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## Incompletely Informed Shorebirds That Face a Digestive Constraint Maximize Net Energy Gain When Exploiting Patches — [Source link](#)

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**Published on:** 01 May 2003 - The American Naturalist (University of Chicago Press)

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*Published in:*  
 American Naturalist

*DOI:*  
[10.1086/374205](https://doi.org/10.1086/374205)

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*Document Version*  
 Publisher's PDF, also known as Version of record

*Publication date:*  
 2003

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

van Gils, JA., Schenk, I. W., Bos, O., & Piersma, T. (2003). Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *American Naturalist*, 161(5), 777-793. <https://doi.org/10.1086/374205>

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# Incompletely Informed Shorebirds That Face a Digestive Constraint Maximize Net Energy Gain When Exploiting Patches

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Submitted June 3, 2002; Accepted October 28, 2002;  
Electronically published May 2, 2003

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**ABSTRACT:** Foragers that feed on hidden prey are uncertain about the intake rate they can achieve as they enter a patch. However, foraging success can inform them, especially if they have prior knowledge about the patch quality distribution in their environment. We experimentally tested whether and how red knots (*Calidris canutus*) use such information and whether their patch-leaving decisions maximized their long-term net energy intake rate. The results suggest that the birds combined patch sample information with prior knowledge by making use of the potential value assessment rule. We reject five alternative leaving rules. The potential encounter rate that the birds choose as their critical departure threshold maximized their foraging gain ratio (a modified form of efficiency) while foraging. The high experimental intake rates were constrained by rate of digestion. Under such conditions, maximization of the foraging gain ratio during foraging maximizes net intake rate during total time (foraging time plus digestive breaks). We conclude that molluscivore red knots, in the face of a digestive constraint, are able to combine prior environmental knowledge about patch quality with patch sample information to obtain the highest possible net intake over total time.

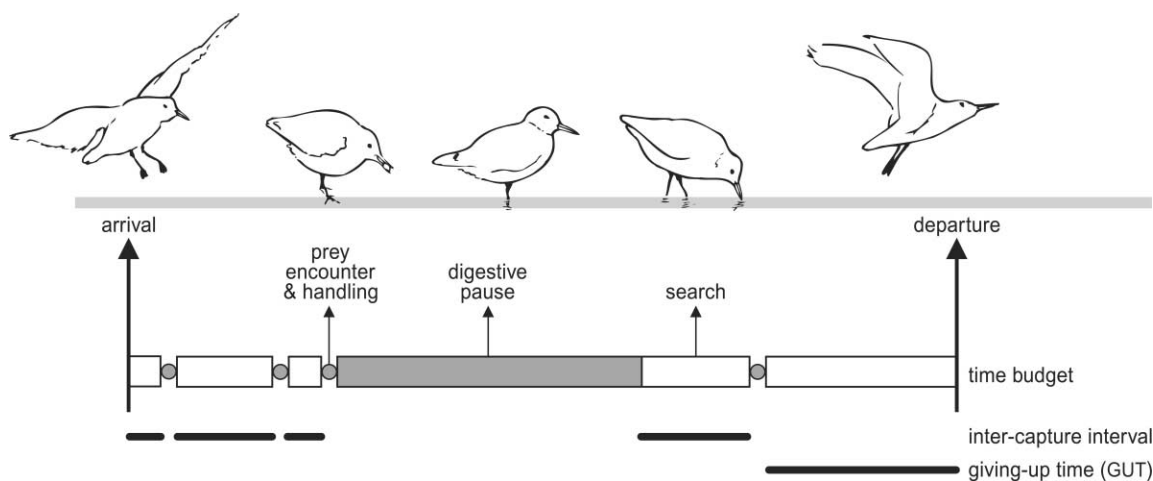
**Keywords:** incomplete information, digestive constraint, giving-up density, optimal foraging, marginal value theorem, currency.

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To model the interactions between foragers and their prey, ecologists have made a number of simplifying assumptions. Prey items are generally supposed to be distributed in clusters, the so-called patches, and are located at random positions in such patches. The area between patches is taken to be devoid of prey. Foragers are expected to maximize their rate of energy intake. In the simplest model, the ideal free distribution model (Fretwell and Lucas 1970), foragers do not spend time and energy traveling between patches, and they know the energy intake rate that can be achieved in each patch. They should and can always select the patch where they obtain the highest intake rates. Feeding in a patch where energy is gained at a lower rate than can be achieved elsewhere is a form of lost opportunity (Stephens and Krebs 1986). More realism is added in the model using the marginal value theorem (MVT; Charnov 1976), where it is acknowledged that it takes time to travel between patches and that foragers do not know the intake rates in all patches beforehand. They only know the intake rate in the current patch and the long-term intake rate achievable in their environment (a rate that also takes travel time into account). Search within patches is random, and because of prey depletion, foragers experience diminishing returns. If foragers aim to maximize their long-term energy intake, they should skip (or leave) a patch when the instantaneous intake rate is lower than the achievable long-term intake rate.

The idea of using an instantaneous intake rate as a currency to decide on patch departure is only applicable when energy intake comes as a continuous flow, for example, in birds feeding on nectar (Gass and Roberts 1992). In contrast, if prey are discrete items found at irregular, stochastic moments (fig. 1), the instantaneous intake rate between prey encounters is 0, and a strict interpretation of MVT predicts that all patches will be left immediately on arrival. Thus, foraging models for discrete prey situations have been developed, which we review.



**Figure 1:** Possible feeding scenario in a patch. Between arrival and departure, a forager encounters four prey at stochastic moments in time. Before each prey capture (*filled circle*; width of circle denotes handling time), a forager has to spend some time searching (*open bar*). After a number of prey have been found (in this case, three), the forager cannot ingest more prey since its stomach is full. It needs to pause in order to process and digest these prey items (*filled bar*). Intercapture interval is the search time it takes to find a single prey (*solid lines*). Search time between the last encounter and departure is called giving-up time (*GUT*). Several of these foraging parameters (*GUT*, total number of prey found in relation to invested search time) could inform the forager about prey density in this patch.

### Departure Rules When Foraging on Discrete Prey Items

#### *Prescient*

The problem of immediate departure was circumvented by assuming that foragers are prescient; that is, they can instantly recognize in what type of patch they are feeding by using sensory cues (e.g., vision, olfaction; Valone and Brown 1989). On arrival, such foragers instantly know how many prey a patch contains, and they thus know how many prey to take from each patch type in order to leave all patches at similar instantaneous encounter rates. As a result, all patches are left at similar giving-up densities (*GUD*; Brown 1988).

The problem for foragers that feed on hidden discrete prey items is the instant recognition of a patch type (i.e., initial prey density). However, as foraging success contains information about a patch (so-called patch sample information; Valone 1991), foragers can try to estimate the instantaneous intake rate (Oaten 1977). Discrete prey items require some handling time before they can be ingested. If we assume that the expected handling time of discrete prey items is known to the forager, estimates of instantaneous intake rate transform into estimates of instantaneous encounter rate (Holling 1959). We review how incompletely informed foragers could estimate encounter rates in depleting patches.

#### *GUT*

Giving-up time (*GUT*) is defined as the length of the search interval between the last encountered prey item and patch departure (fig. 1). The *GUT* rule predicts that a forager leaves a patch when the search time for the next prey item takes longer than a critical time interval, the *GUT*. The reciprocal of *GUT* is a measure of encounter rate, and some authors thought that a fixed *GUT* was predicted by *MVT* (e.g., Krebs et al. 1974). McNair (1982) corrected this mistake. He showed that animals that instantly recognize patch quality should use longer *GUT*s in initially richer patches so that they would effectively leave patches at a constant instantaneous encounter rate. Thus, although *GUT* might be an easy measure of instantaneous encounter rates (it only demands keeping track of time since the latest prey encounter), the estimate obtained is biased.

#### *Current Value Assessment with Prior Knowledge*

Foragers are able to obtain unbiased estimates of instantaneous encounter rates when they know the frequency distribution of initial prey densities in their environment, that is, when they know what to expect. Updating this prior expectation with patch sample information on the elapsed total search time and the number of prey found leads to an unbiased estimate of instantaneous encounter rate (Iwasa et al. 1981; see app. A for technical details).

Updating prior knowledge with newly obtained information is generally called Bayesian updating. Foragers that leave depleting patches at constant estimates of instantaneous or current encounter rates make use of the so-called current value assessment rule (Olsson and Holmgren 1998). In contrast, prescient foragers leave their patches at constant true instantaneous encounter rates.

