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Gain curves in depletable food patches: A test of five models with European starlings

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ABSTRACT

A forager's gain curve, the cumulative number of prey harvested from a patch as a function
of time spent in the patch, influences optimal patch departure rules and interpretations of
patch use data. We describe models of five different search strategies that yield different gain
curves. Hence they would influence a forager's decision for patch departure differently and,
consequently, how researchers should interpret patch residence times and giving-up densities.
However, the models are virtually impossible to separate based on data of the gain curves *per se*.
Therefore, we develop a series of diagnostic tests that can be used to discriminate among
models. These tests consider how the instantaneous harvest rate within patches depends on
initial (IPD) and current prey density (CPD) and search time. We applied these tests to data
collected from European starlings (*Sturnus vulgaris*) foraging in experimental food patches of
known initial prey density. The starlings' harvest rate increased with CPD, an indication of
diminishing returns. However, a given CPD yielded a lower instantaneous intake rate the higher
the IPD. Thus, the two models most commonly assumed in foraging studies, systematic
and random search, can be unequivocally rejected. Instead, we found support for a new model,
negative stirring, in which the starlings spoil their own future foraging returns by aggregating
the remaining prey items as they search.

Keywords: European starling, foraging, gain function, giving-up density, *Sturnus vulgaris*.

INTRODUCTION

When exploiting a depletable food patch, a forager must decide when to abandon the present
patch and seek another (Charnov, 1976; Green, 1980; McNamara, 1982; Brown, 1988). The
decision should be influenced by its gain curve within the patch, which specifies the relation-
ship between harvest and time spent exploiting the patch. A forager's gain curve emerges
as a complex interplay between the food patch's structural properties, the abundance
and distribution of food within the patch, the forager's sensory abilities and the forager's
mechanics of patch exploitation. We considered five different gain curves that can emerge
from this interplay. All of them produce a decelerating relationship between gain and time

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(four are smoothly decelerating and one is piecewise linear). They all produce a similar and excellent fit to harvest data from depletable food patches (Fig. 1).

Models of patch use (MacArthur and Pianka, 1966; Charnov, 1976) have enhanced our understanding of how animals perceive and respond to resource availability (Charnov, 1976), predation risk (Gilliam and Fraser, 1987; Brown, 1988), alternative inputs into fitness (Brown, 1992) and to their own fitness prospects (Clark, 1994; McNamara and Houston, 1994; Olsson and Holmgren, 1999). Information on patch use reveals aspects of foraging behaviour (Marschall *et al.*, 1989; Brown and Alkon, 1990; Morgan and Brown, 1996), diet choice (Brown and Morgan, 1995), the foragers' information processing (Valone and Brown, 1989; Alonso *et al.*, 1995; Olsson *et al.*, 1999), habitat selection (Kotler *et al.*, 1991; Hughes and Ward, 1993; Morris, 1997) and species co-existence (Brown, 1989; Brown *et al.*, 1994; Guerra and Vickery, 1998; Kotler and Brown, 1999). These models require and assume that resource availability declines considerably during the course of foraging. A further assumption, which is fundamental to many of the above studies (Brown, 1988) yet rarely tested, is that the instantaneous energy intake rate, or harvest rate, is positively and simply related to the current prey density of the patch. Such a relationship implies that the harvest rate in the patch declines as the remaining resources disappear. One way of depicting this is by the slope of the gain curve (Fig. 1). If the gain curve decelerates, then the instantaneous harvest rate declines as the patch is depleted and the current prey density provides an estimate of the forager's harvest rate. If so, then giving-up densities (the remaining density of food when the forager leaves a patch) within natural and experimental food patches provide a surrogate for quitting harvest rates. Giving-up densities can often be measured relatively easily, whereas quitting harvest rates cannot (Brown, 1988).

Due to the similarity among model gain curves, they may seem interchangeable, at least as long as comparisons are not made across patches of different initial prey densities. However, to the foraging animal and to behavioural ecologists interested in inferring or predicting ecological processes from patch use data (Munger, 1984; Tome, 1988; Brown and Mitchell, 1989; Kotler and Brown, 1990; Morgan *et al.*, 1997; Fryxell and Lundberg, 1998), each gain curve has different and important consequences. As a forager attempts to leave each patch at the same or some prescribed quitting harvest rate, some of these gain curves predict a positively density-dependent, a negatively density-dependent or a density-independent resource harvest. If two resource items co-occur in patches, some of these gain curves predict short-term apparent competition or indirect mutualism (Kotler and Holt, 1987) among resource species. The pattern of giving-up densities among patches that vary in initial prey density (IPD) or foraging costs (e.g. predation risk) will be strongly influenced by the forager's gain curve in the patch. For these reasons, it is important to develop theory and tests for investigating the nature of a forager's gain curve whether from naturally occurring or experimental food patches. However, to test among gain curves requires investigations of other attributes of the models with respect to the effect of current prey density (CPD), IPD and total search time in the patch (t) on inter-capture intervals (or the reciprocal, which estimates current harvest rate, f). This is our goal.

The two search modes most often considered in foraging studies are random (e.g. Holling, 1959) and systematic (e.g. Green, 1980). However, between these extremes exists a suite of other biologically reasonable gain curves that may be influenced by IPD, CPD and t. In expanding on these possibilities, consider two food patches that are identical in all respects except for IPD: one has 100 units of food and the other has 50, initially. Assume that a forager has harvested each of these patches down to a CPD of 25 (75% and 50% of the

food has been removed from each, respectively). Which of the two patches will currently offer the highest instantaneous harvest rate? Under the assumption of random search, each offers the same current harvest rate. Under the assumption of systematic search, the rich patch, despite 75% depletion, will continue to offer twice the encounter rate with food items. Neither extreme may be reasonable for ungulates browsing shrubs (Åström *et al.*, 1990), shorebirds probing for invertebrates in the sand (Goss-Custard *et al.*, 1995), *Paramecium* harvesting bacteria (Decamp and Warren, 1998) or small mammals in experimental food patches (e.g. seedtrays: Brown, 1988; Kotler, 1992; Bowers and Breland, 1996).

In the next section, we consider random, systematic and three additional search modes. Because we cannot compare among the models based solely on their gain curves (they are so similar!), we develop predictions and tests for each based on their more subtle properties with respect to the effects of IPD, CPD and t on current harvest rates. We then show how the models and tests can be applied to actual data by using patch use data from starlings foraging in experimental food patches that varied in IPD. The data from video recordings provide accurate information on CPD, t and inter-capture intervals. From these data, it is possible to successfully separate among the models.

THE MODELS

The modelling produces four sets of predictions (Figs 2–5) and statistical tests (Table 1). The four tests provide null models for the different search modes (opportunities to reject a model by rejecting the null model) as well as four different opportunities to refute or support each model. While representing a strong inference (Platt, 1964) approach to testing

Table 1. The four sets of statistical tests

	Diagnostic test for:			
	Systematic[a]	Random[b]	Ratio[c]	Crypto & Stirring[d]
Model	$A_s = a + \beta CPD + \gamma t$	$A_r = a + \beta IPD + \gamma t$	$r = a + \beta x + \gamma IPD + \delta n$	$y = at + \beta t IPD$
Systematic	$\beta = 0; \gamma = 0$	$\beta = 0; \gamma > 0$	$\beta = 0; \gamma > 0; \delta = 0$	$a < 0; \beta = 0$
Random	$\beta = 0; \gamma < 0$	$\beta = 0; \gamma = 0$	$\beta < 0; \gamma > 0; \delta < 0$	$a < 0; \beta = 0$
Ratio	$\beta > 0; \gamma < 0$	$\beta < 0; \gamma = 0$	$a > 0; \beta < 0; \gamma = 0; \delta = 0$	$a < 0; \beta > 0$
Crypto	$\beta = 0; \gamma < 0$	$\beta = 0; \gamma < 0$	$\beta < 0; \gamma > 0; \delta < 0$	$a < 0; \beta = 0$
Stirring	$\beta < 0; \gamma < 0$	$\beta < 0; \gamma < 0$	$\beta < 0; \gamma > 0; \delta < 0$	$a < 0; \beta > 0$
Significant results	$\beta < 0; \gamma < 0$	$\beta < 0; \gamma = 0$	$\beta < 0; \gamma > 0; \delta < 0$	$a < 0; \beta > 0$

Note: The entries in the table body are the predictions from applying the diagnostic test for the model of a given column to data collected from a forager adopting the strategy of a given row. The Greek letters (a–δ) refer to the predicted regression coefficients applying the linear models representing the diagnostic tests. These linear models are shown in the third row of the table head. The underlined entries along the diagonal of the table are the null hypotheses, i.e. the relations expected if testing the data from a forager, using a given strategy, using the correct diagnostic test for that model. For example, if applying the diagnostic test for systematic search (first column), both β and γ are significantly less than zero and one may conclude that the forager does not use a systematic search strategy, but perhaps negative stirring. The other tests should be applied to verify this. The bottom row of the table summarizes the results from the foraging experiment. Relations indicated by '<' or '>' are significant at $P = 0.002$ or less.
[a] A_s is the ratio of f/IPD, [b] A_r is the ratio of f/CPD, [c] r is the square root of f and x is the ratio of n/IPD, [d] y is ln(CPD/IPD).

among gain curves, our battery of tests allows for solid refutation (Brown, 1993) of all five models, perhaps indicating the operation of some other undescribed gain curve. After applying the tests to actual data (as we will do for starlings), a model should either be refuted (hopefully multiple times) or supported by all four tests.

