of gain $G_{\min}$ is more robust to uncertainty with s than with s':

$$s \succ s' \quad \text{if} \quad \widehat{\alpha}(s, G_{\min}) > \widehat{\alpha}(s', G_{\min}) \tag{6}$$

An opportunity cost is paid when the animal chooses one patch over another: the animal forgoes the advantage which the rejected patch might have yielded. Robustness is obtained in exchange for the opportunity cost. Robustness to the uncertain future, $\widehat{\alpha}(s, G_{\min})$, is a measure of confidence in survival. The animal's fitness is enhanced by enhancing the confidence that the selected patch will yield at least the critical level of energy. The patch-selection rule in relation (6) states that more confidence in survival is preferable over less confidence.

Evaluating the robustness. We now evaluate the robustness function of eq.(5) with the info-gap model of eq.(4). We assume that the animal needs a positive amount of energy ($G_{\min} > 0$) and that the estimated rates of energy gain are positive ($\widetilde{g}_i > 0$). One finds that the robustness functions for the two choices of s are:

$$\widehat{\alpha}(0, G_{\min}) = \begin{cases} 1 - \dfrac{G_{\min}}{\widetilde{g}_0 t} & \text{if } G_{\min} \leq \widetilde{g}_0 t \\ 0 & \text{else} \end{cases} \tag{7}$$

$$\widehat{\alpha}(1, G_{\min}) = \begin{cases} 1 - \dfrac{G_{\min} + c}{\widetilde{g}_1 t} & \text{if } G_{\min} \leq \widetilde{g}_1 t - c \\ 0 & \text{else} \end{cases} \tag{8}$$
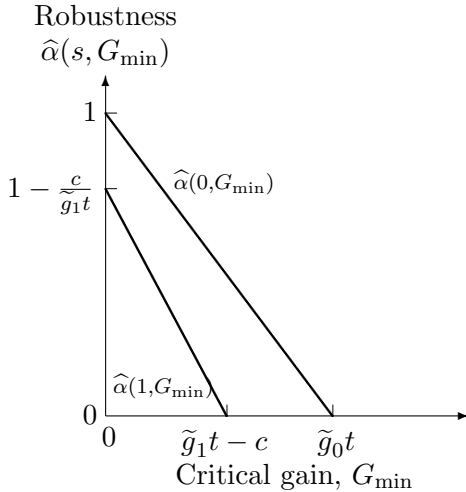

Figure 1: Robustness versus critical gain, if $\widetilde{g}_1 t - c < \widetilde{g}_0 t$ for which the nominal (and MVT) choice is $s = 0$.
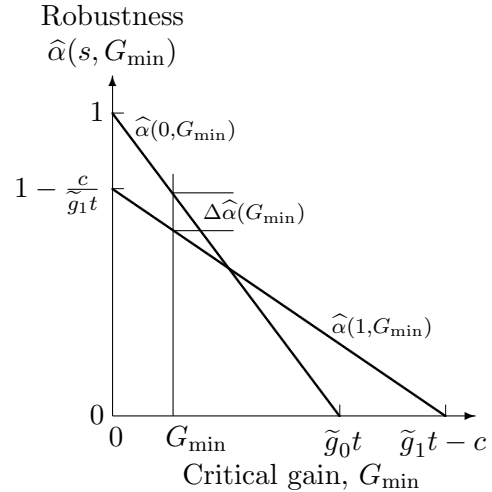
Figure 2: Robustness versus critical gain if $\widetilde{g}_1 t - c > \widetilde{g}_0 t$, for which the nominal (and MVT) choice is $s = 1$.

These robustness functions are shown in fig. 1 for $\widetilde{g}_1 t - c < \widetilde{g}_0 t$ and in fig. 2 for the case that $\widetilde{g}_1 t - c > \widetilde{g}_0 t$. These figures show how the robust-satisficing strategy selects between the two choices, $s = 0$ (stay in the current patch) and $s = 1$ (move to the new patch), based on the criterion of greater robustness, relation (6).