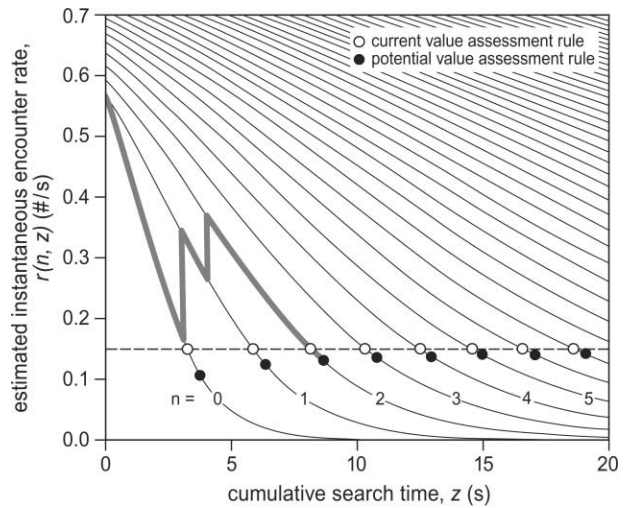
Here we will consider environments where the variance in prey densities exceeds the mean (i.e., contagious distributions), which is how they are most commonly found in nature (Pielou 1977). In such environments, the characteristics of the current value assessment rule are a decline in the estimate when searching proceeds without success (suggesting that the patch contains few or no prey and thus yields a low instantaneous encounter rate) and an increase in the estimate with every new prey found (suggesting that the patch contains additional prey; fig. 2).

*Potential Value Assessment with Prior Knowledge*

Intuitively, one would expect that the aforementioned rule offers uncertain foragers the highest possible intake rates, since it enables unbiased estimates of instantaneous prey encounter rates. However, McNamara (1982), Green (1988), and Olsson and Holmgren (2000) showed that an even better rule exists for uncertain foragers in contagious environments. Because of the potential increase in the estimated instantaneous encounter rate when a prey is encountered, Bayesian foragers striving for maximum long-term intake rates should not base their departure decision on estimates of such current encounter rates. Instead, they should initially be somewhat reluctant to leave a patch and accept low estimates on instantaneous encounter rates (fig. 2; app. B). In this way, foragers await new information in the form of prey encounters and thus take into account the chance that the estimated instantaneous encounter rate will rise in the near future. Foragers that make use of this so-called potential value assessment rule (Olsson and Holmgren 1998) leave their patches at constant estimates of potential encounter rates, that is, the encounter rate over the remainder of the patch visit. As estimates become more reliable when search time proceeds (because more information is gathered), the potential rise in estimated encounter rate becomes smaller over time; new information no longer changes the estimate much. Therefore, with time, the potential value of the patch approaches the current value (fig. 2).

*Current and Potential Value Assessment without Prior Knowledge*

As simple alternatives to the latter two assessment rules, we introduce current and potential value foragers that ig-



**Figure 2:** Unbiased estimation of instantaneous rate of prey encounter by current value assessment rule, assuming prior knowledge. Solid thin lines indicate how the estimate declines with cumulative search time ( $z$ ) and increases with the number of prey found ( $n$ ). When a forager enters a patch ( $z = 0, n = 0$ ), it expects the environmental average instantaneous encounter rate. In this particular example (*thick gray line*), the forager finds two prey items and leaves at a critical estimate of instantaneous encounter of  $0.15 \text{ s}^{-1}$  (*open circles*; dashed line is plotted just to make clear that all circles are at  $0.15 \text{ s}^{-1}$ ). A forager using the potential value rule uses these current estimates on instantaneous encounter rates in a more conservative way. This makes such a forager slightly more successful than a current value forager, since it reduces the chance of leaving a good patch too early. It takes into account the chance that current estimate rises again in the near future, which occurs when a prey is found. Since potential rise in the estimate is largest in the initial phase of patch exploitation (i.e., most can be learned when not much is yet known), it is here where the difference between current estimate and potential estimate is largest. If the forager in this example aims to leave at a potential encounter rate of  $0.15 \text{ s}^{-1}$ , it should stay about half a second longer than the current value forager (solid circles indicate, for different values of  $n$ , a potential encounter rate of  $0.15 \text{ s}^{-1}$ ).

nore prior knowledge. Such foragers estimate current or potential encounter rate by simply keeping track of elapsed search time and number of prey found in a patch as described but have no expected frequency distribution on prey density with which to compare this information (app. C).

Uncertain foragers pay missed opportunity costs when collecting information; they cannot obtain the maximum intake rates that prescient foragers achieve. Among incomplete information models, potential value foragers that make use of prior knowledge achieve highest long-term intake rates. Since current value foragers that make use of prior knowledge ignore the chances of potential future information, they obtain somewhat lower intake rates (Olsson and Holmgren 2000). Since GUT foragers base their decisions on the least amount of information (only

a little part of the entire search period, no prior knowledge), their long-term intake rates are even lower (Green 1987). Current and potential value foragers that ignore prior knowledge achieve lowest long-term intake rates (mainly because they underestimate the likelihood of being in a poor patch, which is high in contagious environments). Given that prior information on the frequency of prey densities can be collected effectively and quickly (Rodríguez-Gironés and Vásquez 1997) and that updating with patch sample information requires little neuronal capacity (Holmgren and Olsson 2000), we expect that net rate-maximizing foragers that feed on hidden prey make use of the potential value assessment rule that takes prior knowledge into account.

We will assess the departure rule used by foragers by calculating what the perceived encounter rates at departure would be if they were estimated by foragers that made use of the considered rule (e.g., reciprocal of GUT as perceived encounter rate for GUT foragers). When we do this for the rule that is being used, we should empirically find that the encounter rates at which patches are left are constant for all initial prey densities. For rules that are not used, we should find significant variation among patches with different initial prey densities. Thus, we reject that a rule is used if we find that estimated encounter rate at departure varies with initial prey density. This approach of inference should allow for solid refutation of competing models (Brown 1993).

#### What Critical Encounter Rate Should Be Applied across All Patches?

No matter which of the aforementioned departure rules is used by a forager, a forager should decide on the critical departure encounter rate below which it leaves its patches. We shall refer to the continuous range of critical departure encounter rates as options. As will be explained, the optimal critical departure encounter rate with respect to energy intake depends on environmental and physiological constraints acting on the forager.

Each option  $i$  is characterized by an average number  $n_i$  of prey found per patch and an average amount of search time  $z_i$  invested per patch. If we assume the energy content of the prey to be unity and handling time  $h$  and travel time  $\tau$  between patches to be constant, long-term gross energy intake rate  $b_i$  for option  $i$  is given by

$$b_i = \frac{n_i}{z_i + n_i h + \tau}. \quad (1)$$

We expect foragers to select the option that yields highest long-term energy intake rate. When different foraging activities (searching, handling, and traveling) vary in their

associated metabolic rate ( $c_z$ ,  $c_h$ , and  $c_r$ , respectively), each option is associated with a different long-term metabolic rate  $c_i$  given by

$$c_i = \frac{c_z z_i + c_h n_i h + c_r \tau}{z_i + n_i h + \tau}. \quad (2)$$

Here we expect foragers to select the option that yields the highest long-term net energy intake rate  $\gamma_i = b_i - c_i$ .

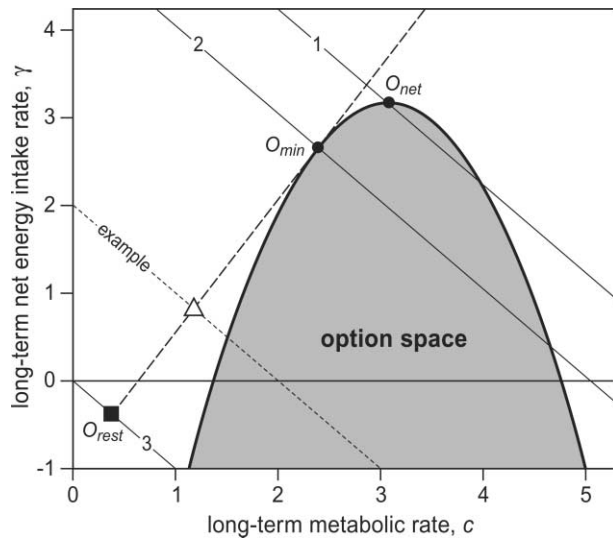
In many situations, foragers cannot sustain maximum net energy intake rates over long periods of time because of digestive constraints (Jeschke et al. 2002). McNamara and Houston (1997) graphically showed that such constrained optimal foragers should select a different option than do unconstrained optimal foragers. They plotted  $\gamma$  as a function of  $c$  (fig. 3) so that lines with a slope of  $-1$  represent lines of equal gross energy intake rates  $b$ , the value being given by the intercept. If  $\hat{b}$  is the maximum long-term gross energy intake rate set by the digestive constraint, depending on the value of  $\hat{b}$ , three scenarios are possible. First, when  $\hat{b} \geq b_{\text{net}}$ , a forager faces no digestive constraint since intake rates will never exceed  $b_{\text{net}}$  (which is gross intake rate at option  $O_{\text{net}}$ ; fig. 3). Thus, it should choose option  $O_{\text{net}}$ , which maximizes net intake for unconstrained foragers. Second, when  $b_{\text{min}} \leq \hat{b} < b_{\text{net}}$ , a forager should choose an option between  $O_{\text{min}}$  and  $O_{\text{net}}$ , such that  $b_i = \hat{b}$  ( $b_{\text{min}}$  is gross intake rate at option  $O_{\text{min}}$ ; fig. 3). If searching for prey in patches is cheaper than traveling between patches ( $c_z < c_r$ ), constrained net rate maximizers should give up patches at lower (estimated) encounter rates than do unconstrained net rate maximizers. Third, when  $\hat{b} < b_{\text{min}}$ , the forager should rest part of the time ( $O_{\text{rest}}$ ) and forage at  $O_{\text{min}}$  otherwise, such that  $b_i = \hat{b}$ . So, as long as the forager compensates by resting part of the time, short-term intake rates can exceed  $\hat{b}$ . If we define  $r_i$  as average time spent resting, then