Despite the striking similarities among the models in the shape of their gain curves in the state space of cumulative harvest versus time spent searching for food (Fig. 1), the models begin to reveal striking differences in alternative state spaces such as $f/$IPD versus t (Fig. 2), $f/$CPD versus t (Fig. 3), $f^{1/2}$ versus $n/$IPD (where n is cumulative harvest, Fig. 4) and $\ln($CPD$/$IPD$)$ versus t (Fig. 5). Two models that may appear similar in one state space diverge strikingly in another. The ways in which the models appear different based on the relationships of CPD, IPD, t and n with f form the basis for the battery of four tests.

The first three models, which have previously been described in the literature, will receive only a brief description below. The remaining two are new and will be treated in more detail.

Systematic search

Systematic search (Fig. 1, solid straight line) has been invoked when criticizing approaches that assume random search (e.g. Green, 1980). It occurs when a forager avoids returning to the same spot in a patch, once that spot has been searched. By avoiding previously exploited regions of the patch, the forager should be able to maintain a constant rate of harvest throughout its bout in the patch. Systematic search requires a more or less directed search path. Furthermore, the risk of committing a mistake and searching the same spot twice must be independent of the area of the patch already searched. By directing search effort towards virgin areas of the patch, the forager maintains a constant harvest rate from the patch that is proportional to initial prey density. The gain curve of such a forager is linear, as it is simply the product of the forager's searching efficiency, A, the initial prey density and the time spent searching in the patch, t:

$$n_s = \begin{cases} A\text{IPD}t & \text{for } t \le T \\ A\text{IPD}T & \text{for } t > T \end{cases} \tag{1}$$

(Fig. 1, solid straight line). Once the entire patch has been searched, at time T, a certain fraction of prey will have been harvested, AT, and no more prey are to be found. The instantaneous intake rate of a systematic forager, f_s, is given by:

$$f_s = \begin{cases} A\text{IPD} & \text{for } t \le T \\ 0 & \text{for } t > T \end{cases} \tag{2}$$

A systematic searcher maintains the same intake rate throughout a patch visit, despite the declining current prey density. A systematic searcher does not experience diminishing returns while searching, until the patch has been completely searched. This means that giving-up densities will not correspond to quitting harvest rates in any simple fashion.

We may rearrange equation (2) to yield a null-model for the systematic forager:

$$A = \frac{f_s}{\text{IPD}} \tag{3}$$

If a forager searches patches in a truly systematic fashion, then the ratio of feeding rate to IPD should be constant for all search times ($t < T$) and prey densities (Fig. 2a, Table 1). The test for systematic search is a general test for diminishing returns in which the forager's harvest rate, f, declines as the patch depletes. For this reason, the test separates systematic search from the other four models, which all predict the ratio f/IPD to decrease with t (Fig. 2b–e).

Here we would like to suggest several ways of relaxing the assumptions of systematic search. We may think of a forager that is not entirely capable of discriminating between previously searched and unsearched areas. Such a forager may still have a linear gain curve provided that the risk of committing a mistake is independent of the area of the patch that has been searched. If, instead, the risk of committing a mistake is proportional to the area of the patch searched, the forager will experience diminishing returns and its gain curve will converge with that of random search. A third scenario may be a forager whose risk of mistake is independent of area searched but, after having searched once, it searches the whole area again, and again. Each time it makes a new round it will have a lower harvest rate – that is, the gain curve will be piecewise linear with every piece at a lower slope than the previous one. If the patch is searched only once, this is true systematic search; if the patch is searched an infinite number of times, it converges with random. As these variations to systematic search converge with either of the pure strategies (systematic or random), and IPD, CPD and t will not influence f in any ways different from the pure strategies, we will not pursue these models further.

Random search

Random search is the most commonly assumed search mode in theories of patch use (e.g. Holling, 1959; Charnov, 1976; Brown, 1988). Under random search, the forager is equally likely to search any spot in the patch at any time, regardless of where it has been searching previously. Hence, the encounter probability on any given prey item is only given by A and independent of IPD, CPD and t. With random search, the forager faces diminishing returns from harvesting the patch. Its gain curve will be given by:

$$n_r = \text{IPD}(1 - e^{-At}) \tag{4}$$

(Fig. 1, solid curve) and its instantaneous intake rate by:

$$f_r = A\text{IPD}e^{-At} = A\text{CPD} \tag{5}$$

As the current prey density declines, so does the expected intake rate. From the perspective of giving-up density analyses, random search has the desirable property of providing a perfect match between instantaneous intake rate and prey density.

For purposes of data analysis, we may rearrange the above equation to:

$$A = \frac{f_r}{\text{CPD}} \tag{6}$$

Random search predicts that the ratio of harvest rate to CPD should be independent of IPD and search time – if not, we may reject this model (Fig. 3b, Table 1). Systematic search predicts that the ratio f/CPD increases with time (Fig. 3a); the other three models all predict that this ratio decreases with time (Fig. 3c–e).
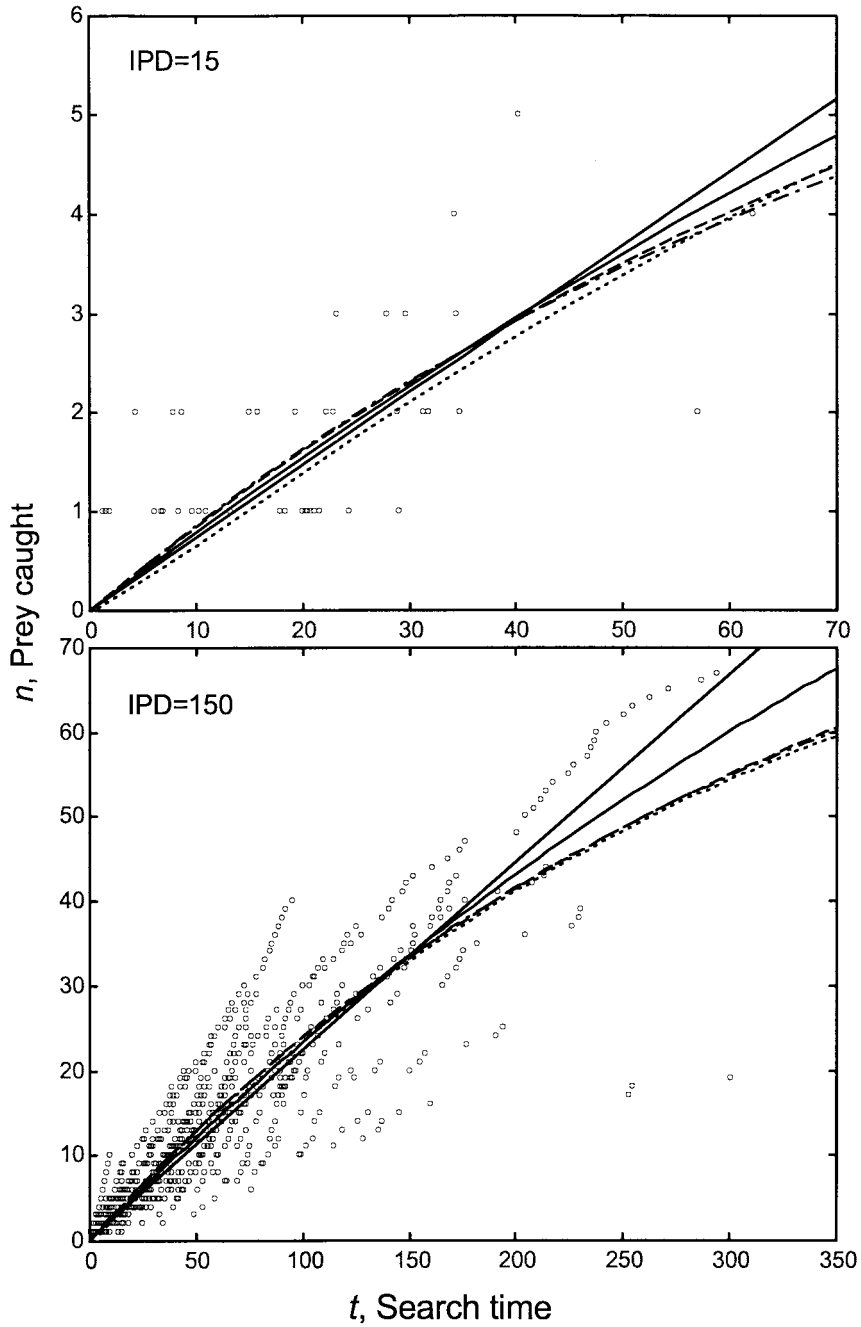
Fig. 1. The gain curves, i.e. the cumulative number of prey items harvested as a function of time spent searching in the patch. Separate panels are shown for each initial prey density, IPD. All the models
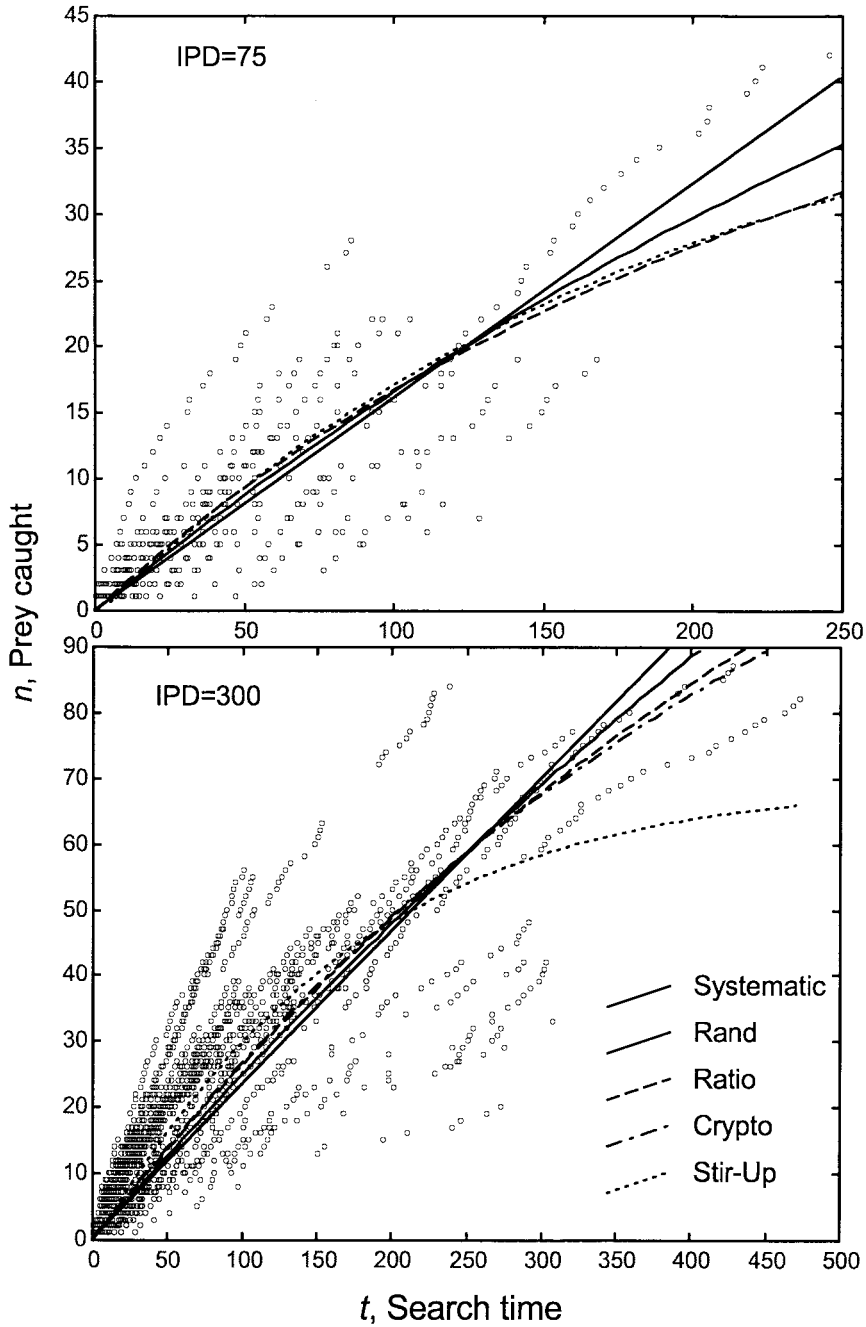
presented in the text have been fitted to the data, separately for each IPD. The models are: systematic search (solid straight line), random search (solid curve), ratio (dashed curve), crypto (dash-dotted curve) and stirring (dotted curve).
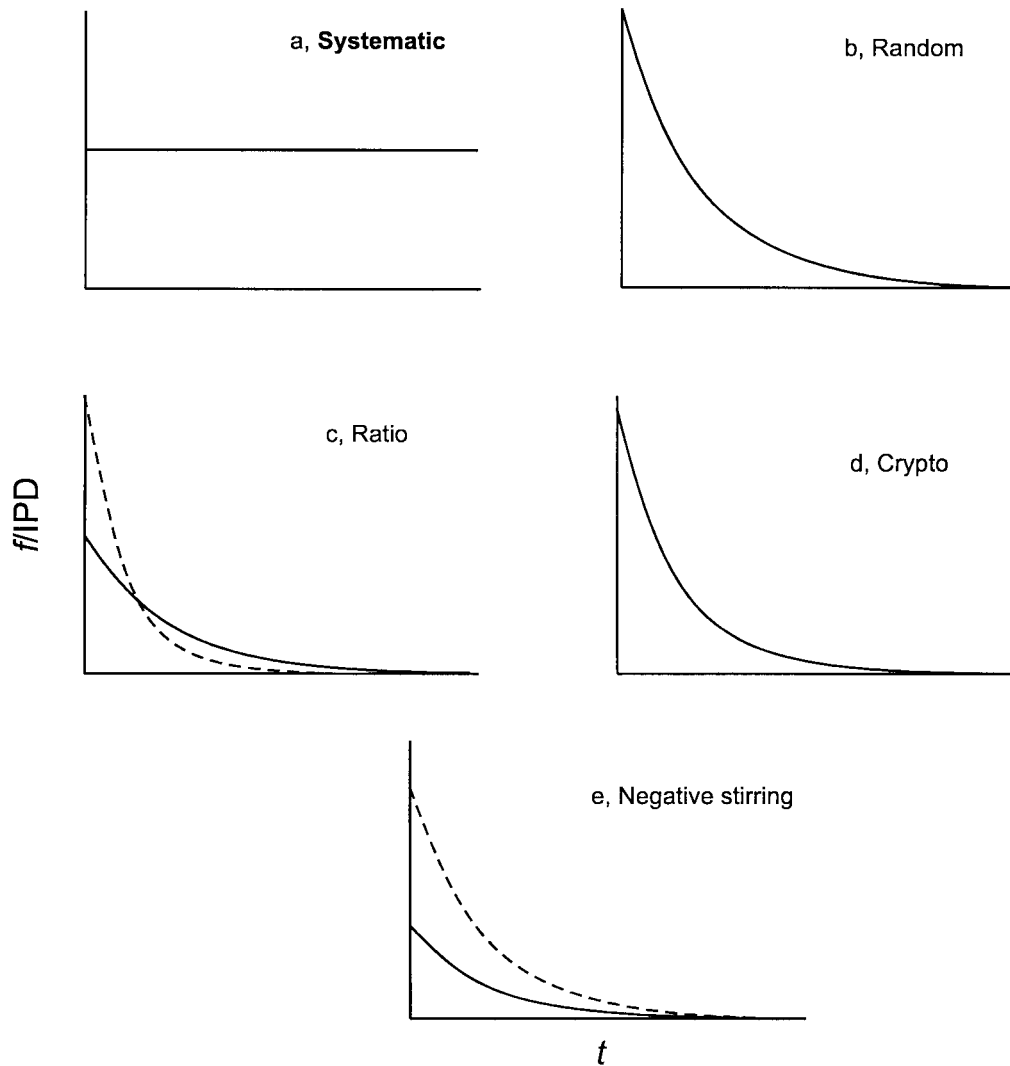
Fig. 2. Graphical representation of the diagnostic test for systematic search, i.e. the ratio of instantaneous intake rate, f, to initial prey density, IPD, as a function of search time, t (cf. the first column of Table 1). Solid lines = high initial prey density and dashed lines = low prey density. In case only one line is shown, high and low density yield the same result. If the forager actually uses a systematic search strategy (a), f/IPD is predicted to be constant with search time and equal between IPDs.

Ratio-dependent harvest

When patch size, rather than prey density within patches, determines variability in IPD (measured as initial numbers of prey per patch), then all patches may offer the same initial instantaneous intake rate, but small patches will deteriorate more quickly (Åström *et al.*, 1990). Recalling the example from the Introduction, the poor patch with 50% food remaining would be far more valuable than the rich patch with just 25% left. The gain curve of Åström *et al.* (1990) is given by:
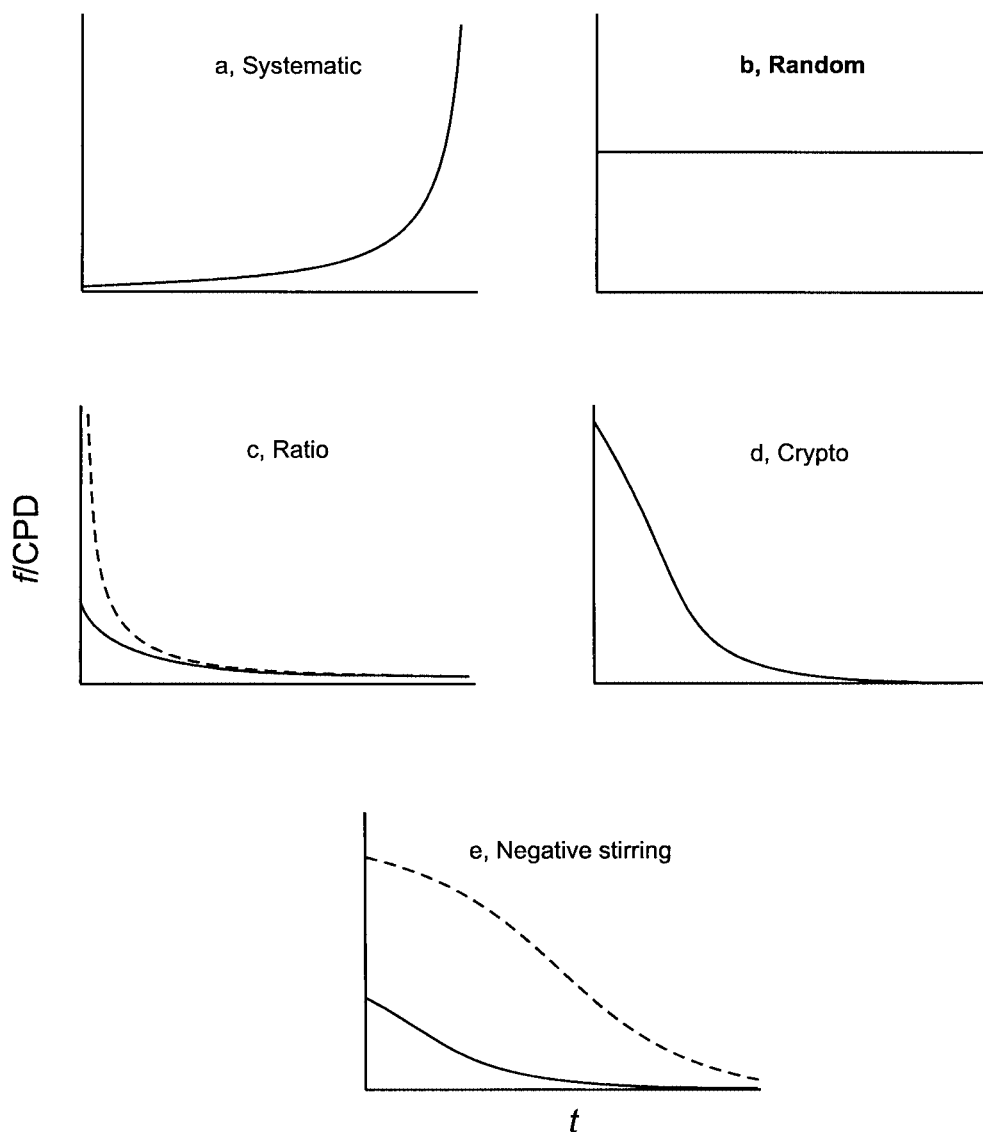
Fig. 3. Graphical representation of the diagnostic test for random search, i.e. the ratio of instantaneous intake rate, f, to current prey density, CPD, as a function of search time, t (cf. the second column of Table 1). Solid lines = high initial prey density and dashed lines = low prey density. In case only one line is shown, high and low density yield the same result. Only if the forager uses random search is f/CPD predicted to be independent of t and IPD (b).