In fig. 1 we see that $s = 0$ is always preferred, which is also the MVT recommendation since $\widetilde{g}_1 t - c < \widetilde{g}_0 t$.

In fig. 2 we see that the choice $s = 1$ is more robust and hence preferred if only low robustness against uncertainty is required, while the choice $s = 0$ is preferred if large robustness is required. The crossing of robustness curves in fig. 2 implies reversal of preference between the options which those curves represent. That is, the choice indicated by the marginal value theorem, eq.(1), holds here only if uncertainty is low. If, however, uncertainty is high, then the info-gap robust-satisficing (IGRS) recommendation is to stay, while the MVT recommendation is to move since $\widetilde{g}_1 t - c > \widetilde{g}_0 t$.

Time to move. We can carry this example one step further, and make some testable predictions. This is based on the idea of **robustness premium**, $\Delta\widehat{\alpha}(G_{\min})$, which is illustrated in fig. 2. The robustness premium of decision $s = 0$ (stay put), over decision $s = 1$ (move), is the increment in robustness which is guaranteed by $s = 0$ over the robustness which is guaranteed by $s = 1$. The robustness premium is a function of the critical gain requirement $G_{\min}$ and is formally defined as:

$$\Delta\widehat{\alpha}(G_{\min}) \quad = \quad \widehat{\alpha}(0, G_{\min}) - \widehat{\alpha}(1, G_{\min}) \tag{9}$$

Strategy $s = 0$ is preferred, in terms of robust-satisficing, over strategy $s = 1$, if and only if $\Delta\widehat{\alpha}(G_{\min})$ is positive.

$\Delta\widehat{\alpha}(G_{\min})$ is a somewhat complicated function because $\widehat{\alpha}(0, G_{\min})$ and $\widehat{\alpha}(1, G_{\min})$ are each piecewise linear as seen in eqs.(7) and (8). Nonetheless one can readily establish the following necessary and sufficient condition for positive robustness premium:

$$\Delta\widehat{\alpha}(G_{\min}) > 0 \ \text{ if and only if } \begin{cases} \widetilde{g}_0 t \leq \widetilde{g}_1 t - c & \text{and} \quad G_{\min} < \dfrac{c\widetilde{g}_0}{\widetilde{g}_1 - \widetilde{g}_0} \leq \widetilde{g}_0 t \\ & \text{or} \\ \widetilde{g}_0 t > \widetilde{g}_1 t - c & \text{and} \quad G_{\min} < \widetilde{g}_0 t \end{cases} \tag{10}$$

The upper conditions on the right correspond to fig. 2 and the lower conditions correspond to fig. 1. In the upper condition, the term $c\widetilde{g}_0/(\widetilde{g}_1 - \widetilde{g}_0)$ is the value of $G_{\min}$ at which the robustness curves cross in fig. 2. Decision $s = 0$ is more robust than $s = 1$ when $G_{\min} < c\widetilde{g}_0/(\widetilde{g}_1 - \widetilde{g}_0)$, which must be less than $\widetilde{g}_0 t$ in order for $\widehat{\alpha}(0, G_{\min})$ to be strictly positive.