$$b_i = \hat{b} = \frac{n_i}{z_i + n_i h + \tau + r_i}, \quad (3)$$

and if we define  $c_r$  as metabolic rate while resting, then

$$c_i = \frac{c_z z_i + c_h n_i h + c_r \tau + c_r r_i}{z_i + n_i h + \tau + r_i}. \quad (4)$$

Thus, in the third scenario, while foraging at option  $O_{\text{min}}$ , animals maximize the foraging gain ratio  $b/(c - c_r)$  during foraging in order to maximize net energy intake rate over total time (Hedenström and Ålerstam 1995; Houston 1995; Ydenberg and Hurd 1998; Nolet 2002). They should give up patches at lower (estimated) encounter rates than in the second scenario (again, if  $c_z < c_r$ ). However, unlike the second scenario, this encounter rate does not vary with



**Figure 3:** McNamara and Houston's (1997) solution for a forager maximizing its long-term net energy intake rate  $\gamma$  while digestively constrained. When we plot  $\gamma$  as a function of long-term metabolic rate  $c$ , lines with a slope of  $-1$  represent lines of similar gross energy intake rates  $b$ , with the intercept representing the level of  $b$  (as  $\gamma = b - c$ ). Digestive constraints  $\hat{b}$  are constraints on gross energy intake rates and are thus represented by such lines. Shaded area denotes continuous option space available while foraging; solid square denotes resting option. Note that any shape of foraging option space is conceivable; we chose a hump-shaped space (as did McNamara and Houston 1997). When a digestive constraint only delimits long-term gross energy intake rates larger than  $b_{net}$  (above line 1), the forager actually faces no constraint and should always feed at option  $O_{net}$ . Somewhat lower, when  $b_{min} \leq \hat{b} < b_{net}$  (between lines 1 and 2), the forager should feed slower at an option between  $O_{min}$  and  $O_{net}$ , such that  $b = \hat{b}$ . When a digestive constraint delimits gross energy intake rates that are below  $b_{min}$  (between lines 2 and 3), the forager should rest part of the time ( $O_{rest}$ ) and feed at  $O_{min}$  otherwise, such that  $b = \hat{b}$ . The  $O_{min}$  is found by constructing a tangent from  $O_{rest}$  to the shaded area (dashed line). In that case, average long-term net intake rate is maximal at the intersection of the tangent line and the digestive constraint line (triangle for an example  $\hat{b}$ ).

$\hat{b}$  but is constant. Instead, depending on  $\hat{b}$ , foragers should vary their time spent resting in order to arrive at  $b_i = \hat{b}$ .

In this article, we experimentally tested what rule a medium-sized shorebird, the red knot (*Calidris canutus*), uses when exploiting patches. We tested for prescient, GUT, current value assessment excluding and including prior knowledge, and potential value assessment excluding and including prior knowledge. We offered hidden prey to assure uncertainty about prey densities, and we therefore predict that red knots make use of the rule that offers highest intake rates to uncertain foragers, the potential value assessment rule including prior knowledge. In addition, we tested what option red knots select, given the rule they use (i.e., which threshold encounter rate). We offered high prey densities to ensure that intake rate would

actually be constrained by rate of digestion, and we consequently predict that the birds maximized the foraging gain ratio while feeding. Finally, to see whether our experimental conclusions were consistent with the prey consumption patterns in the field, we measured initial and giving-up densities in patches that were fed on by flocks of free-living red knots.

### The Study Species and Its Prey

Red knots are an ideal species for studying patch use decisions. Their total and available prey stocks are readily quantified (Zwarts et al. 1992; Piersma et al. 1993a, 1993b, 1994), individual patch residence times can be measured in the field by radiotelemetry techniques (van Gils and Piersma 1999; van Gils et al. 2000), they can easily be trained to forage in experimental aviary settings (Piersma et al. 1995a), and we have considerable knowledge on rates of energy expenditure (Piersma 2002). Red knots feed on hard-shelled bivalve prey, which they ingest whole. The internal processing of the bulky, useless shell material causes the birds' rate of ingestion to be constrained by their rate of digestion when feeding at high prey density patches (Zwarts and Blomert 1992; J. A. van Gils, T. Piersma, A. Dekinga, and M. W. Dietz, unpublished manuscript).

Bivalves live buried in intertidal mudflats, and their densities obey a contagious distribution (Piersma et al. 1993b). In the absence of correlated surface features (J. A. van Gils, personal observation), it would appear impossible for red knots to instantly recognize patch quality. Instead, we expect red knots to make use of patch sample information to update existing prior knowledge.

### Material and Methods

#### The Experimental Birds and Housing Conditions

Four red knots of the *islandica* subspecies (Piersma and Davidson 1992), captured with mist nets on February 19 and 20, 1999, near Texel, were used during the experiment. Three of them were in their second calendar year, and one was at least in its third. Their bill lengths varied between 32.8 and 35.6 mm and their average body mass between 119 and 126 g. We housed them in a large outdoor aviary. On April 30, 1999, 3 wk before the experiment, we moved them to the experimental outdoor aviary (7 m  $\times$  7 m surface area and 3 m high), where they became used to feeding on mussels (*Mytilus edulis*) buried in the experimental patches.

Patches consisted of large buckets (65 cm high, 30 cm diameter) that were filled with sediment collected in the western Wadden Sea (Mokbaai, Texel). Since we wanted

the patches to be depleted quickly, we reduced the actual surface area of the patches to 83 cm<sup>2</sup> by covering the top of each bucket with a plastic disk that was open in the middle. This also minimized disturbance to the induced pressure prey detection system of red knots (Piersma et al. 1998) by edge effects and treading. Although these patches may seem small, we know that red knots in the field probe in similarly sized surfaces for a considerable time, in spite of the large scale over which their daily feeding trips take place (Piersma et al. 1993*b*). In addition, the prey we offered were tiny relative to the size of the patch (covering about 0.1% of the total surface area when buried). The patches were placed on the floor of a basin filled with seawater to a level just below the top of the buckets. During the day (from 0800 hours to 2100 hours), the birds had access to a smaller aviary with a sand-covered floor (4 m × 1 m surface area and 2 m high). Here the birds could drink freshwater. During the night, we locked the birds in this high-tide roost cage. They received no food until the experimental arena was opened the next morning. Total available feeding time per day (13 h) was selected such that the birds' energy budget would be in balance (given the parameters listed in table 1).

### The Prey

Small mussels were scraped from North Sea basalt piers at Texel. After washing off most of the attached organic material, we sieved them through a set of sieves with different mesh sizes. For the experiment, we selected medium-sized mussels (mean length ± SE = 10.8 ± 0.2 mm,  $N = 54$ ). Mussels were stored in clean seawater basins at temperatures between 5° and 12°C. We collected a fresh batch of mussels twice a week. To obtain energetic values of the prey, we measured ash-free dry mass by incinerating the dried fleshy part of the mussels at 550°C (for details of methods, see Piersma et al. 1993*b*).