$$n_{\mathrm{\hat{a}}} = \mathrm{IPD}\left(1 - \frac{1}{1 + (At/\mathrm{IPD})}\right) \tag{7}$$

(Fig. 1, dashed curve), which simplifies to:

$$n_{\mathrm{å}} = \frac{A\mathrm{IPD}t}{\mathrm{IPD} + At} \tag{8}$$

The instantaneous intake rate is:

$$f_{\mathrm{å}} = \frac{A\mathrm{IPD}^2}{(\mathrm{IPD} + At)^2} \tag{9}$$

As CPD = IPD − *n*, which expands to:

$$\mathrm{CPD} = \frac{\mathrm{IPD}^2}{\mathrm{IPD} + At} \tag{10}$$

we may rewrite equation (9) as:

$$f_{\mathrm{å}} = A\left(\frac{\mathrm{CPD}}{\mathrm{IPD}}\right)^2 \tag{11}$$

This model predicts diminishing returns, not as a function of CPD but as a function of the squared proportion of items left in the patch.

   As the current prey density is the initial prey density minus the number of prey caught, we may obtain the following expression as a diagnostic test for the model:

$$\sqrt{f_{\mathrm{å}}} = A - A\frac{n}{\mathrm{IPD}} \tag{12}$$

Under the ratio model, the square root of the instantaneous intake rate should be a linear function of the proportion of the prey items harvested, and the intercept of this relationship should be independent of IPD and *n* (Fig. 4c, Table 1). The other four models predict an increasing intercept with IPD (Fig. 4a, b, d, e).

Crypto

Search may be random within a patch, but not all items may be equally detectable either because of variability in crypticity or in accessibility among food items. For example, some prey may be hidden deeper into the substrate than others. Over time, the forager's mean encounter probability will decline as items that are easier to find are preferentially harvested relative to items that are harder to find. For such a forager, the poor patch foraged to 25 items will yield a higher current harvest rate than the rich patch foraged to 25 items.

   We may think of a model in which we have several types of prey (types $i = 1, 2 \ldots l$) that differ in how detectable they are to the predator. That means that each prey type offers its own specific searching efficiency, A_i. Furthermore, we may assume that initially a fixed proportion, p_i, of the prey items in the patch belong to type *i*. The remaining number of type *i* after the forager has spent some time, *t*, searching the patch is given by:

$$\mathrm{IPD}\, p_i \mathrm{e}^{-A_i t} \tag{13}$$

The forager's gain curve will be:
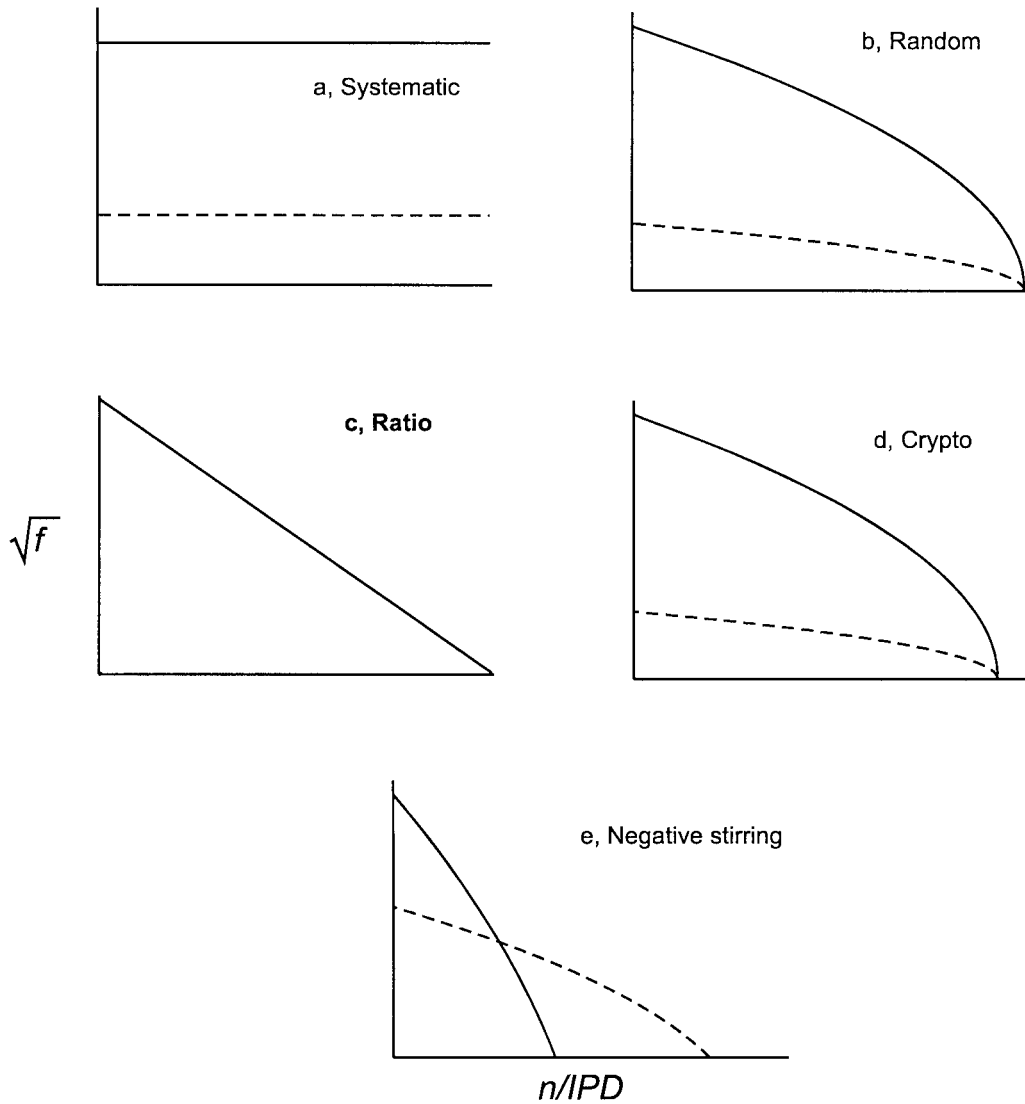
Fig. 4. Graphical representation of the diagnostic test for the ratio model, i.e. the square root of instantaneous intake rate, $f^{1/2}$, as a function of the proportion of prey caught, n/IPD (cf. the third column of Table 1). Solid lines = high initial prey density and dashed lines = low prey density. In case only one line is shown, high and low density yield the same result. If the forager conforms to the ratio model (c), $f^{1/2}$ should depend only on n/IPD and in the same manner for all levels of IPD.

$$n_c = \text{IPD}\left(1 - \sum_{i=1}^{I} p_i e^{-A_i t}\right) \tag{14}$$

(Fig. 1, dash-dotted curve), where IPD is the total prey density of all prey types. The expression for the forager's (total) instantaneous intake rate including all prey types is:

$$f_c = \text{CPD} \frac{\sum_{i=1}^{l} A_i p_i \mathrm{e}^{-A_i t}}{\sum_{i=1}^{l} p_i \mathrm{e}^{-A_i t}} \tag{15}$$

where CPD refers to the remaining density of all prey types taken together. The predator experiences diminishing returns while foraging in the patch, although the relationship between CPD and f will differ depending on IPD.

To develop a testable null hypothesis for this model, we can make use of the fact that the current prey density in the patch (of all prey types) is:

$$\text{CPD} = \text{IPD} \sum_{i=1}^{n} p_i \mathrm{e}^{-A_i t} \tag{16}$$

The proportion of remaining prey in the patch is:

$$\frac{\text{CPD}}{\text{IPD}} = \sum_{i=1}^{n} p_i \mathrm{e}^{-A_i t} \tag{17}$$

Hence, this ratio is predicted to be independent of IPD and only dependent on t.