	1	2	3	4	5	6	7
	Differential productivity	Remaining foraging time	MVT condition	MVT strategy	Critical gain	Robustness premium	Robust satisficing strategy
A	$\widetilde{g}_0 > \widetilde{g}_1$	$t \geq 0$	$\widetilde{g}_0 t > \widetilde{g}_1 t - c$	$s = 0$	$G_{\min} \leq \widetilde{g}_0 t$	$\Delta\widehat{\alpha}(G_{\min}) > 0$	$s = 0$
B	$\widetilde{g}_0 < \widetilde{g}_1$	$t < \dfrac{c}{\widetilde{g}_1 - \widetilde{g}_0}$	$\widetilde{g}_0 t > \widetilde{g}_1 t - c$	$s = 0$	$G_{\min} \leq \widetilde{g}_0 t$	$\Delta\widehat{\alpha}(G_{\min}) > 0$	$s = 0$
C	$\widetilde{g}_0 < \widetilde{g}_1$	$t > \dfrac{c}{\widetilde{g}_1 - \widetilde{g}_0}$	$\widetilde{g}_0 t < \widetilde{g}_1 t - c$	$s = 1$	$G_{\min} < \dfrac{c\widetilde{g}_0}{\widetilde{g}_1 - \widetilde{g}_0}$	$\Delta\widehat{\alpha}(G_{\min}) > 0$	$s = 0$
D	$\widetilde{g}_0 < \widetilde{g}_1$	$t > \dfrac{c}{\widetilde{g}_1 - \widetilde{g}_0}$	$\widetilde{g}_0 t < \widetilde{g}_1 t - c$	$s = 1$	$G_{\min} > \dfrac{c\widetilde{g}_0}{\widetilde{g}_1 - \widetilde{g}_0}$	$\Delta\widehat{\alpha}(G_{\min}) < 0$	$s = 1$

Table 1: Strategy choices based on robust-satisficing, eq.(10), and the MVT, eq.(1).

The implications of the robustness premium in eq.(10) are summarized in table 1. We now explain the four rows of this table.

Row A. First consider $\widetilde{g}_0 > \widetilde{g}_1$, which means that, according to available estimates, the current patch is more productive than the next patch. Thus $\widetilde{g}_0 t > \widetilde{g}_1 t - c$, so the condition of fig. 1 holds. Eq.(10) implies that the robustness premium is positive for all $G_{\min} \leq \widetilde{g}_0 t$. Hence $s = 0$ is the preferred robust-satisficing strategy, provided the required gain $G_{\min}$ is not greater than $\widetilde{g}_0 t$. This agrees with the MVT recommendation.

Row B. Now suppose $\widetilde{g}_0 < \widetilde{g}_1$ and that $t < c/(\widetilde{g}_1 - \widetilde{g}_0)$. Thus again $\widetilde{g}_0 t > \widetilde{g}_1 t - c$, so the condition of fig. 1 holds. Hence $s = 0$ is the robust-satisficing preferred strategy, provided the required gain $G_{\min}$ is not greater than $\widetilde{g}_0 t$. This agrees with the MVT recommendation.

Row C. Again suppose $\widetilde{g}_0 < \widetilde{g}_1$ but now $t > c/(\widetilde{g}_1 - \widetilde{g}_0)$. Now $\widetilde{g}_0 t < \widetilde{g}_1 t - c$, so the condition of fig. 2 holds. Hence $\Delta \widehat{\alpha}(G_{\min}) > 0$ and $s = 0$ is preferred only if $G_{\min} < \dfrac{c\widetilde{g}_0}{\widetilde{g}_1 - \widetilde{g}_0} \leq \widetilde{g}_0 t$. This disagrees with the MVT recommendation.

Row D. Finally, suppose $\widetilde{g}_0 < \widetilde{g}_1$ and that $t > c/(\widetilde{g}_1 - \widetilde{g}_0)$. Again $\widetilde{g}_0 t < \widetilde{g}_1 t - c$, so the condition of fig. 2 holds. Now $\Delta \widehat{\alpha}(G_{\min}) < 0$ and $s = 1$ is preferred if $G_{\min} > \min \left[\dfrac{c\widetilde{g}_0}{\widetilde{g}_1 - \widetilde{g}_0}, \widetilde{g}_0 t \right]$. This agrees with the MVT recommendation.

Do foragers optimize or satisfice? Which strategy, MVT optimization or info-gap robust-satisficing, best describes foraging behavior? Comparing columns 4 and 7 of table 1 we see that the two models agree in rows A, B and D, and disagree in row C. That is, discrimination between robust-satisficing and MVT-optimizing must concentrate on situations defined by this disagreement.

We will reject info-gap robust-satisficing and not reject MVT if, under the conditions of row C and columns 1, 2 and 5, PRTs correspond to, or are shorter than, MVT predictions.