### The Experiment

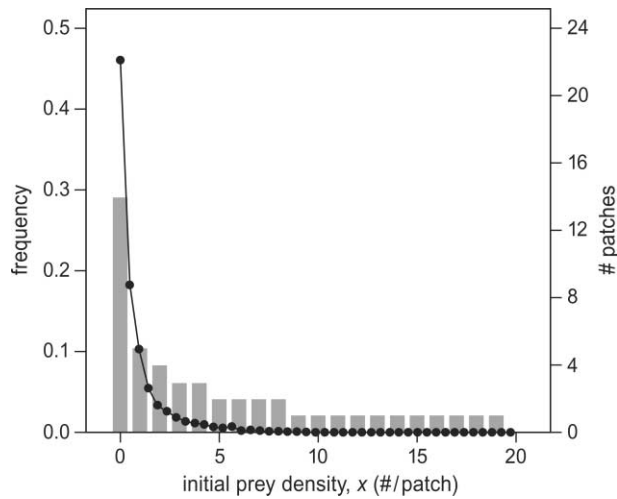
The number of mussels issued per patch followed a negative binomial distribution (a specific form of contagious distributions; app. A) that was kept constant throughout the experiment ( $\alpha = 0.6$ ,  $\beta = 0.12$ , range = 0–19). Average prey density was selected such that the birds' intake rate would be constrained by their rate of digestion (on the basis of Piersma et al. 1995*a* and J. A. van Gils, T. Piersma, A. Dekinga, and M. W. Dietz, unpublished man-

**Table 1:** Listing of model parameters needed to predict optimal departure encounter rates for the six considered leaving rules

Parameter	Definition	Value	SI unit	Obtained
$\alpha$	$\alpha$ parameter negative binomial distribution (overdispersion coefficient)	.6	...	Experimentally offered
$\beta$	$\beta$ parameter negative binomial distribution	.12	...	Experimentally offered
$a_x$	Searching efficiency (as a function of initial prey density $x$ )	$10^{-0.21}x^{-0.84}$	patch s <sup>-1</sup>	Measured
$\tau$	Travel time between patches	.47	s	Measured
$h$	Handling time	1.69	s	Measured
$f$	Flesh mass prey (AFDM)	9.8	mg	Measured
$\varepsilon$	Energy density prey flesh mass	22	J mg <sup>-1</sup> AFDM	J. Samuels and T. Piersma, unpublished data
$d$	Digestion efficiency	.725	...	Piersma 1994
$p$	Prey acceptance probability	.79	...	Measured
$\hat{i}$	Long-term maximum rate of ingestion	.033	s <sup>-1</sup>	J. A. van Gils, T. Piersma, A. Dekinga, and M. W. Dietz, unpublished manuscript
$c_r$	Metabolic rate during resting	2.5	W	Wiersma and Piersma 1994
$c_z$	Metabolic rate during searching	3	W	Piersma 2002
$c_h$	Metabolic rate during handling	3	W	Piersma 2002
$c_t$	Metabolic rate during traveling	13	W	Kvist et al. 2001

Note: AFDM = ash-free dry mass. The 13 h of daily feeding time that we allowed is just sufficient to balance energy income with outcome as maximum long-term gross intake rate during daily foraging period =  $\hat{b} = \hat{i}d\varepsilon = 5.2$  W, and long-term metabolic rate  $c_i = 2.7$  W. Note that  $c_i$  is based on time allocation to different behaviors (fig. 6C) and is in agreement with unpublished data (2.9 W) of M. Poot and T. Piersma (see Piersma 2002).





**Figure 4:** We offered prey densities per patch that followed a negative binomial distribution, with an average of five prey per patch and an overdispersion coefficient  $\alpha$  of 0.6 (which makes  $\beta = 0.12$ ). This meant that the bulk of the 48 experimental patches contained zero or only a few prey and that only a few patches contained many prey (gray bars). For comparison, we plotted the frequency distribution of patch qualities in the field (solid circles connected with a line). From 12,165 core samples collected in 1996–2000 in the field (western Dutch Wadden Sea), we selected ingestible size classes of the three most abundant prey species (*Macoma balthica*, *Cerastoderma edule*, and *Mytilus edulis*). These prey were distributed slightly more contagious ( $\alpha = 0.3$ ) than in the experiment.

uscript). From this distribution, we drew 48 prey densities (fig. 4). Each of the 48 patches was randomly assigned one of these densities. To prevent the birds from learning the position of profitable patches, we made new density assignments before each trial. Before each trial, we filled the patches to the assigned density. We buried the mussels at a fixed depth of 2 cm by pushing them with a little rod into the sediment. All trials ran with solitary individuals; in the meantime, the other three birds were locked in the high-tide roost cage. We performed one trial per bird per day. Over the total period, each trial was repeated six times per bird, which led to 24 trials in total. A trial ended when the focal bird had visited all 48 patches at least once. To avoid any effect of the bird’s possible anticipation to the end of a trial, we only analyzed the first 20 patch visits. Revisits were excluded from analysis, since the bird might memorize the number of prey remaining when it left the patch.

Trials were recorded by a Hi-8 video camera from a blind. We time coded copies of the tapes, which enabled us to analyze the behavior of the birds to the nearest 0.04 s in slow motion with the Observer package (Noldus Information Technology 1997). We scored the patch where the focal bird was located, the moments of prey encounter,

search time between prey encounters, flight time between patches, prey handling time, and time spent doing other things (mainly resting).

To keep the experimental environment as constant as possible ( $\alpha$  and  $\beta$  of the negative binomial distribution of initial prey densities), we kept the birds in a closed economy (Hursh 1980). This meant that the birds had to obtain their entire daily food ration in the experimental setup (see also note in table 1). To keep a stable patch quality distribution when we were not doing trials, we regularly refilled patches to their initial prey density. To acquaint the birds to the  $\alpha$  and  $\beta$  of the prey density distribution, we “trained” them on this distribution for 2 wk before the experiment.

### Testing for Random Search

Essential for the model we wanted to test is the principle of diminishing returns: the decline in encounter rate when a patch gets depleted. This principle holds for foragers that search a patch randomly. Random search implies that the inverse of intercapture interval  $T_s$  (s) is a linear function of current number of prey in the patch (patch<sup>-1</sup>), with the slope defined as instantaneous area of discovery  $a$  (patch s<sup>-1</sup>), also called the searching efficiency (Hassell 1982):

$$\frac{1}{T_s} = a(x - n). \quad (5)$$

The current number of prey in the patch equals  $x$  (the initial number of prey) minus  $n$  (the number of prey already found). If search is random, the encounter process has Markov property, in which case  $T_s(x - n)$  should be exponentially distributed (Marschall et al. 1989). However, in an experiment such as ours where foragers are allowed to leave patches, there is a good chance that such a distribution will be biased toward short intercapture intervals, since the birds are likely to give up patches after a long interval of not finding a prey item. This makes the last, unsuccessful search interval (i.e., giving-up time) a censored observation; true intercapture intervals are uncensored observations. Thus, censoring occurs when data on the duration of a certain activity (such as searching for a prey) are interrupted (e.g., by flying off the patch; Haccou and Hemerik 1985). Since we wanted to quantify the unbiased distribution of intercapture intervals, we took these censored giving-up times into account. Such data can be handled by survival analysis, where giving-up times get a censor value of 0 and true intercapture intervals get a censor value of 1 (Haccou and Meelis 1992). For each patch visit, we tested whether the distribution of  $T_s(x - n)$  (including censored data) deviated from exponentiality

**Table 2:** ANOVA in searching efficiency  $a$  ( $\log_{10}$  transformed, nested GLM)

Variable	SS	df
Bird	1.07*	3
Trial (bird)	2.70*	20
$\log_{10}(x)$	14.27*	1
Visit number	.20	1
Error	13.55	222

Note: Bird and trial are treated as category variables, and  $\log_{10}$ -transformed initial prey density  $x$  and visit number as continuous variables. SS = sum of squares, df = degrees of freedom. The relationship with initial prey density is given by  $\log(a) = -0.21 - 0.84 \log(x)$ .

\*  $P < .05$ .

by using the adjusted Kolmogorov-Smirnov test for exponentiality with an unknown mean (Haccou and Meelis 1992). For each patch, we obtained the maximum likelihood estimator of the mean  $T_s(x - n)$ , the reciprocal of  $a$ , the searching efficiency. To obtain normally distributed data, we log transformed searching efficiencies and tested for significant variance among birds, trials, and patches using nested general linear models (GLM) in SYSTAT 10 (Systat Software).

#### *Testing between Patch Departure Rules*

For each of the six patch departure rules, we tested whether encounter rates at patch departure estimated by each rule varied between initial prey densities  $x$ . Thus, we calculated encounter rates that would be perceived by red knots if they were using the considered rule. A significant dependence on  $x$  would refute the possibility that the birds made use of the considered rule, since each rule predicts a constant threshold encounter rate at patch departure.

Since prescient foragers know their true instantaneous encounter rate while foraging, the "estimated" departure encounter rate for prescient foragers was calculated as the observed giving-up density (GUD) times the initial prey density specific searching efficiency  $a_x$ . Departure encounter rates as estimated by GUT foragers were calculated as the reciprocal of the observed giving-up time. We calculated the departure encounter rate estimated by current value foragers by combining the offered frequency distribution on initial prey density with the observed cumulative number of prey found ( $n$ ) and cumulative search time ( $z$ ) at departure, as explained in appendix A. Future estimates of current encounter rate (i.e., after a patch was left) were used as inputs to calculate potential encounter rate at departure (app. B). Encounter rates as perceived by current and potential value foragers that ignore prior knowledge were calculated only from observed cumulative number of prey found ( $n$ ) and cumulative search time ( $z$ ) at departure (app. C). We square root transformed all six ex-

pressions of estimated encounter rates to meet normality requirements of ANOVAs. The analyses were performed using nested GLM.