Regardless of the variance in prey crypticity, a fixed amount of search time will yield the forager the same proportion of a patch's resources independent of IPD. In fact, the relationship between $\ln(\text{CPD/IPD})$ should be roughly linear with t [over a large range of t, the logarithm of the summation of equation (17) will approximate the sum of the logarithms, which does describe a linear relationship]. For the crypto model, we obtain a negative relationship between $\ln(\text{CPD/IPD})$ and t that goes through the origin (Fig. 5d, Table 1). Systematic and random search also predict a similar relationship (Fig. 5a, b). However, the ratio and stirring models predict that the slope of the relationship will become less steep with IPD (Fig. 5c, e).

Patch stirring

The presence or searching activity of the forager may reduce the quality of a patch in addition to the removal of prey items. One possible such mechanism is the following: Consider a predator, such as the starling, that searches for prey items by probing a hole into the substrate to expose the hidden items. Assume that, initially, the prey have some spatial distribution in the patch and that, in each hole that the predator opens, it can take only one item. Assume also that the remaining items, which were initially in the area that the predator opened but did not catch, are shuffled to the sides. Then, by the act of probing the predator actually increases aggregation because the remaining prey items will be aggregated in between the spaces where the starling probed. Then, the poor patch at 25 is better than the rich patch with the same number of food items. This is negative stirring. Positive stirring may also be possible, when prey become progressively easier to find as the forager searches the patch. However, it will not be considered here.

Let the size of the hole that the forager peeks into be A. Then, the expected number of items in that hole is $m = A\text{CPD}$. Assume that the distribution of items in holes belongs to a
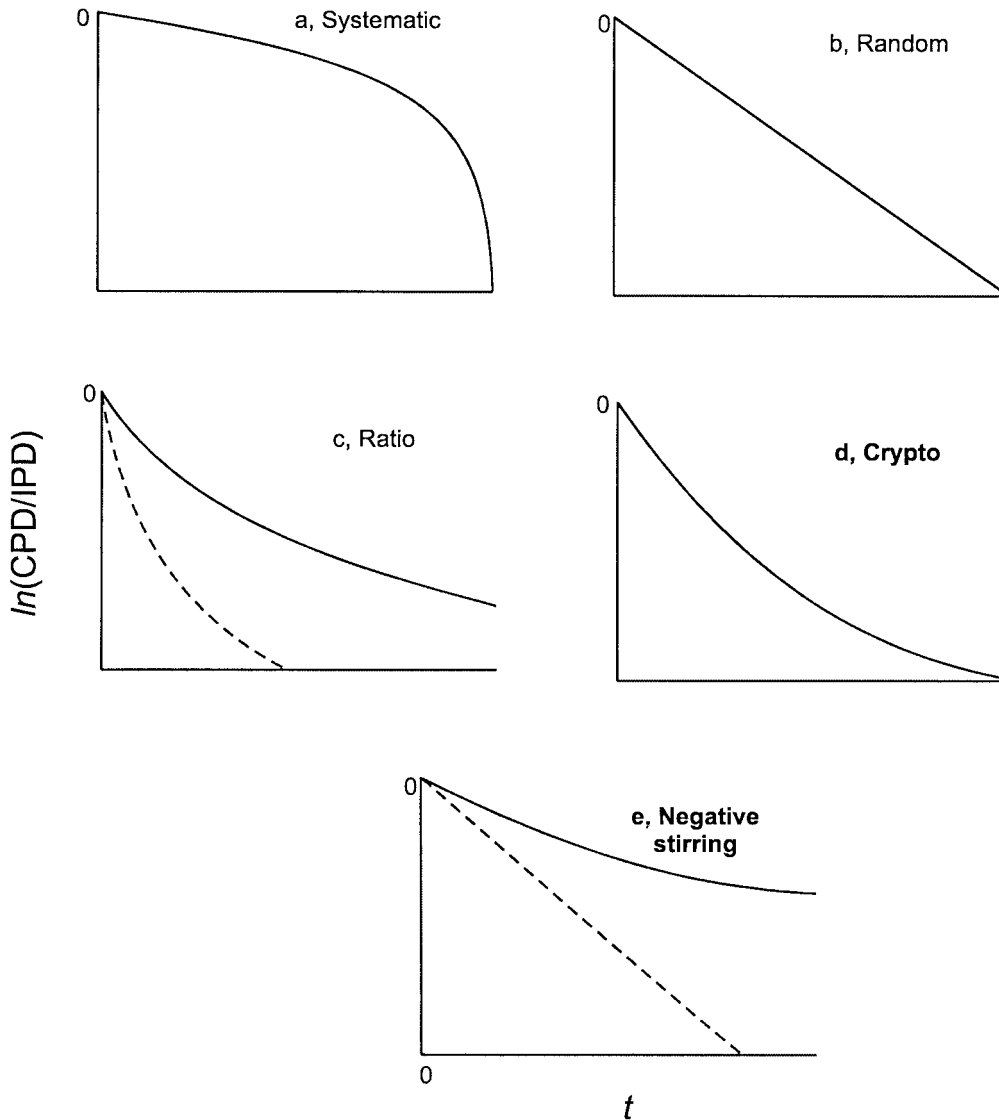
Fig. 5. Graphical representation of the diagnostic test for crypto and stirring, i.e. the logarithm of the proportion of prey left in the patches [ln(CPD/IPD)] (cf. the fourth column of Table 1). Solid lines = high initial prey density and dashed lines = low prey density. In case only one line is shown, high and low density yield the same result. All models (a–e) obviously predict the proportion of prey left to decline with search time. However, crypto (d) and stirring (e) can be separated by the effect of IPD that is predicted by stirring but not crypto.

negative binomial distribution with parameters m and k, where k is an over-dispersion parameter (Pielou, 1977). With very large k, the distribution converges with the Poisson; with small k, it describes the distribution of heavily clumped items.

The probability of finding no prey items in a hole of size A would then be:

$$p_0 = \left(\frac{k}{k + A\text{CPD}}\right)^k \tag{18}$$

We may describe the 'shuffling' of the forager by letting

$$k = k_0 e^{-bt} \tag{19}$$

where k_0 is the initial value of k in a virgin patch, t is the time spent searching the patch, and b is a parameter describing the decline in k with time. A lower value of k means a greater extent of clumpedness.

If the forager finds one prey item each time the area of the hole contains at least one item, then the instantaneous intake rate is $1 - p_0$, that is:

$$f_u = 1 - \left(\frac{k_0 e^{-bt}}{k_0 e^{-bt} + A\text{CPD}}\right)^{k_0 e^{-bt}} \tag{20}$$

Unfortunately, there is no analytical solution to this model's gain curve (Fig. 1, dotted curve). However, numerically a gain curve can be produced for any given set of parameters. For this model, the proportion of prey items remaining in the patch (CPD/IPD) depends on t and IPD (Fig. 5e, Table 1). For the crypto model, CPD/IPD depends only on IPD and not t (Fig. 5d). Although we could not develop a null statistical model for stirring, the differing effects of t on CPD/IPD for stirring versus crypto allows us to distinguish the models using the same diagnostic test.

METHODS

Aviaries, birds and their husbandry

We collected 12 female starlings from the wild during spring 1999 and we divided them into four groups of three birds. The birds were caught in the Revinge study area of southern Sweden (55°43′ N, 13°30′ E) and kept in aviaries nearby. Each group of three birds inhabited an aviary of approximately 8 m^2. Birds were colour-marked using acrylic paint on their greater coverts. Between experiments, the birds were fed mealworms buried in sand during the day and poultry starter pellets during the night. Fresh water was available *ad libitum* for drinking and bathing. We regularly checked the birds' weights to ensure good health and sufficient feeding.

The patches

During the experiments, each aviary was supplied with four experimental food patches. These consisted of square wooden trays, 25 cm wide and 3.5 cm deep. The patches were prepared by covering the bottom with a 1 cm deep layer of moist sand. On this layer a fixed weight of freeze-killed mealworms was evenly distributed. By killing the worms before the experiment, we eliminated the possibility that any of the patch properties and subsequent starlings' behaviours were influenced by prey mobility. Each of the trays of an aviary

received one of four initial prey abundances of 1, 5, 10 and 20 g respectively (approximately 15 mealworms per gram). Finally, the worms were covered with an additional 2.5 cm of moist sand.

The protocol

The food patches were placed at four fixed positions on the floor in each aviary. To prevent the birds from learning between experiments which tray contained the highest prey density, we rotated the positions of the individual trays each time.

The foraging behaviour of the birds was videotaped for 1 h from the time when the patches were presented to the birds. The videotapes were subsequently analysed using Noldus Observer Video Pro 4 (Noldus Information Technology, 1995). From colour marking it was possible to identify individual birds on the tapes. The time that each bird spent in each patch was classified into the following behaviours: searching (walking or standing with beak directed below horizontal), probing (actively probing into the sand to find prey items), handling (extracting a specific prey item from the sand, handling it in the beak and swallowing it), scanning (standing or walking upright with beak directed above horizontal) and other activities (usually preening or interacting with other birds in the patch). These other activities represented a tiny fraction of the birds' total time in the patches. Behaviours outside the patches were not classified. Usually, a prey item was found following a number of probing and searching events. The total time spent on these two activities between the capture of two successive prey items we considered the inter-capture interval (ICI). The inverse of this is the instantaneous capture rate while searching (i.e. $f = 1/\text{ICI}$). This is the rate of prey capture during active searching only. While it does not consider the effects of handling time and scanning time on harvest rate, f is the relevant metric for testing among the models' predictions in Table 1.