We will reject MVT and not reject robust-satisficing if the patch residence time exceeds the MVT prediction only when all of the following three conditions hold:

1. The current patch is estimated to have sub-average rate of gain (row C, column 1).

2. Much time remains for foraging (row C, column 2).

3. The organism is in a situation of 'low stress' meaning that the critical gain need not be too great (row C, column 5).

We stress that only in this 3-fold constellation do the two models disagree: the MVT strategy is to move ($s = 1$) while the robust-satisficing strategy is to stay put ($s = 0$). Note, however, that such constellations may be very common, perhaps prevailing, for most animals during their foraging activities. Evidence discussed in the next section will indicate that field studies usually correspond to the constellation in row C of Table 1 and may therefore be interpreted as supporting exclusively one or the other of these theories.

4   Evidence from Foraging Studies

We surveyed the literature,[1] and selected all studies that satisfied the following two criteria: 1. The study provides field- or lab-test of the MVT. 2. Results of the study enable direct comparison between MVT-predicted PRT and actual PRT. We found that 26 studies satisfied these criteria, representing a diverse range of taxa, of which 24 were used previously in Nonacs (2001).

We inspected all these articles, to assess if they comply with the set of conditions that characterizes row C in Table 1, and if their results may rightly serve to distinguish between the two models.

The first condition (column 1) is 'gain in current patch is less than average'. If the gain in the current patch is more than average, then both models would prescribe a stay. All surveyed studies met this simple condition.

The second condition is that much time remains for foraging (column 2). In both types of studies that we evaluated, field observations and lab experiments, foragers were followed for a long period during each day of study; typically, multiple sessions totaling several hours were carried out daily. In some of these studies, results of the last foraging hour were not used in the analysis (Kamil et al 1988; Lima 1985), and these studies fully met condition #2. In other studies, the animals were free to continue foraging after the hours of formal trials (Roitberg and Prokopy 1982). All the surveyed studies contained numerous trials or observations in each day of the study. Thus, apparently, the vast majority of the data from each study reflect situations where there is much time left for foraging.

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[1]We used the ISI web of science to select all items with the keyword 'Marginal Value Theorem' published from 1977 onward.

The third condition (column 5) is that the critical gain, which is the minimal gain required to ensure survival, is relatively low, and the animal is not on a tight budget. In the present context, quantifying the critical gain is not feasible. However, there are indications that this condition is met in most, if not all, of the surveyed studies. Some studies of lab experiments report that the animals had unrestricted access to water and food throughout the period of the experiment (Devries et al 1989; Lima 1985; Ydenberg 1984). In other studies, the animals had a diet that kept them at 80–90% percent of their original body-weight (Cassini et al 1990; Hanson and Green 1989; Kamil et al 1993; Todd and Kacelnik 1993). In general, the animals were kept in benign conditions, without predation risk. Another indication that the lab conditions were not too harsh for the animals is that all animals in all these studies survived the entire experiment period, and not a single death was reported. In conclusion, there seems to be a general matching between the conditions in row C of Table 1 and the conditions of most (if not all) experiments, at least during most of the experimental period.

The studies were classified according to whether their empirical average PRT values were longer than MVT predictions (and thus supportive of IGRS), equal to MVT predictions, or inconsistent with both MVT and IGRS. Details of all studies appear in the on-line appendix.

19 studies reported significantly longer than MVT-expected PRTs, as predicted by the IGRS but not by the MVT, possibly reflecting row C in Table 1. Row C represents that constellation of conditions in which IGRS and MVT have different predictions, and it is here that evidence can distinguish between these two models. An additional 4 studies reported average PRTs similar to predictions of the MVT model. Three additional studies contradicted both models, indicating either shorter PRTs than MVT predictions, or shorter and longer PRTs in rich and poor patches, respectively. In summary, the preponderance of the evidence is consistent with the info-gap robust-satisficing paradigm and conflicts with the predictions of the MVT.