#### *Testing for Net Intake Rate Maximization*

To predict the optimal departure encounter rate (i.e., the option) for the rule that was observed, we needed parameters of the birds' time and energy budget. These parameters were either measured in the experiment or obtained from other studies (table 1). We obtained values for  $h$  (handling time per encountered prey),  $\tau$  (travel time between two patches), and  $p$  (proportion of encountered prey ingested) by nested GLM analyses of log-transformed ( $h$  and  $\tau$ ) and arcsine-square root-transformed ( $p$ ) averages per trial (following Krebs 1999). We used the parameters to simulate 30,000 patch visits (in True BASIC). We ran these simulations for each rule and a range of realistic departure encounter rates to relate long-term net intake rate to departure encounter rate (by using eqq. [3] and [4]).

#### *Patch Exploitation in the Field*

From October 5 to 12, 1996, we measured reductions in prey densities caused by flocks of red knots feeding in our study area, the western Dutch Wadden Sea (53°15'N, 5°19'E). By using exclosures, we compared initial prey densities with giving-up densities at nine different sites. At each site, we put up a fence of sticks and ropes around an area of 100 m<sup>2</sup> to locally exclude flocks of foraging red knots. If flocks of knots had fed just next to these exclosures (within 10 m; checked by presence of footprints and fecal droppings) during the next low-tide period, we compared prey densities in the exclosures (initial prey density) and just next to the exclosure where the birds had fed (GUD) at the end of that low-tide period. We chose such short exploitation periods of 2–5 h to avoid possible effects of prey emigration. We only compared densities of harvestable *Mya arenaria* (depth <4 cm, shell length 3–20 mm), a bivalve species that was fed on most in that year at those sites. One sample comprised 50 subsamples taken with a core of 1/56 m<sup>2</sup> surface area (such subsample sizes guarantee standard errors that are  $\pm 10\%$  of the mean; Piersma et al. 1993b).

## Results

#### *Testing for Random Search*

Out of the 480 patch visits (4 birds  $\times$  6 trials bird<sup>-1</sup>  $\times$  20 visits trial<sup>-1</sup>), 248 visits yielded at least two intercapture intervals (either censored or not), which were minimally

**Table 3:** Sum of squares of estimated encounter rate at patch departure for the six proposed rules (square root transformed; nested GLM)

Variable	df	Prescient	GUT	Current		Potential	
				No prior knowledge	Including prior knowledge	No prior knowledge	Including prior knowledge
Bird	3	.19	.18	.86*	.27*	.73*	.30*
Trial (bird)	20	1.97	3.91*	4.31*	1.36*	2.89*	1.50*
<i>x</i>	1	12.03*	.71*	2.69*	.29*	2.22*	.07
Error	455	34.96	31.33	31.16	12.46	20.80	12.56

Note: Bird and trial are treated as category variables, initial prey density *x* as a continuous variable; df = degrees of freedom, GUT = giving-up time.

\* *P* < .05.

required to test for exponentiality of the distribution of  $T_s(x - n)$ . With the adjusted Kolmogorov-Smirnov test, only four distributions (2%) deviated from exponentiality at the *P* = .05 level. We combined significance probabilities of each separate test by a method proposed by Sokal and Rohlf (1995) to show that overall these 248 distributions did not deviate from exponentiality (i.e., we compared test statistic  $-2\sum \ln P = 236.8$  with  $\chi^2_{2 \times 248}$ ).

Each distribution yielded a maximum likelihood estimator of searching efficiency *a*. A nested GLM revealed significant variation among birds and trials (table 2). However, these differences were small and only due to one out of six between-bird comparisons and five out of 276 between-trial comparisons (Bonferroni’s pairwise comparison). Most variation in searching efficiency could be explained by the negative effect of initial prey density,  $\log(a) = -0.21 - 0.84 \log(x)$ . No effect was detected of the rank number within a trial of the successive patch visits.

#### Testing between Patch Departure Rules

When taking away effects of bird and trial, “perceived” encounter rates at departure varied significantly with initial prey density when assuming prescient knowledge (table 3). These presciently estimated and thus true instantaneous encounter rates went up with initial prey density (fig. 5A). Poor patches were visited for longer than predicted and were thus left at lower prescient encounter rates (most extreme: empty patches, which were predicted to be skipped by prescient foragers, were visited shortly by the birds). We can thus reject the hypothesis that red knots are prescient foragers. Nor did the birds make use of the GUT rule, since reciprocals of GUT (perceived encounter rate if they were GUT foragers) went down with initial prey density (table 3; fig. 5B). Red knots did not behave as current value foragers, since perceived departure encounter rate went down (without prior knowledge; fig. 5C) or up (with prior knowledge; fig. 5D) with initial prey

density (table 3). Nor did the birds estimate potential encounter rate while ignoring prior knowledge; this expression for encounter rate at departure related negatively to initial prey density (table 3; fig. 5E). Only when encounter rate was expressed for potential value foragers that do make use of prior knowledge did we find encounter rates at departure to be independent of initial prey density (table 3; fig. 5F).

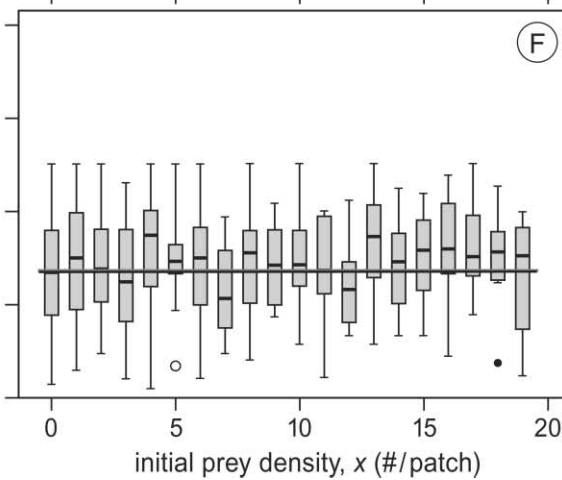
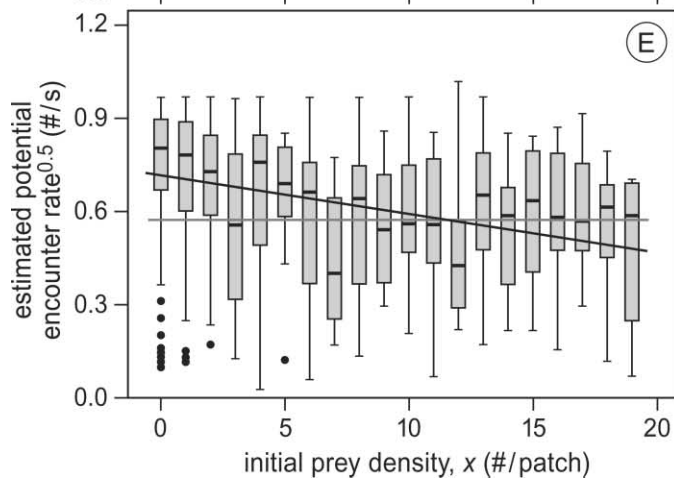
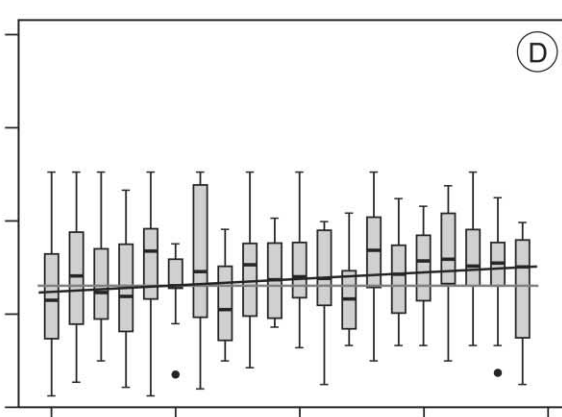
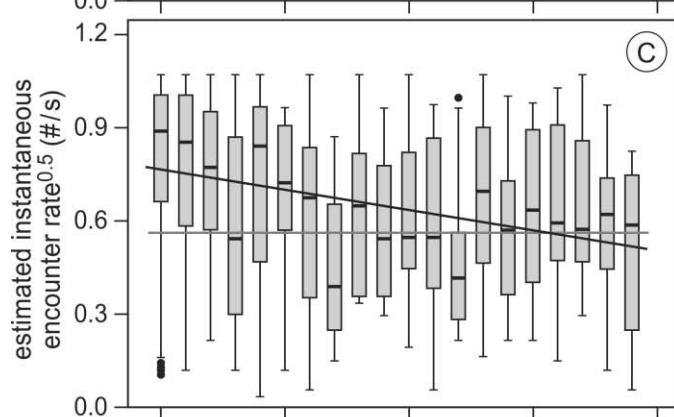
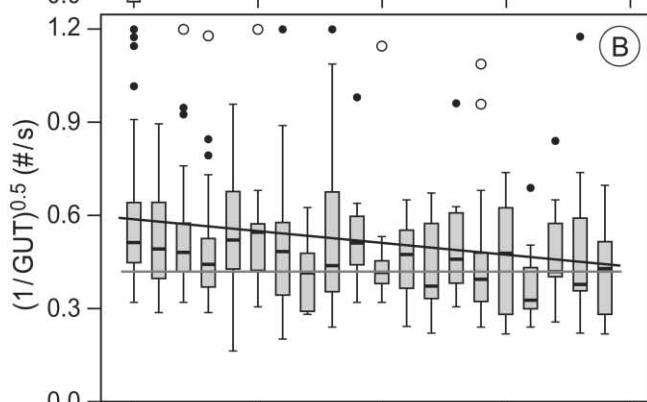
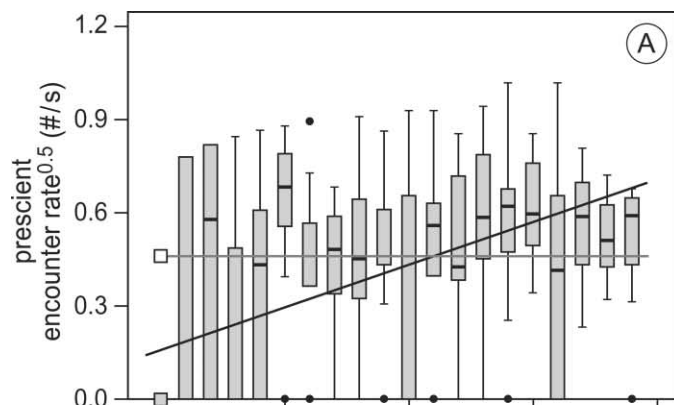
#### Testing for Net Intake Rate Maximization