We omitted from our analyses the rare events when all three birds simultaneously occupied the same patch. At such times, mutual interference sometimes disrupted foraging.

Statistical analyses

The data analyses conform as much as possible to the four statistical models described in Table 1. Like most foraging models, predictions apply to the individual; that is, the models predict that data from each individual should follow the relations presented in Table 1. Thus, each diagnostic test was run separately for each individual to obtain the individual estimates of the coefficients. These estimates were then tested against the null hypothesis of zero using a t-test. Accordingly, $n = 12$ in all cases.

RESULTS

Analysing gain curves

We estimated the fit of the five proposed gain curves to the data using non-linear regression of the number of prey caught to search time using each model (Fig. 1). Separate analyses were made for each IPD-level. All models provide a good fit to the data:

- systematic search: r^2(IPD = 15) = 0.82, r^2(IPD = 75) = 0.86, r^2(IPD = 150) = 0.90, r^2(IPD = 300) =0.87;
- random search: r^2(IPD = 15) = 0.83, r^2(IPD = 75) = 0.87, r^2(IPD = 150) = 0.91, r^2(IPD = 300) = 0.88;
- ratio: r^2(IPD = 15) = 0.83, r^2(IPD = 75) = 0.86, r^2(IPD = 150) = 0.91, r^2(IPD = 300) = 0.89;
- crypto: r^2(IPD = 15) = 0.83, r^2(IPD = 75) = 0.87, r^2(IPD = 150) = 0.91, r^2(IPD = 300) = 0.89;
- stirring: r^2(IPD = 15) = 0.83, r^2(IPD = 75) = 0.87, r^2(IPD = 150) = 0.91, r^2(IPD = 300) = 0.91.

For the crypto model, we made the simplifying assumptions that only two types of prey were available in the patches and that they were equally common. Using the quality of fit by the different models to the data provides a dubious means for rejecting or accepting a model. A good fit is inevitable as a result of the strong linear component of each gain curve and of the data. As in the predictions of Table 1, it is the more subtle, non-linear effects that provide diagnostic tests for each model.

Tests of predicted relations

A summary of the following results is presented in the bottom row of Table 1. Coefficients presented in the text (α, β and γ) are those corresponding to the table.

Assuming systematic search, the ratio of instantaneous intake rate to initial prey density (f/IPD) should be the estimate of searching efficiency, and hence be unaffected by current prey density and search time (Fig. 2). In contradiction to this prediction, search efficiency declined significantly with both current prey density ($\beta = -1.7 \times 10^{-5}$, $t = -10.57$, $P < 0.0005$) and search time spent in the patch ($\gamma = -1.85 \times 10^{-5}$, $t = -9.66$, $P < 0.0005$). Hence, we may reject systematic search as being applicable to the starlings foraging from the experimental food patches. The results from this test accord best with the negative stirring model.

If we consider the diagnostic test for random search, the ratio of instantaneous intake rate to current prey density (f/CPD) should estimate searching efficiency. This ratio should be independent of IPD and t (Fig. 3). However, the ratio of f/CPD decreased significantly with initial prey density ($\beta = -2.7 \times 10^{-5}$, $t = -7.68$, $P < 0.0005$) and was unaffected by search time spent in the patch ($\gamma = -2.5 \times 10^{-5}$, $t = -0.935$, $P = 0.4$). These results refute random search and accord best with the ratio or negative stirring model.

Under the assumption that the instantaneous intake rate depends only on the squared proportion of prey items left in the patches, all fresh patches should yield the same instantaneous intake rate (Fig. 4). Under the ratio model, the drop in instantaneous intake rate should be steeper for lower IPDs. None of these predictions were supported (γ: $t = 4.48$, $P = 0.001$; δ: $t = -1.71$, $P = 0.12$). Thus, removing the interaction term (δ), we found that intake rate decreased with the number of prey caught in the patch ($\beta = -0.005$, $t = -6.73$, $P < 0.0005$) and increased with IPD even for fresh patches ($\gamma = 0.00078$, $t = 4.15$, $P = 0.002$). These results reject the ratio model and accord with the random, crypto and negative stirring models.

Finally, if the crypto model applies, then the proportion of prey remaining in a patch (CPD/IPD) should decline with search time independently of initial prey density. In

contrast, we found that the decline in (the logarithm of) this proportion was less steep for higher initial prey densities ($\beta = 1.26 \times 10^{-5}$, $t = 7.39$, $P < 0.0005$), which is the prediction given by the stirring model (Figs 5 and 6). As predicted by all of the models, the decline in CPD/IPD with search time was significantly less than zero ($a = -0.0072$, $t = -9.70$, $n = 12$, $P < 0.0005$). These tests reject the crypto model and accord with the ratio and stirring models.

The four tests provided a rejection of the systematic search, random search, ratio and crypto models. All of the tests fit the predictions of the negative stirring model.

Satiation

An alternative possibility is that internal state or satiation influences searching efficiency. We tested this idea by including the cumulative number of prey eaten during the entire experiment as an independent variable to the diagnostic tests of the systematic and random search models. This extension did not alter any of the conclusions. For systematic search we found that, as before, the ratio of instantaneous intake rate to IPD declined with CPD and search time ($\beta = -1.8 \times 10^{-5}$, $t = -11.12$, $P < 0.0005$; $\gamma = -1.2 \times 10^{-5}$, $t = -5.39$, $P < 0.0005$), only now it also decreased with number of prey items eaten ($d = -2.3 \times 10^{-5}$, $t = -3.46$, $P = 0.005$). For random search, the ratio of instantaneous intake rate to current prey density declined with IPD and search time, but was independent of number of prey items eaten ($\beta = -3.0 \times 10^{-5}$, $t = -6.41$, $P < 0.0005$; $\gamma = -1.6 \times 10^{-5}$, $t = -2.17$, $P = 0.053$; $d = 4.4 \times 10^{-5}$, $t = 1.90$, $P = 0.08$). Satiation does not appear to influence encounter probabilities in any consistent manner, or in ways that would alter any conclusions.

Handling and scanning times

The five models explicitly consider the effects of patch properties on search times and search efficiencies. However, none of the models explicitly consider handling time or scanning times. In the simplest case, handling time may be a constant that measures the amount of time that is required to retrieve and consume an encountered prey item. As such, it will be independent of patch properties and forager satiation. Scanning may serve to reduce perceived predation risk or to gain information on the whereabouts and activities of the other birds. Within and among foraging bouts, patch properties and forager satiation may influence the optimal scan rate for predators (e.g. Brown, 1999; Lima and Bednekoff, 1999). Both handling time and scanning times will influence time spent in each food patch, and thus will influence the forager's overall harvest rate.

