

# Paying for information: partial loads in central place foragers

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**Abstract** Information about food sources can be crucial to the success of a foraging animal. We predict that this will influence foraging decisions by group-living foragers, which may sacrifice short-term foraging efficiency to collect information more frequently. This result emerges from a model of a central-place forager that can potentially receive information on newly available superior food sources at the central place. Such foragers are expected to return early from food sources, even with just partial loads, if information about the presence of sufficiently valuable food sources is likely to become available. Returning with an incomplete load implies that the forager is at that point not achieving the maximum possible food delivery rate. However, such partial loading can be more than compensated for by an earlier exploitation of a superior food source. Our model does not assume cooperative foraging and could thus be used to investigate this effect for any social central-place forager. We illustrate the approach using numerical calculations for honeybees and leafcutter ants, which do forage cooperatively. For these examples, however, our results indicate that reducing load confers minimal benefits in terms of receiving information. More-

over, the hypothesis that foragers reduce load to give information more quickly (rather than to receive it) fits empirical data from social insects better. Thus, we can conclude that in these two cases of social-insect foraging, efficient distribution of information by successful foragers may be more important than efficient collection of information by unsuccessful ones.

**Keywords** Central place foraging · Information center · Recruitment · Partial loads · Honeybees · *Apis mellifera*

## Introduction

Intuition suggests that information may sometimes be as valuable as material goods. From an evolutionary perspective, this should only be the case if, ultimately, possession of information leads to an increase in fitness. Moreover, the extent to which individuals are willing to forfeit material goods to obtain information should reflect the value of that information (Stephens 1989; Dall et al. 2005).

In the context of foraging, for example, an individual might sacrifice resources by adopting a less productive foraging strategy to obtain information that will result in a greater gain of resources in the long term. This could happen, for example, through the adoption of submaximal loads before returning from a food source to a central place (Núñez 1966; Schmid-Hempel et al. 1985). Many foragers collect resources to deliver them to a central place such as a nest or a colony (Orians and Pearson 1979). Theory predicts that if food sources offer constant reward rates, foragers should load themselves maximally before returning to the central place (Kacelnik et al. 1986; Stephens and Krebs 1986; Ydenberg and Schmid-Hempel 1994). How-

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ever, if the reward rates decrease with the time that the forager spends at the food source, the forager may perform better by departing without a full load. This reduction in load depends on travel time between the central place and the food source: with shorter travel time, smaller loads should be collected (Orians and Pearson 1979; Kacelnik et al. 1986; Wetterer 1989).

Load sizes have been studied in detail in honeybees foraging on artificial food sources (Núñez 1966, 1970, 1971, 1982; Schmid-Hempel et al. 1985; Wolf and Schmid-Hempel 1989; Wolf et al. 1989; Balderrama et al. 1992; Varju and Núñez 1993). Even with constant reward rates, honeybees frequently seem to adopt submaximal loads, i.e. they do not fill their crop to capacity but return to the hive with a partial load. This contradicts the predictions of simple optimal foraging models (Kacelnik et al. 1986; Ydenberg and Schmid-Hempel 1994). Deviations from the load size that maximises rate have also been observed in leafcutter ants (Roces and Núñez 1993; Burd 1996a). Three explanations for these results have been offered.

1. Mass-dependent costs: even though the crop can be loaded at a constant rate, the energetic cost of carrying ever greater loads from flower to flower during a foraging trip effectively may mean that honeybees experience diminishing returns as they load a fuller crop (Schmid-Hempel et al. 1985; Wolf and Schmid-Hempel 1989). The existence of such higher energetic costs of carrying loads is controversial (Balderrama et al. 1992; Kacelnik 1993; Rocés and Núñez 1993; Moffatt and Núñez 1997; Moffatt 2000 and see also Cuthill and Kacelnik 1990).
2. Information exchange: the submaximal delivery rate associated with a partially filled crop may be the price paid for more rapid information updating at the colony (Núñez 1966, 1970, 1971, 1982). Bees are able to communicate the quality and location of food sources to nestmates at the colony (Frisch 1967), and foragers returning there may thus give or receive information about superior food sources that have become available.
3. Interactions between workers: in leafcutter ants, cutting smaller fragments of leaf might reduce congestion at cutting sites (Burd 1996b). Burd and Howard (2005) extend this argument to include interactions between above-ground and below-ground workers at the nest site and conclude that a model based on overall colony performance predicts the observed fragment size.