Given that the knots made use of the potential value assessment rule with prior knowledge, and given the parameter values listed in table 1, the birds’ long-term net intake rate would have been maximized by application of a departure potential encounter rate of 0.17 prey s<sup>-1</sup>. The observed potential encounter rate at departure (0.167; 95% confidence interval [CI] 0.151–0.184; intercept from analysis presented in table 3) did not differ from this predicted value (*P* > .7; fig. 6; note that  $[0.167]^{1/2} = 0.41$ , which is plotted on the Y-axis).

As a check of whether the rate of digestion that we implemented into the model (an estimate of which was obtained elsewhere; J. A. van Gils, T. Piersma, A. Dekinga, and M. W. Dietz, unpublished manuscript) matched the observed rate of digestion in this experiment, we compared predicted percentage of time that could be spent foraging (searching, handling, and traveling) with the data (fig. 7). The observed average (18.8%; 95% CI 16.8–20.8, calculated per trial) did not differ from predicted 20.4% (GLM analysis with arcsine-square root-transformed percentages).

#### Patch Exploitation in the Field

At all nine sites, we found higher prey densities in enclosed areas (*x*, initial prey densities) than in neighboring open areas where flocks of knots had fed (GUD; fig. 8). Absolute number of prey consumed went up with initial prey density, but the proportion of prey consumed was indepen-



dent of initial prey density, as indicated by a slope not different from one in the relation between log-transformed GUD and log-transformed  $x$  ( $\log[\text{GUD}] = -0.13 + 1.01 \log[x]$ ;  $N = 9$ ;  $R^2 = 0.87$ ;  $P < .0005$ ; 95% CI of slope 0.66–1.36).

## Discussion

### Departure Rules

In the aviary experiment, red knots updated prior knowledge with patch sample information by making use of the potential value assessment rule: patches were left at constant potential encounter rates, independent of initial prey density (fig. 5F; table 3). The other five expressions for departure encounter rate varied with initial prey density and were therefore rejected (fig. 5A–5E; table 3). In addition, for each of the five rejected rules, the relationship with initial prey density was consistent with the assumption that red knots updated prior knowledge with the potential value assessment rule.

It is clear why the birds were not behaving as prescient foragers, since this requires patches to be instantly recognized. With hidden buried prey, the knots had to collect patch sample information about patch quality to get to know a patch. This is most obvious in poor patches ( $<5$  prey patch $^{-1}$ ); prescient foraging predicts those patches to be skipped (0 prey patch $^{-1}$ ) or exploited for only a short while (1–4 prey patch $^{-1}$ ). However, in those patches, the birds stayed longer than the prescient model predicted, such that true instantaneous encounter rate at departure fell below the prescient optimum (dashed horizontal line in fig. 5A). Only for rich patches ( $>5$  prey patch $^{-1}$ ) were observed departure encounter rates close to the prescient optimum. This can be interpreted as a bird getting to know the patch after having spent some time foraging in it.

At the other extreme, the GUT rule leads to suboptimal intake rates in uncertain environments. Giving-up times comprise only a little part of the entire search process, and because of the stochastic nature of prey encounters, even

in rich patches long intercapture intervals can occur, which makes it a suboptimal rule. The observed decline in the reciprocal of GUT with initial prey density (fig. 5B), which allowed us to reject the GUT rule, has been observed by others (Wildhaber et al. 1994) and was predicted by the prescient, discrete-prey version of MVT (McNair 1982) and by Bayesian models (R. F. Green, personal communication).

Since the proposed current and potential value assessment rules make use of information collected during the entire search process, chances for over- and underestimates are reduced by these rules (fig. 5C–5F), especially when making use of prior knowledge on the frequency distribution of initial prey densities (fig. 5D, 5F). Ignorance of such prior knowledge makes foragers unaware of the fact that most patches in contagious environments are poor. Thus, if prior knowledge was ignored but poor patches were left as quickly as the experimental birds actually did, this would be perceived as leaving too soon (i.e., at too high encounter rates; fig. 5C, 5E).

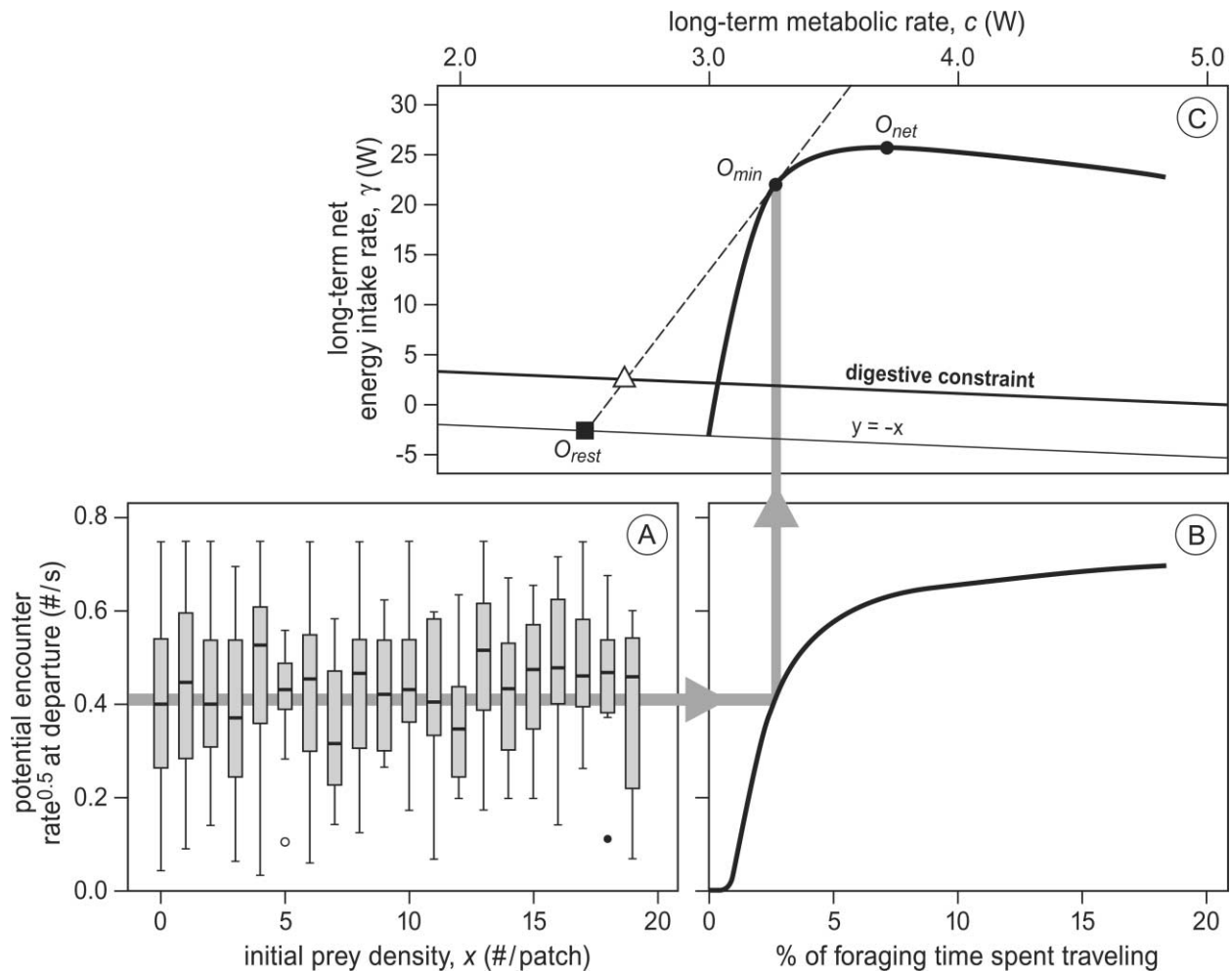
Using prior knowledge makes the birds aware of high chances for being in a poor patch. Using the potential value rule instead of the current value rule reduces the likelihood of too rapid “conclusions” about the state of the patch. Exactly as the data show (fig. 5D), potential value foragers that take prior knowledge into account on average would be predicted to leave bad patches at lower estimated instantaneous encounter rates than good patches. This provides additional evidence that the birds coped with uncertainty in the best possible way.