5   Discussion

The notion of optimization in animal behavior, as well as in economics, refers to the principle of maximizing gain, which determines animal and human decision making (studied by ethologists and economists, respectively). This concept has long been employed as a paradigm: it is well embedded in our world-view and it directs the way researchers conceive their discipline and interpret their results. This way of thinking is appealing, perhaps because it prescribes a very simple answer to the question 'how much?', an answer which is always precise: 'as much as possible'.

Theories based on optimization strategies are readily tested because they entail precise predictions. This vulnerability to falsification is a virtue for a scientific theory, as Popper has described in his analysis of the methodology of science (Popper 1965). Theories based on satisficing rather than optimization sometimes suffer from lack of falsifiability, which has rightly been pointed out to be a serious deficiency of these theories (Stephens and Krebs 1986, p.180). One contribution of this paper is to develop a model of foraging behavior based on robust-satisficing and to show its vulnerability to falsification against observation.

The notion of optimization as a paradigm of actual behavior has been questioned on the grounds of 'bounded rationality' (Simon, 1955), referring to limitations on the ability of an animal (or a person) to find an optimal solution. Limitations may stem from (1) imperfect information, (2) imperfect information-processing capabilities and (3) environmental variability in space and time. Knight (1921) stressed that information may be so deficient, and conditions may be so variable, that probabilistic models are inaccessible: under severe uncertainty one simply cannot choose a probability distribution.

The approach adopted here, info-gap robust-satisficing, is one possible quantification of bounded rationality and Knightian uncertainty. A solution that is good enough for the animal to survive, even if sub-optimal, may be more robust (in the sense developed here) than a gain-optimizing solution. We have derived and discussed such a solution in section 3. Given the uncertainties mentioned above, a reliable and adequate solution is preferable to an optimal but unreliable solution.

It might be argued that robust-satisficing due to information limitations or processing constraints

is congruent with optimal foraging with these constraints. After all, optimal foraging theory has never assumed that animals have perfect knowledge of the environment, or intricate mathematical capabilities to calculate optimal solutions (Stephens and Krebs 1986). However, optimal foraging theory implicitly assumes mechanisms of foraging choice that approximate optimal strategies (Stephens and Krebs 1986). In contrast, the present work shows that a gain-optimizing strategy which is based on models with non-probabilistic Knightian info-gaps may have low or zero robustness to those info-gaps. A strategy with positive robustness may differ from a gain-optimizing strategy, as illustrated in fig. 2. A satisficing strategy does not try to approximate a gain-optimal solution, and may choose a sub-optimal strategy (Janetos and Cole 1981). As we have seen, a robust-satisficing strategy can be sub-optimal in gain but more robust (and hence more reliable) than the optimal strategy. The robust-satisficing approach to animal decision making is distinct from optimal foraging. It prescribes quantitative predictions that sometimes differ from those of optimal foraging, and, as exemplified here for patch-leaving rules, may correspond better to available data.

Nonetheless the info-gap robust-satisficing strategy entails Pareto optimization:[2] trading-off one (or several) variables against another variable, which defines a surface of optimal or maximally efficient options. Pareto optimal surfaces are shown in figs. 1 and 2 in which energy gain is traded-off against robustness to uncertainty. The importance of state variables in biological modelling has been emphasized by Mangel and Clark (1988). Robustness can be viewed as an additional state variable, along with other state variables such as energy gain, physiological state, reproductive status, predation risk, etc. All these other state variables are substantive physiological or environmental parameters which impact the fitness of the individual in the objective and concrete struggle for survival. The substantive state variables all interact, through traditional biological laws, in ecological processes.

Robustness is qualitatively different. Robustness is epistemic,[3] not physiological or environmental. It impacts fitness in a distinctive manner. Robustness assesses the reliability with which a given strategy will achieve specified goals. Since these goals — e.g. energy requirements — relate directly to survival, the assessment of reliability of achievement is pertinent to survival when the animal must choose a strategy.

The fitness-value of robustness can be explained syllogistically as follows.