In this paper, we offer a formalisation of the information-based argument. In particular, we explore the implications of a model under which a forager returning early from a food source (with a submaximal load) may receive information about a superior food source that has become available.

## The model

We consider a central place forager with two different potentially available food sources. We assume that source 1 is always available, whereas source 2 is available intermittently. Availability of source 2 is signalled by information present at the central place. In the case of a social insect forager, this could be through communication with a nestmate at the colony (the central place). In non-cooperative foragers, it could be through observation of other successfully foraging individuals (Brown et al. 1991). We assume that the forager should maximise the overall rate at which food is delivered to the central place, and analyse how the potential availability of information affects the time,  $s$ , that the forager should spend at source 1 on each trip, and the resulting load,  $G(s)$ . We also investigate the extent to which the optimal behaviour increases the overall delivery rate.

Source 1 is modelled using a standard food patch foraging model (Charnov 1976; Stephens and Krebs 1986). We write  $r(t)$  for the rate at which the forager gains food when the current time on the source is  $t$  (and assume  $r(t) > 0$ ),  $G(t)$  for the total food collected up to time  $t$  on the current trip (i.e. the load carried), and  $\tau$  for the travel time for a single round trip from the central place to the source and back. We consider three qualitatively different types of forager/food source behaviour:

- a Constant-unlimited Model, where  $r(t)$  is assumed constant (say  $r_0$ ), and the forager's loading capacity is unconstrained;
- a Diminishing Returns Model, where  $r(t)$  is assumed to be strictly decreasing with  $t$ ;
- a Capacity-limited Model: a particular case of the general Diminishing Returns Model where we assume  $r(t)$  decreases very slowly (and is nearly constant) up to a time corresponding to a maximal load  $G_{\max}$ , and steeply decreases to 0 after that.

The Constant-unlimited Model may be thought to reflect an idealised resource that offers a constant supply of food and an idealised forager with infinite loading capacity. Although clearly unrealistic, it provides an elegant and striking theoretical illustration of the impact of information. In reality, a forager will eventually leave a patch either because the resource gets depleted by the forager (the general Diminishing Returns Model) or because there is a limited amount of food available each time the resource is visited and/or the forager has a limited loading capacity (the Capacity-limited Model). Although the motivation for the two models with non-constant reward rate is different, the mathematical analysis is exactly the same (as under both models  $r(t)$  is assumed to be strictly decreasing with  $t$ ) and results will only be

stated for the Diminishing Returns Model. Numerical results are presented for all three models using appropriate illustrative parameter values.

We assume that each time the forager returns from source 1, there is a certain probability that information will be present, indicating the availability of source 2. This probability will generally depend on the length of time the forager has been away. We write  $P(s)$  for the probability that such information is present when the forager returns from a round trip of total length  $s$  to source 1. For clarity of presentation, we will assume that source 2 becomes available at rate  $\lambda$ , so that  $P(s) = 1 - e^{-\lambda s}$ . In this case, the expected time until source 2 is again available is  $1/\lambda$ . However, the results can be shown to extend directly to a wider class of models for  $P(s)$ .

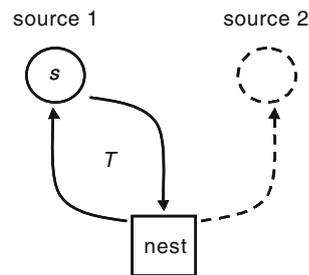
To allow for a variety of interpretations and applications, source 2 is modelled somewhat schematically in terms of the time spent at the source and the average rewards received. If a forager arrives at the central place and no information is present, then it immediately returns to source 1. If information is present, then the forager exploits source 2 until the source is no longer available. This takes an expected time  $T$ , and may include several trips by the forager. The forager then starts visiting source 1 again, irrespective of the information state when the forager finished on source 2. We write  $\gamma_2$  for the overall rate at which food is gained at source 2, so the expected total food gained from source 2 at each exploitation period is  $\gamma_2 T$ .