### Discrete Patches

In nature, the bivalve prey of knots live in continuous, nondiscrete patches in extensive mudflat systems (Piersma et al. 1993b). It is therefore surprising that the birds in the experiment were able to make use of a departure rule that is thought to be valid for discrete patches only, that is, for situations where no prey occur between patches. The potential value assessment rule has been verified only for woodpeckers that feed in more or less discrete patches,

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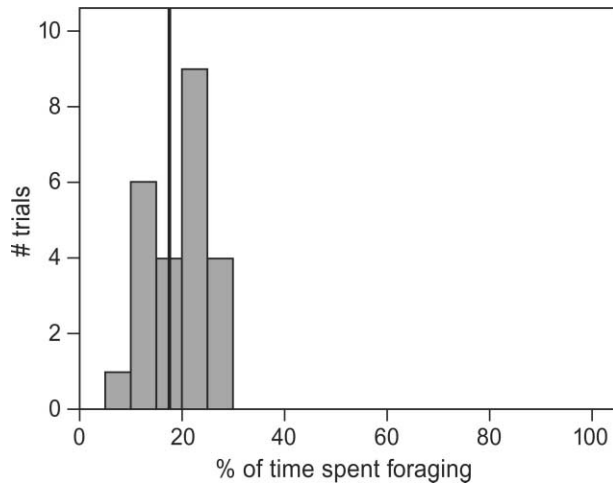
**Figure 5:** Relating observed six expressions of (square rooted) encounter rate at patch departure to initial prey density. For each graph, we have plotted linear regression line through observed encounter rates (*thin solid line*) and predicted optimal departure encounter rate (*gray horizontal line*) on the basis of the experimental environment and the level of the knots' digestive constraint. *A*, Prescient encounter rates went up with initial prey density. All patches except for empty ones (*open square*) should be visited according to the prescient model; gray square in origin of graph indicates that the birds visited even empty patches (where, of course, prescient encounter rates were 0). *B*, Reciprocals of giving-up times (*GUT*) go down with initial prey density; that is, the birds persisted longer after last prey encounter in initially rich patches. The few square rooted encounter rates on the upper horizontal axis were actually  $>1.2$  (1.3–2.9) but were given a value of 1.2 for reasons of presentational clarity. *C*, Current value foragers that ignore prior knowledge would perceive departure encounter rates that declined with initial prey density. *D*, Current value foragers that consider prior knowledge would perceive only a slight increase in departure encounter rates with initial prey density. *E*, Potential value foragers that ignore prior knowledge would perceive departure encounter rates that declined with initial prey density. *F*, Departure encounter rate as perceived by potential value foragers that consider prior knowledge is constant across initial prey density. Observed mean potential encounter rate (*thin solid horizontal line*) does not differ from optimal value (*gray horizontal line*).



**Figure 6:** To see why red knots selected the optimal encounter rate to depart from patches, we constructed a link to their energy budget. A, Potential encounter rate that the birds selected as their critical measure to leave depleting patches (this graph is essentially the same as fig. 5F). Width of gray bar denotes 95% confidence interval (CI) around the mean. The departure encounter rate relates directly to the percentage of foraging time that is spent traveling (horizontal axis in B). This is because the selected departure encounter rate is a measure of the minimal quality that a forager “demands” of its patches. High demands (high departure encounter rates) lead to short patch residence times (cf. fig. 2), and since travel times are fixed, this leads to the forager spending much of its time traveling. There is an optimal departure encounter rate that leads to highest long-term net intake rates  $\gamma$  (vertical axis in C), since the forager could devote too much or too little time to traveling. Since traveling is more expensive than spending time in patches, we can linearly translate relative time spent traveling into a long-term metabolic rate (horizontal axis in C), which allows us to plot the available options in a dimension proposed by McNamara and Houston (1997). Now the effect of the digestive constraint on the optimal option is clearly visible. Since  $\gamma$  cannot exceed the experimentally determined constraint line (J. A. van Gils, T. Piersma, A. Dekinga, and M. W. Dietz, unpublished manuscript), alternating between feeding in option  $O_{min}$  and spending time in rest  $O_{rest}$  leads to highest possible  $\gamma$  (triangle). As gray 95% CI bar shows, the birds selected this option.

the branches of trees (Lima 1984; Olsson et al. 1999). Our study demonstrates that discrete patch rules could function in nondiscrete patch situations as well and that red knots possess the cognitive architecture to make use of the potential value assessment rule. In fact, in a theoretical article, Arditi and Dacorogna (1988) show that any arbitrary prey distribution should be exploited like prey in discrete patches: harvest until (estimated) encounter rate has

dropped below a critical level. As pointed out by Kacelnik and Bernstein (1988, p. 253), “When patches do not exist, optimal foragers should invent them.” The scale over which a forager should and can base its estimate remains unclear. Schmidt and Brown (1996) showed that the finer the scale of perception, the higher the intake rates. However, a forager will always be perceptually constrained below some finer scale, a threshold that Kotliar and Wiens



**Figure 7:** Observed percentages of total time the birds spent foraging (searching, handling, and traveling). This distribution does not differ from the predicted value for constrained net rate maximizers (solid vertical line), which is calculated from a priori determined level of the digestive constraint.

(1990) called “grain.” We consider unraveling the decision making in nondiscrete patches as one of the challenges of contemporary optimal foraging theory.

*Variation in Searching Efficiency*

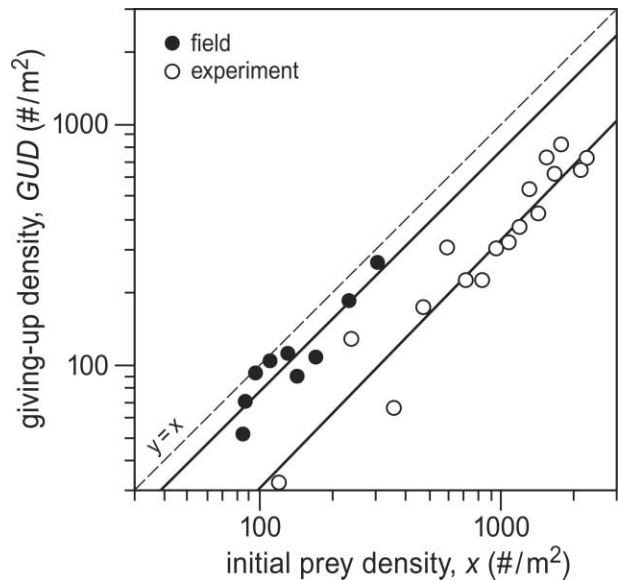
Olsson and Holmgren (2000) showed that the proportion of prey consumed by potential value foragers increases with initial prey density. Although the experimental red knots behaved as potential value foragers, they consumed a fixed proportion of the available prey (fig. 8). This unexpected result is due to the negative relationship between searching efficiency and initial prey density (table 2). This makes the rate of prey encounter at a given prey density lower in rich patches than in poor patches. Consequently, rich patches should be left at higher giving-up densities (GUD) than poor patches, leading to the proportion of prey taken away from rich patches being lower than predicted by a constant searching efficiency (such as modeled by Olsson and Holmgren 2000) and approaching the proportion taken from poor patches. A similar pattern of prey consumption was found in the field (fig. 8), which is probably due to the same mechanism.