1. Sufficient energy intake is necessary for survival.

2. More reliable sufficient intake is preferable over less reliable sufficient intake when the animal selects a patch.

3. Thus maximal reliability of sufficient intake is an optimal selection strategy.

The robust-satisficing strategy (maximize robustness of adequate energy gain) will coincide with the classical energy-optimizing strategy when the robustness curves do not cross, as in fig. 1. However, robust-satisficing and energy-optimization can differ when robustness curves cross, as in fig. 2.

Of course, it is also true that more energy is better than less energy. The point is that both energy and robustness are necessary properties of a good decision. In other words, the animal's optimization problem is a Pareto trade-off of robustness against energy, rather than a pure energy-optimization problem. Attempting solely to optimize energy intake may endanger the animal because a maximal energy-intake strategy has zero robustness to info-gaps.

Optimization takes many forms. For instance, new optimization criteria reflect the effect on foraging decisions of competitive or cooperative interactions among foragers (Giraldeau and Caraco 2000). The present work does not contribute to social foraging theory, but shares with that body of work the revision of classical optimization criteria. We have shown that by considering the Knightian

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[2] "Pareto optimality, the state of a system ... when there is no alternative in which there is at least one person better off and no one worse off." Oxford English Dictionary.

[3] Epistemic: "of or relating to knowledge or knowing; cognitive" (Webster's Dictionary); "Of or relating to knowledge or degree of acceptance" (Oxford English Dictionary). Much work on decision under uncertainty distinguishes between epistemic and objective (real world) uncertainty. See Helton and Oberkampf, 2004.

uncertainties — info-gaps — which confront the forager, the classical optimization problem becomes embedded in a Pareto trade-off of robustness vs. energy gain.

Our syllogistic argument for the fitness-value of robust-satisficing applies to any optimization strategy, including stochastic optimization. The specific implementation of info-gap robust-satisficing developed in this paper focusses on uncertainty in the gain rates g in a deterministic analysis of energy intake. A similar argument could focus on uncertainty in probability functions, e.g. uncertain tails of a probability density. A stochastically optimal strategy may have low robustness to uncertainty in the functions upon which it is based. This would imply that a patch with sub-optimal but adequate and reliable intake may be preferred over a patch with optimal but unreliable intake. Once again, the preference between robust-satisficing and optimization depends, as in our example, on whether, and where, the robustness curves cross.

We have argued that epistemic limitations imply that performance should be satisficed rather than optimized. 'Satisficing' is the satisfaction of minimal requirements or specifications: making the performance good enough, as distinct from optimizing the performance. Satisficing leaves additional design degrees of freedom open with which to enhance the robustness of the system. Engineers use design specifications to robustly satisfice: meet design-code requirements rather than optimize performance. Satisficing and bounded rationality were introduced into economics by Simon (1997) who recognized the infeasibility of optimization in many contexts. Similarly, Alchian (1977, p.16) points out the impossibility of reliably planning the maximization of profit in dynamic environments. The attainment of global optimization in biological systems is unlikely in light of the vast number of genotypal possibilities (Holland 1975, pp.9, 17).

The seeds of the idea of satisficing can be found in Darwin's thought. Darwin (1872, chap.12) observed that alien species colonized in a new region can dominate successful aborigines due to the newcomers' superior fitness which, as Simon (1983, p.69) pointed out, illustrates that evolutionary success is a measure of comparative advantage rather than universal optimality. The search for 'comparative advantage' is a satisficing strategy (don't optimize, just beat the competition), suggesting that biological systems may evolve by balancing performance against robustness-to-info-gaps rather than by optimizing functionality. The outcome of Darwinian evolution is the survival of the more fit over the less fit, not necessarily of the *most* fit, which again illustrates the importance of comparative advantage rather than optimality. As we have seen in our analysis of foraging, sub-optimal decisions can be more robust than, and hence preferable to, performance-optimal decisions. Darwin (1872, p.378) also pointed to the "great fact" that similar habitats in the Old and New Worlds have "widely different ... living productions!". Optimization would tend to produce similar phenotypes under similar constraints; robust satisficing produces diversity due to the added degrees of freedom associated with performance-sub-optimality.