Note that the only decision in the model is how much time the forager spends at source 1 on each trip,  $s$ .

**Analytical results**

**Overall delivery rate**

The assumptions described above are such that a forager will make a number of trips to source 1 until source 2 opens (Fig. 1). It will then exploit source 2 for the duration that it remains open ( $T$ ), and after that resume foraging on source 1. We call the time from the forager’s return from the just-expired source 2 to the next time it returns from the expired source 2 a reward cycle. For a given fixed foraging time  $s$  at source 1 on each trip, the number of trips in a reward cycle follows a geometric distribution: the forager will make, on average,  $1/P(s+\tau)$  visits to source 1 between exploitation periods of source 2. Each of these visits takes a total trip time (foraging plus journey) of  $s+\tau$ , and each earns a reward  $G(s)$ . A reward cycle also includes a period of exploitation of source 2. This lasts for total time  $T$  and returns a total reward  $T\gamma_2$ . The expected length of the whole cycle is then  $[(s+\tau)/P(s+\tau)]+T$ . The expected reward during



**Fig. 1** The model assumes a forager performing trips to source 1 (travel time  $\tau$ , collecting food for time  $s$ ) until information about a source 2 becomes available. Source 2 is then visited until it expires after time  $T$ . Then visits to source 1 are resumed. Delivery rate (including travel) for source 1 is  $\gamma_1=G(s)/(s+\tau)$ ; for source 2 the reward rate is  $\gamma_2$

the cycle is  $[G(s)/P(s+\tau)]+T\gamma_2$ . The overall delivery rate  $\Gamma(s)$  for a particular foraging time  $s$  ( $s \geq 0$ ) is therefore:

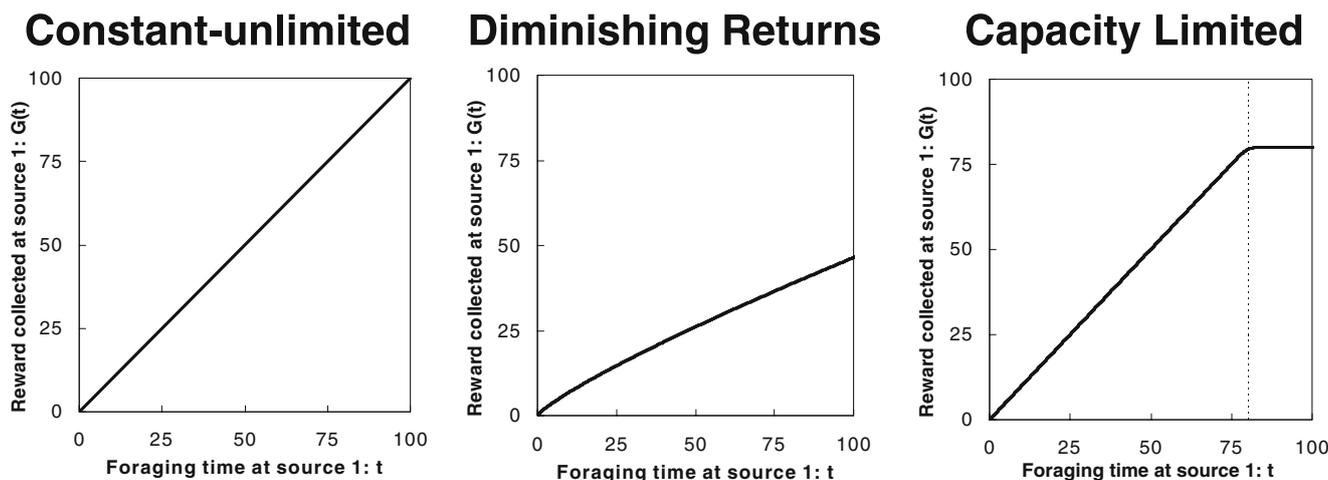
$$\Gamma(s) = \frac{[G(s)/P(s + \tau)] + T\gamma_2}{[(s + \tau)/P(s + \tau)] + T} \tag{1}$$