Although not an explicit part of our models, our data allow us to test for the effects of patch properties and forager satiation on handling and scanning times. To investigate these effects, we entered IPD, CPD, search time and total number of prey caught (satiation) as independent variables in a multiple regression with the fraction of time spent scanning between prey captures as the dependent variable. The proportion of time spent scanning was independent of IPD ($t = 1.39$, $P = 0.2$), had a tendency to decline with CPD ($t = -2.19$, $P = 0.051$), increased with search time ($t = 2.43$, $P = 0.034$) and decreased with satiation ($t = -2.64$, $P = 0.023$). The decline in scanning with CPD is consistent with theory, but the decline in scanning with satiation is anomalous (Brown, 1999).
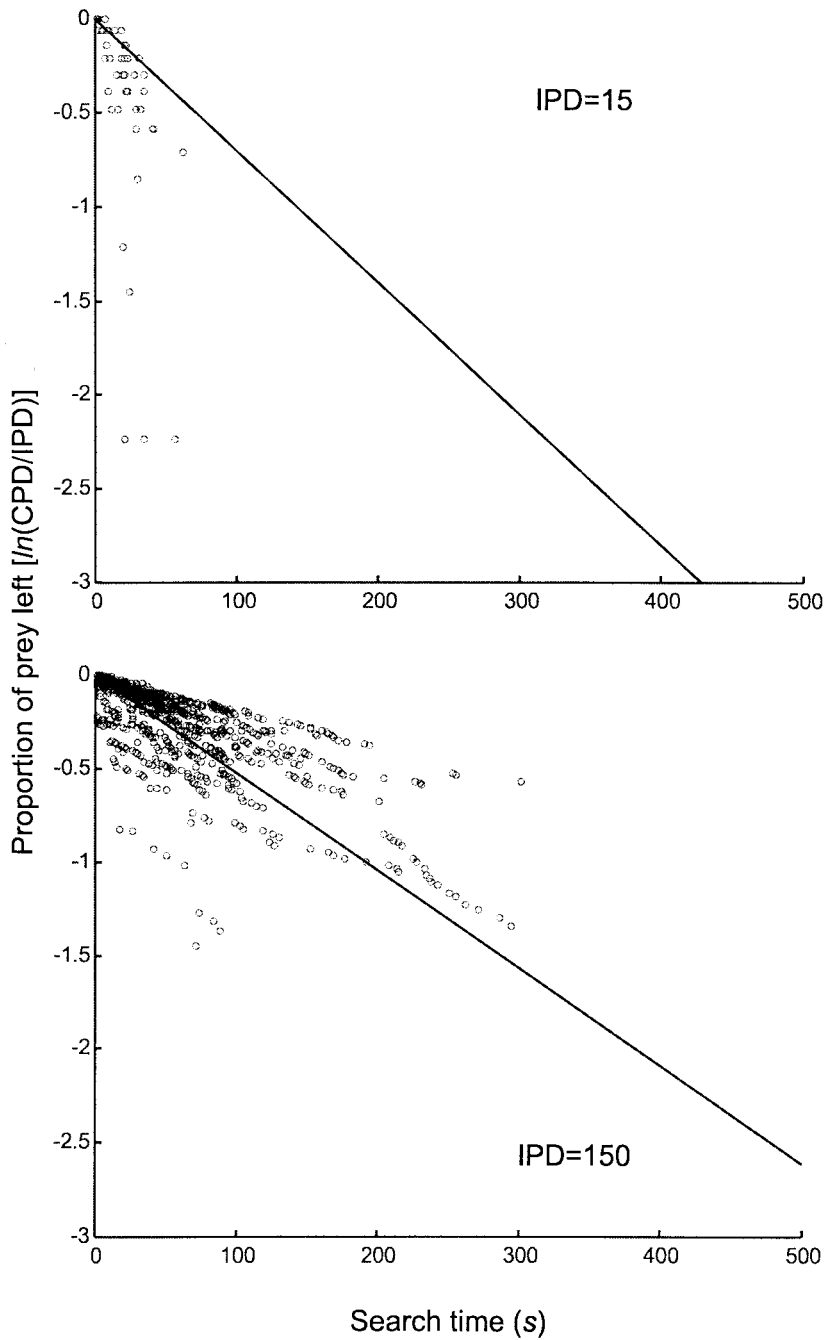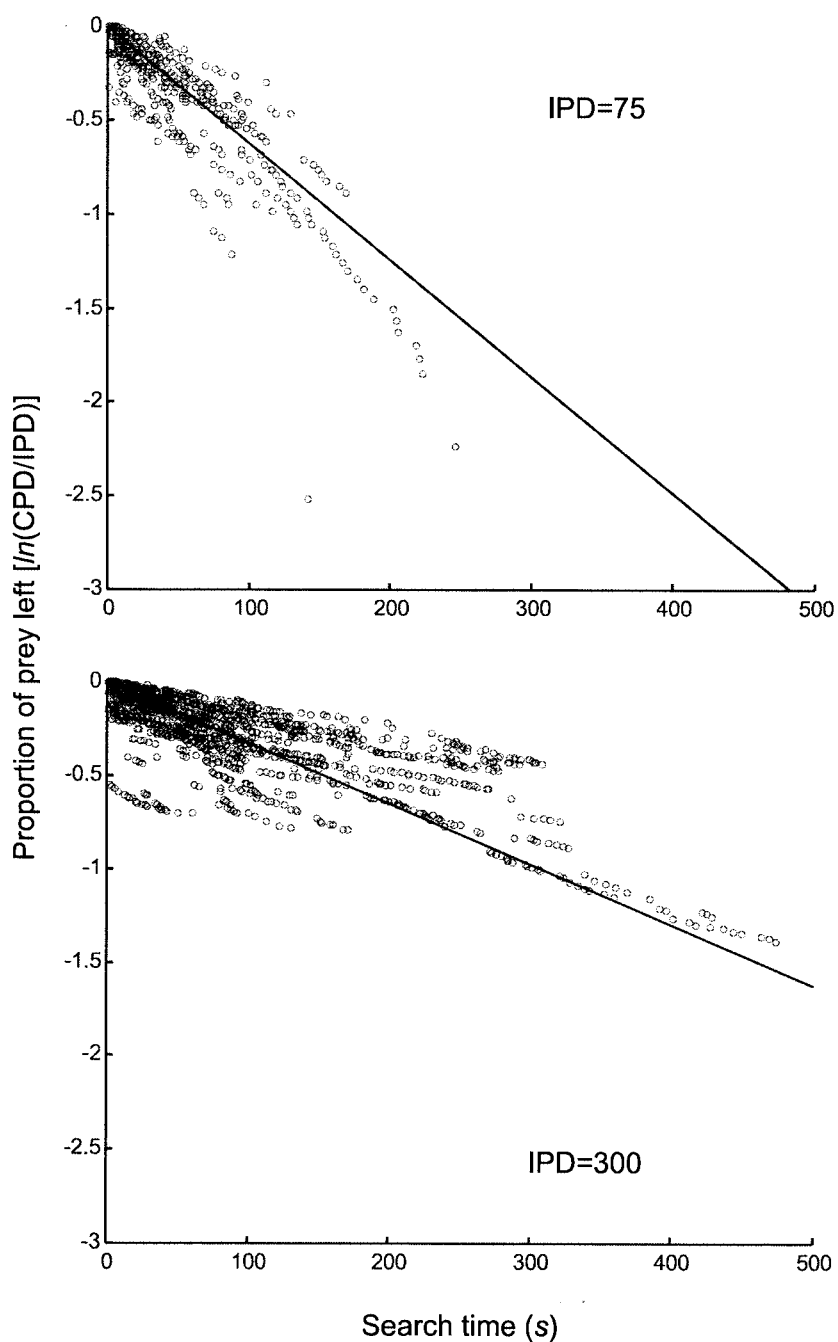
Fig. 6. The natural logarithm of the proportion of prey items left in the patches as a function of time spent in the patches. Separate panels are shown for the patches with different IPD. The lines shown are

from the fit of the regression model $y = at + \beta t$IPD. Different slopes depending on IPD (significant interaction term) is diagnostic for the stirring model (cf. Fig. 5e).

We performed the same analysis using handling time as the dependent variable. Handling time increased with satiation ($t = 7.30$, $P < 0.0005$). In addition, handling time had a tendency to decrease with IPD ($t = -2.03$, $P = 0.068$) and increase with CPD ($t = 2.00$, $P = 0.071$). Handling time was unaffected by search time ($t = -0.24$, $P = 0.8$). The increase in handling time with satiation may represent a property of crop or gut filling. As the bird's crop or gut fills, it may take longer to process and ingest each additional mealworm. This increase in handling time with satiation may explain the decline in scanning with satiation. If handling time provides some scanning information (handling and scanning may not be entirely exclusive activities), then the increased handling time may have partially substituted for scanning.

DISCUSSION

By measuring the inter-capture intervals (separate from time spent scanning or handling) of starlings searching for mealworms in the sand matrix, we were able to use diagnostic tests to evaluate the five models. We found that the starlings' foraging behaviour:

- rejected systematic search, as the current harvest rates scaled for IPD declined with both CPD and t (in complete accord with negative patch stirring);
- rejected random search, as current harvest rate declined with IPD (in accord with the ratio-dependent model and negative patch stirring);
- rejected ratio-dependent harvest, as the intercept of the relationship between f and the proportion of prey captured (i.e. n/IPD) increased with IPD and decreased with n (in accord with random, crypto or negative stirring);
- rejected crypto, as the decline in the (log-transformed) ratio of CPD to IPD with time was steeper for lower IPDs (in accord with the ratio-dependent and negative patch stirring models).

Hence, based on these four tests, we can unequivocally refute the systematic search, random search, ratio-dependent harvest and crypto models. In all cases, the starling data support the predictions of negative patch stirring.

In the present experiment, starlings experienced diminishing returns while feeding in the patches, but not in the simple manner predicted by pure random search. Rather, the instantaneous intake rate appeared to be affected by the time spent in the patch *per se*. For a given CPD, a patch that had a high IPD yields a lower harvest rate than one with a low IPD.

There are several examples in the literature supporting the models we have described here. Foraging patterns consistent with systematic search have been shown in a few cases, including nectar-feeding birds (Kamil, 1978) and ants (Veena and Ganeshaiah, 1991) visiting inflorescences, and woodpeckers (Lima, 1984) and doves (Baum, 1987) using artificial food patches. In all of these cases, the food patches (artificial or natural) were spatially simple. This is perhaps not surprising, as pure systematic search requires the forager to be good at discriminating between virgin and previously exploited parts of the patches. In complex or ambiguous patches, or in foragers with a small brain (Adler and Kotar, 1999), the requirements for systematic search may not often be met.

Åström *et al.* (1990) found that moose foraging on birch (*Betula*) shrubs conformed very well to the ratio model described above. They verified this conclusion by testing a prediction

from the model concerning optimal time spent per patch, and were able to reject an alternative model that assumed instantaneous harvest rates to be independent of initial conditions. A patch such as a birch shrub may have properties similar to that of a prey individual, and hence the consumption of resources from a shrub-patch may be similar to partial prey consumption. There may be certain very clear similarities between a standard patch use scenario and partial prey consumption (Wilson, 1976), such as diminishing returns. However, as visualized by Åström *et al.* (1990) and shown above, when the size of the patch (or prey) varies rather than the density of resources within the patch (as would be the case for most 'standard' patches), some important features of the gain curves will differ between scenarios. As shown in Fig. 7, by applying a constant quitting harvest rate to the ratio model (which should apply for partial prey consumption), giving-up densities would be expected to increase with increasing initial size of the prey or patch.

Other studies have reported foraging patterns consistent with random search (Munger, 1984; Tome, 1988; Marschall *et al.*, 1989; Kotler and Brown, 1990; Li *et al.*, 1992). However, few of these studies verified diminishing returns (concave down gain function) by rejecting a linear gain function (Kotler and Brown, 1990), and only one (Marschall *et al.*, 1989) tested for random search.

Consequences of different gain curves

Regardless of its gain curve, a forager should attempt to leave a depletable food patch when its potential harvest rate in the patch no longer exceeds the sum of its metabolic, predation and missed opportunity costs of foraging (Brown, 1988; Olsson and Holmgren, 1998). At this point of departure, the forager leaves behind some remaining food (i.e. giving-up density, GUD), has harvested a certain amount of food ($n = \text{IPD} - \text{GUD}$) and has expended a certain amount of time. Time expended will include time spent searching for food in the patch, t, time spent handling food items, $h(n)$, and time spent scanning.