The info-gap robust-satisficing strategy defined in section 3 could be modified in many ways. One could use a different performance function than eq.(2), for instance by including the time of transit between patches. One could use a different info-gap model than eq.(4) for uncertainty in the anticipated gain rates $\widetilde{g}_i$, for instance by allowing lower uncertainty in the current patch than in the unvisited patch. One could also modify the robustness function in eq.(5) to include satisficing on several parameters, not only the total remaining foraging gain. This paper aims to demonstrate the power and the potential of IGRS strategies, which might find other manifestations in foraging, as well as in other areas of biology including, for instance, mate selection, nest-building techniques, predator-evasion strategies, and so on.

6   References

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7   On-Line Appendix: Summary of Empirical Studies

Empirical studies that tested MVT predictions against actual data are summarized in on-line appendix tables A1–A3. Articles in these tables are classified into one of three categories. (1) Reports where, on average, data are in agreement with MVT predictions of leaving time, and in conflict with IGRS predictions, are labelled 'MVT'. (2) Reports in which the average stay in patch was substantially longer than prescribed by MVT are labelled 'IGRS' to indicate support for the info-gap robust-satisficing paradigm over MVT. (3) Reports in which the average stay in the patch was smaller than prescribed by MVT, or where stay was longer in poor patches while shorter in rich patches are labelled 'None' to represent their contradiction of both the MVT and IGRS models.

On-line appendix tables A1–A3 are based on Nonacs (2001), with several modifications: (a) Several studies that were irrelevant for testing MVT (classified '?' by Nonacs 2001) were not included here. (b) Two studies cited by Nonacs (2001) as indicating longer stay (Kacelnik 1984) and shorter stay (Hodges and Wolf 1981) than predicted by MVT, were not included in these tables because of very few data in the former, and equivocal data (in the present context) in the latter. (c) Two studies that tested MVT, not mentioned in Nonacs (2001) were added to the tables (Davison and McCarthy 1994; Devries et al 1989).

Source	Animal	Settings	Results	Fit
Best & Bierzzychu-dek 1982	Bumblebee (*Bombus flavifrons*)	Natural patches of flowers. The number of flowers visited before leaving the inflorescence is recorded.	High variability; number of flowers visited not different from MVT predictions.	MVT
Cassini et al. 1990	Armadillo (*Chaetophracus vellerosus*), Guinea pig (*Cavia porcellus*)	Two patches, one better than the other. Animals must move between patches. Numerous trials with both species.	Departures from MVT predictions, significant always in staying too long, not vice versa.	IGRS
Cassini et al. 1993	Guinea pig (*Cavia porcellus*)	Patches where gain declines with time. Animals move between patches.	PRTs longer than predicted by MVT.	IGRS
Cowie 1977	Great tit (*Parus major*)	Several patches all of equal initial quality. Travel times and costs varied.	PRTs are variable. Average PRT was similar to MVT predictions in 5 experiments; and significantly longer (by 20–50%) in 7 experiments.	IGRS
Crowley et al. 1990	Bluegill Sunfish (*Lepomis macrochirus*)	Artificial macrophyte patches, fish prey on chironomids.	PRTs longer than predicted by 4–157%.	IGRS
Cuthill et al. 1994	Starlings (*Sturnus vulgaris*)	Patches of equal quality, with variable travel times within a trial.	PRTs identical to MVT predictions in 11 of 12 birds	MVT
Davison & McCarthy 1994	Pigeons *Columba livia*	Lab simulation of patches where reward probability varies	PRTs consistently longer than MVT predictions	IGRS
Devries et al. 1989	Bluegill Sunfish (*Lepomis macrochirus*)	Artificial macrophyte patches, fish prey on chironomids.	PRT consistently longer than MVT predictions.	IGRS

On-line appendix table A1. Summary of empirical studies.