Negative effects of initial prey density on searching efficiency were also found in an experimental study on starlings (Olsson et al. 2001) and two other studies on red knots (W. K. Vahl, unpublished manuscript; J. A. van Gils, T. Piersma, and J. van der Meer, unpublished manuscript). We propose that the reduction in searching efficiencies in richer patches is due to the longer residence times in such

patches. Disturbance of the structure of the sediment (e.g., holes made by probing, footprints) could make prey harder to detect. Especially in red knots that rely on prey detection based on pore water pressure gradients built up by probing (Piersma et al. 1998), probe holes or footprints might block these gradients. This hypothesis predicts that searching efficiencies decline with increasing search time; reciprocals of searching efficiencies (for a given initial prey density) should deviate from exponentiality. Since we did not find these deviations, the use of a single searching efficiency for a given initial prey density appears justified. It is clear that further investigation needs to be carried out to determine the phenomena causing searching efficiencies to differ between patches and possibly within patches with time and how this should be included in prey density assessment models.

*Decisions on Departure Encounter Rate*

Given the birds’ digestive constraint, their functional response, and the features of the experimental environment (mean travel time, mean and contagiousness in prey densities per patch), the potential encounter rate at departure they chose maximized their net energy intake over total time. In view of the design of the experiment, it is perhaps not surprising that they were maximizing this currency. The birds had to collect all their daily energy in the ex-



**Figure 8:** Giving-up densities (GUD) as a function of a patch initial prey density. Both in the experiment and in the field, more prey was harvested from rich patches than from poor ones. However, the proportion taken did not differ across initial prey densities; slopes of linear regressions (solid lines) on log-log scale do not differ from 1.

perimental food patches that were accessible for only 13 h d<sup>-1</sup>. In addition, the experiment was executed in May when, even in captivity (Piersma et al. 1995b), red knots are preparing for their long-distance migration by putting on a large fuel store. Because the daily available foraging time in the experiment was kept relatively short, we prevented the birds from putting on these stores (see calculation in note of table 1), which kept them eager to feed at the highest possible net gain rates. In view of this fact and the close match between the observed percentage of time spent feeding (18.8%) and the prediction based on a constraint level measured in another experiment (J. A. van Gils, T. Piersma, A. Dekinga, and M. W. Dietz, unpublished manuscript), we can be certain that in this experiment intake rate was constrained by digestion. As McNamara and Houston's (1997) graphical approach shows, in such a case the best option for maximum net energy gain is to maximize the foraging gain ratio while foraging ( $O_{\min}$  in fig. 3) and to spend an amount of time resting ( $O_{\text{rest}}$ ) such that long-term gross intake rate equals  $\hat{b}$ . This is what our experimental birds did (figs. 6, 7).

Although numerous studies have shown that animals maximize their net rate of energy gain (for review, see Stephens and Krebs 1986), to the best of our knowledge, this study is the first to show that energetically constrained foragers maximize the foraging gain ratio while foraging in order to maximize net energy gained over total time. Earlier studies considered maximization of net rate over the foraging period and ignored other activities (e.g., Rovero et al. 2000). Studies that included other activities failed to explain behavior over total time from an energy maximization perspective. For example, Bautista et al. (1998, 2001) found that starlings (*Sturnus vulgaris*) were maximizing net intake rate while foraging but could not explain why the birds spent about 80%–90% of their time resting. We suggest that McNamara and Houston's (1997) graphical approach (which allows also for constraints on sustainable rates of expenditure instead of intake; see, e.g., Piersma 2002) may explain the resting behavior in the starlings studied by Bautista et al. (1998, 2001).

#### Acknowledgments

We would have been unable to collect the data without help from J. Bruin and M. van Meerloo during the experiment and many volunteers during fieldwork. We thank R. F. Green and O. Olsson for encouraging e-mail conversations; A. Dekinga and B. Spaans for helping (handy) hands throughout; G. Driessen and P. Haccou for explaining the basics of survival analysis; and R. H. Drent, J. Fryxell, W. H. Karasov, O. Olsson, W. K. Vahl, J. van der Meer, and an anonymous reviewer for comments. D. Visser is thanked for preparing the figures. The animal ex-

periments complied with Dutch law. Our research was supported by a PIONIER grant of the Netherlands Organization for Scientific Research to T.P.

## APPENDIX A

### Current Value Assessment with Prior Knowledge

When a forager searches randomly through a patch, the prey encounter process has Markov property: the probability to capture a given prey individual in a certain time window depends only on the length of that time window and not on the length of previously unsuccessful search time (Karlin 1966). This leads to exponentially distributed search times between prey encounters. In such a case, the probability that  $n$  prey have been found, given  $z$  time units of search in an initial prey density  $x$ , equals (Olsson and Holmgren 1998)

$$p_n(x, z) = \binom{x}{n} e^{-a_x x z} (e^{a_x z} - 1)^n, \quad (\text{A1})$$

where  $a_x$  denotes the forager's initial prey density-specific searching efficiency (patch s<sup>-1</sup>). We consider prey densities per patch to be contagiously distributed of the negative binomial type (Pielou 1977). Its essence is captured by just two parameters: overdispersion coefficient  $\alpha$ , a measure of the contagiousness of the distribution (the lower  $\alpha$  is, the more contagious the distribution), and  $\beta$  ( $\alpha$  mean<sup>-1</sup>). The probability that a patch initially contains  $x$  prey in a negative binomial distribution is given by

$$p_x(\alpha, \beta) = \binom{\alpha + x - 1}{x} \left( \frac{\beta}{1 + \beta} \right) \left( \frac{1}{1 + \beta} \right)^x, \quad (\text{A2})$$

where

$$\binom{\alpha + x - 1}{x} = \frac{\alpha(\alpha + 1)(\alpha + 2) \cdots (\alpha + x - 1)}{x!},$$

that is, the combinatorial coefficient (Green 1987). Using Bayes' theorem, we can estimate the probability  $I$  that the patch initially contained  $x$  prey items (or contains  $x - n$  prey now), given  $n$  and  $z$ :

$$I_x(n, z) = \frac{p_x(\alpha, \beta) p_n(x, z)}{\sum_{x \geq 0} p_x(\alpha, \beta) p_n(x, z)}. \quad (\text{A3})$$

As calculations become increasingly time consuming with  $x$ , we set  $x_{\max}$  to 170. Since such rich patches are extremely



rare in negative binomial distributions, our distribution approaches the untruncated version.

After multiplying equation (A3) by concurrent encounter rate,  $a_x(x - n)$ , we sum up these products across  $x \geq 0$  to obtain expected instantaneous encounter rate at time  $z$  after  $n$  prey have been found:

$$r(n, z) = \sum_{x \geq 0}^{x_{\max}} I_x(n, z) a_x(x - n). \quad (A4)$$

### APPENDIX B

#### Potential Value Assessment with Prior Knowledge

Although the potential value assessment rule can be modeled in continuous time (Green 1988), we have chosen the somewhat simpler approach of small discrete time steps (sensu Green 1980; Olsson and Holmgren 1998). We selected steps of 0.05 s and adjusted  $a_x$  accordingly.

Given the number of prey remaining in a patch,  $x - n$ , the probability to find  $k$  items during next time unit equals

$$p_k(x, n) = \binom{x - n}{k} e^{-a_x(x - n)} (e^{a_x} - 1)^k. \quad (B1)$$

Note the similarity to equation (A1), which considers the same probability over  $z$  time units. The probability of encountering  $k$  prey items during next time unit, given  $n$  and  $z$ , is the probability of encountering  $k$  prey items during next time unit, given  $x$  and  $n$  (eq. [B1]), times the probability the patch initially contained  $x$  prey, given  $n$  and  $z$  (eq. [A3]), summed across all possible initial prey densities ( $n$  to  $x_{\max}$ ):

$$s_k(n, z) = \sum_{x=n}^{x_{\max}} p_k(x, n) I_x(n, z). \quad (B2)$$

By using backward iteration (Clark and Mangel 2000), we can now calculate the expected number of prey to be found during the expected remaining search time in the patch:

$$EG(n, z) = \sum_{k=0}^{x-n} s_k(n, z) [k + EG(n + k, z + 1)]. \quad (B3)$$

Likewise, the expected remaining search time in the patch equals

$$ET(n, z) = \sum_{k=0}^{x-n} s_k(n, z) [1 + ET(n + k, z + 1)]. \quad (B4)$$

A potential value forager should leave a patch whenever potential encounter rate is below or at its critical potential encounter  $c$ , so when

$$\frac{EG(n, z)}{ET(n, z)} \leq c. \quad (B5)$$

### APPENDIX C

#### Current and Potential Value Assessment without Prior Knowledge

Calculations of current and potential encounter rates estimated by foragers that ignore prior knowledge are similar as in appendixes A and B, respectively, with the subtle difference that equation (A2) is left out of subsequent calculations.

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