Our results imply that giving-up density should be positively related to IPD, as under the negative stirring model, quitting harvest rate, $f(\text{GUD})$, is a negative function of IPD (Fig. 7). Incomplete information can also yield a positive relationship between giving-up density and IPD (Valone and Brown, 1989; Alonso *et al.*, 1995; Olsson and Holmgren, 1998). If foragers must estimate present patch quality as they forage, their optimal behaviour leads to a positive relation between giving-up density and IPD for the most commonly observed patch qualities, even if search is assumed to be perfectly random (Olsson and Holmgren, 1998). In fact, models of patch foraging with incomplete information have only been explicitly investigated under the assumptions of either systematic (Green, 1980, 1984, 1987) or random search (Iwasa *et al.*, 1981; Green, 1988; Olsson and Holmgren, 1998, 1999). How the optimal patch departure, under incomplete information of patch quality, would be influenced by other gain curves remains an interesting and open question.

If there is a positive relation between giving-up density and IPD, then a greater proportion of the prey items initially present may be harvested from low- than high-quality patches. Negatively density-dependent patch exploitation (Morgan *et al.*, 1997; Rodríguez-Gironés and Vásquez, 1997) could result when the search of foragers conforms to negative stirring. However, this conclusion is premature, as it depends on the forager's patch departure rule.
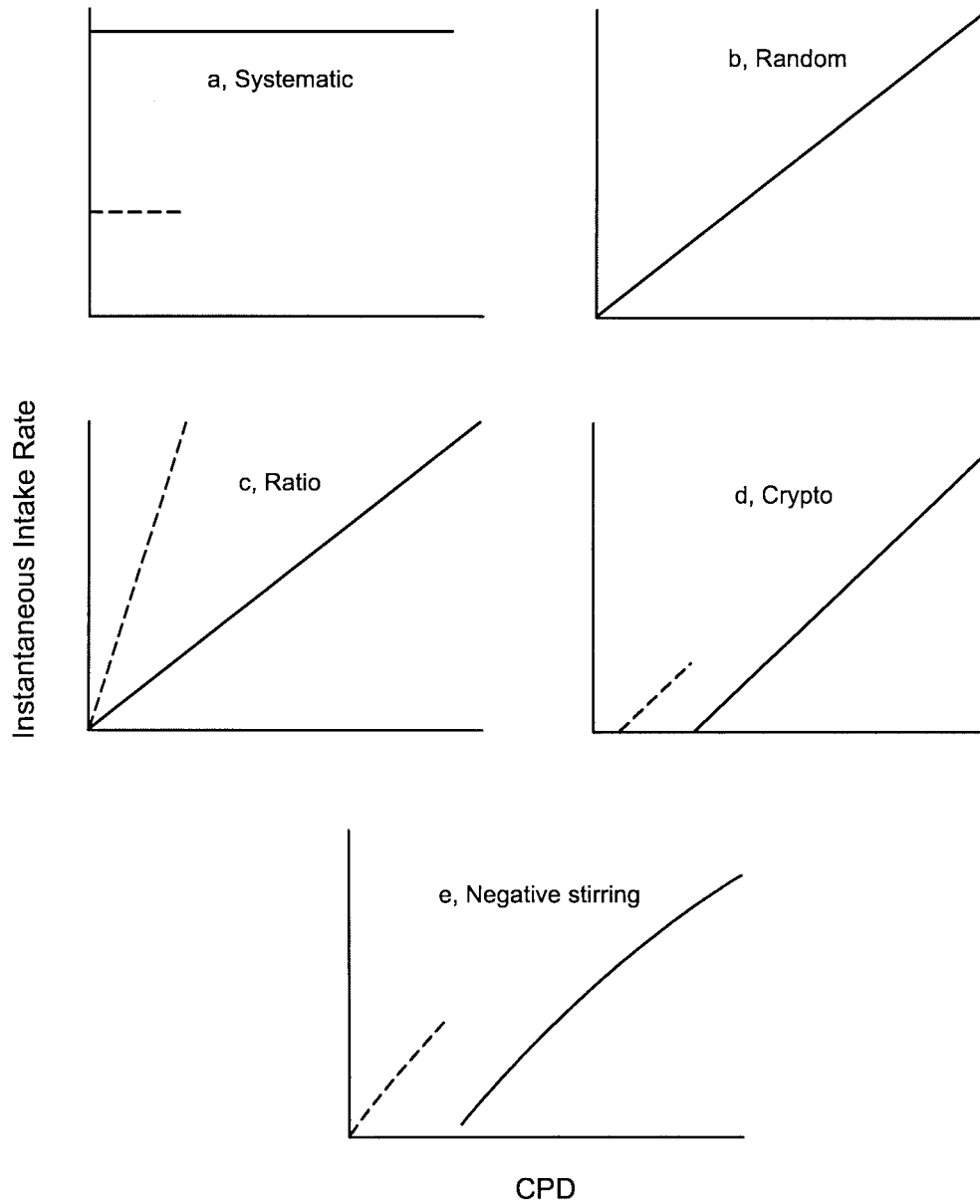
Fig. 7. Predicted relationships between instantaneous intake rate, f, and current prey density, CPD, for each of the five different models. Assuming constant quitting harvest rates, predicted giving-up densities can be found by inserting a horizontal line corresponding to this rate, and finding the value of prey density at the intersections.

The value of giving-up densities as behavioural indicators is based on the assumption that they reflect the quitting harvest rate (Brown, 1988; Olsson and Holmgren, 1999). Our analyses indicate that this relation is not entirely straightforward for starlings foraging in

sand trays, for the reasons given above. This raises some problems in using giving-up density techniques in this case or in other systems where the foragers cause negative stirring by their searching. However, this problem only pertains to experimental studies where patches of different IPDs are provided to the foragers. That is, giving-up density cannot be translated into harvest rates across different IPDs; it can, however, within a single IPD.

Furthermore, in experiments or field studies involving natural patches, much of the problem can be circumvented. The reason is as follows. The patches used in our experiment (sand trays) probably differed in at least three respects from the feeding patches that starlings experience in the wild (e.g. a piece of grassland). First, negative stirring is much less likely to occur, or may occur to a lesser extent, when the prey items are 'kept in place' by roots of grasses and herbs. That means that the parameter b of the stirring model may often be zero or close to zero. Second, a hole made by a probing starling in a natural patch probably rarely contains more than one prey item (that is, m is small because A and/or CPD are small; Whitehead *et al.*, 1995). Under such conditions, the negative stirring model converges with random search, and hence giving-up densities may be rather reliable estimates of harvest rates even across different IPDs.

The precise shape of the gain function and its independence of initial prey density in a patch becomes crucial if one tries to make quantitative inferences of patch residence time (Munger, 1984). Obviously, it is also crucial to have a good appreciation of the gain curve when estimating quantitative parameters such as searching efficiency (Kotler and Brown, 1990). Some previous attempts to parameterize gain curves (e.g. Kotler and Brown, 1990) probably suffered from lack of knowledge of the actual gain curve and an inability to separate handling and scanning times from search time. In a way, these problems act synergistically, in that without separating the different parts of the patch residence time, the diagnostic tests described here cannot easily be applied. However, by using a single initial patch quality, some of the important properties of the gain curves of different species (Kotler and Brown, 1990) can probably be captured in the parameters derived. That is, these estimates can be used to describe that the gain curve of one species is steeper than that of another. However, if the gain curve is in fact not the one assumed by the analysis, there is a great risk that the parameters derived, A for searching efficiency and h for handling time, do not estimate these properties *per se*, but merely some abstract property of the gain curve. Using several initial patch qualities could produce entirely different values for these parameters.

In the present context of the starlings, we probably can derive reliable estimates of the gain curve's parameters. This is because we have confidence in the starling's gain curve. Our data fit all aspects of the negative stirring model very well, and all other reasonable models were falsified.

In our case, handling and scanning times were not constant throughout an experiment. Handling time increased, and scanning decreased, with satiation. It should be noted that scanning and handling are not mutually exclusive. Time spent handling food items probably provides some level of useful vigilance. Satiation – that is, the number of prey items eaten during an experiment – is best thought of as gut fullness and not an internal state that affects the birds' long-term fitness prospects. During our experiment, which lasted 1 h, an individual bird could eat up to approximately 125 mealworms, which corresponds to approximately 8 g. This is obviously much higher than the long-term requirement of starlings. It is probable that, as the birds became increasingly satiated, they shunted time from pure scanning to handling, possibly because of physical constraints that made it more

difficult to swallow the prey, as the gut became fuller. In nature, these levels of gut-fullness may not be common and hence we should perhaps expect handling and scanning times to remain unaltered during foraging.

Part of our interest in starling foraging comes from the growing conservation concerns for the species. In Europe, where it is native, it is declining in numbers for reasons that may at least in part be related to habitat loss (Møller, 1983; Solonen *et al.*, 1991; Feare, 1994). In North America, where it was introduced, it is considered a pest species and may even out-compete natural hole nesters in some areas (e.g. Ingold, 1994). It may therefore be highly interesting to develop a technique for behavioural indicators that works for the species in its many different environments. In appropriate food patches where the gain curve is known, giving-up densities can be used to measure quitting harvest rates. In combination with data on total patch residence times or scanning levels, giving-up densities may provide an effective means of revealing the foragers' own estimates of habitat suitability and fitness prospects (Olsson *et al.*, 1999).

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