Source	Animal	Settings	Results	Fit
Formanowicz 1984	Diving beetle *(Dytiscus verticalis)*	Constant density of prey within a trial. Patch = prey item, with measure being how much prey to consume.	Beetle larvae partially consume prey as predicted at high densities, but handle too long at low prey densities.	IGRS
Hansen & Green 1989	Pigeon *(Columba livia)*	Can switch within a trial between richer and poorer patches.	Stay too long in all patches, in all experiments. Trend is exaggerated when overall habitat quality is poorer.	IGRS
Hansen 1987	Pigeon *(Columba livia)*	Single patch, measuring how long animal stays.	On average, stay too long in all patches, but more so in better patches.	IGRS
Howell & Hartl 1980, 1982; Schluter 1982	Bat *(Leptonycteris sanborni)*	20 artificial flower patches with equal initial volumes. Giving up nectar density measured.	Howell & Hartl interpret results as indicating optimality, but Schluter shows the bats stayed too long.	IGRS
Hubbard & Cook 1978	Parasitoid wasp *(Nemeritis canescens)*	Lab measured departure time from patch.	Variable densities of hosts across patches. Excessive use of less profitable patch which declines with experience.	IGRS
Kamil et al. 1988	Bluejay *(Cyanocitta cristata)*	Patches are either empty or contain one prey item. PRTs measured for the empty patch.	Stayed consistently longer than predictions of a rate-maximization model.	IGRS
Kamil et al. 1993	Bluejay *(Cyanocitta cristata)*	Same as above, except travel times varied.	In all experiments stay too long in empty patches and travel time has an effect when it should not.	IGRS
Lima 1984	Downy woodpecker *(Picoides pubescens)*	Pairs of patches presented, one empty and one with variable amount of prey.	On average, birds sampled too many holes on empty patches and stayed too long.	IGRS
Lima 1985	Starling *(Sturnus vulgaris)*	Pairs of patches presented, one empty and one with variable amount of prey.	Most (15 of 16) birds stayed longer than rate maximization model.	IGRS

On-line appendix table A2. Summary of empirical studies.

Source	Animal	Settings	Results	Fit
Mellgren 1982	Rat *(Rattus norvegicus)*	Variable densities of food in patches.	Rats visit all patches, which results in an overuse of bad patches and under-use of good patches.	None
Munger 1984	Horned lizard *(Phyrnosoma cornutum, P.modestum)*	Field observations. Patches are ant colonies of variable quality.	Large variance in PRTs across individuals, with a mean close to the MVT prediction. On average, animals stayed slightly too long.	MVT
Parker 1978	Dung fly *(Scatophaga stercoraria)*	Field patch. Female: measured length of time spent in copulation.	Males understay in copulation by 14%, but no range of values was given.	None
Pyke 1978	Hummingbird *(Selasphorus rufa, S. platcercus)*	Field artificial inflorescences in patches with identical nectar contents	On average, close to MVT prediction.	MVT
Roitberg & Prokopy 1982	Fruit fly *(Rhagoletis pomonella)*	Large flight cage. Hawthorn trees with set numbers of fruit, but different distances apart across trials.	Variation in individual fly behavior, with most flies consistently staying too long in trees (up to 25 times longer than predicted) and few leaving too early.	IGRS
Todd & Kacelnik 1993	Pigeon *(Columba livia)*	Two patches with different mean travel times.	High variability in PRTs, but on average birds stay too long. No reduction in PRT variance with experience.	IGRS
Tome 1988	Ruddy duck *(Oxynura jamaicensis)*	Either single or two patch densities per trial.	Ducks consistently stay in patches longer than MVT predictions.	IGRS
van Alpen & Gallis 1983	Parasitoid wasp *(Asorbara tabida)*	Variable number of hosts across trials, but single density in patch within a trial.	Too much time spent in low density patches (data in support of this claim are not presented)	IGRS
Ydenberg 1984	Great tit *(Parus major)*	Patches of high or low quality and bird decides when to leave to go to next patch.	On average, birds leave rich patches too quickly and poor patches too slowly.	None

On-line appendix table A3. Summary of empirical studies.