**Optimal foraging time**

We are looking for the maximal delivery rate the forager can achieve,  $\Gamma(s^*)$ , and the corresponding optimal time the forager should stay at food source 1 on each trip,  $s^*$ . For comparison, we call  $t^*$  the optimal time the forager should stay at food source 1 under a standard patch foraging model [with no information exchange and only one food source with the same reward function  $r(t)$ ]. We call the optimal delivery rate corresponding to  $t^*$  for the single source model  $\gamma_1^*$ . If  $s^*$  is smaller than  $t^*$ , then the forager collects a smaller load and thus sacrifices immediate reward for earlier access to information (and better foraging later).

In a standard single-source model, the delivery rate over a round trip to source 1 with foraging time  $t$  and total travel time  $\tau$  is  $G(t)/(t+\tau)$ , where  $G(t) = \int_0^t r(s)ds$  (Charnov 1976; Ydenberg and Schmid-Hempel 1994). Still looking at a single food source, for the Constant-unlimited Model, the reward rate  $r(t)$  is constant ( $=r_0$ ) (Fig. 2), and thus the load collected per time spent on the trip,  $G(t)/(t+\tau)$ , is strictly increasing with foraging time  $t$  for all  $t \geq 0$ . This means that however long the forager stays at the patch, it can always achieve a higher delivery rate if it stayed even longer ( $t^*$  is infinite and  $\gamma_1^*=r(t)=r_0$ ). When  $r(t)$  is strictly decreasing, as in the Diminishing Returns and Capacity-limited models,  $t^*$  is finite and  $\gamma_1^* = G(t^*)/(t^* + \tau) = r(t^*)$ . This is the Marginal Value Theorem, which states that the forager should leave the food source when the reward rate has decreased to the overall rate achieved when travel time is included (Charnov 1976; Stephens and Krebs 1986).

Our two-source model with information exchange makes some predictions that differ from this standard model. To



**Fig. 2** The gain of reward,  $G(t)$ , while at source 1 for time  $t$ , shown for the three models of  $r(t)$  used: Constant-unlimited; Diminishing Returns; and Capacity-limited

find the maximum of  $I(s)$ , i.e. the maximal delivery rate that can be achieved over a reward cycle, we look at its derivative. The maximum of the function  $I(s)$ , and thus the optimal delivery rate, will correspond either to the endpoint of the set of possible  $s$  values, or to the point at which the derivative becomes zero. We find from direct calculation that the derivative of  $I(s)$  in expression (1) has the same sign, and is zero in the same places, as expression (2) below [writing  $P'(s)$  for the derivative of  $P$  with respect to  $s$  and  $\sigma_P(s)$  for  $(P(s)/P'(s)-s)$ ].

$$[r(s)(s + \tau) - G(s)] - (\gamma_2 - r(s)) \frac{TP'(s + \tau)\sigma_P(s + \tau)}{1 + TP'(s + \tau)} \tag{2}$$

We now study how this term changes with  $s$ , and thus which  $s$  would make it zero. For the Diminishing Returns and Capacity-limited models,  $r(s)$  is strictly decreasing with  $s$ . The first term in expression (2) has the same sign as the derivative of  $G(s)/(s+\tau)$ , is positive at  $s=0$ , monotone decreasing for all  $s \geq 0$ , and zero at  $s=t^*$ . If this was the only term,  $I(s)$  would thus be maximised at the same foraging time  $s$  as in the single-source model. In the second term,  $TP'(s + \tau)\sigma_P(s + \tau)/(1 + TP'(s + \tau))$  is positive and strictly increasing in  $s$ , while  $\gamma_2 - r(s)$  is strictly increasing with  $s$  and its value at  $s=t^*$  is positive only if  $\gamma_2 > \gamma_1^* = r(t^*)$ . Moreover, if expression (2) is positive at  $s=0$ , i.e. if  $\gamma_2 < \bar{\gamma}_2$ , where  $\bar{\gamma}_2 = r(0) [1 + \tau(1 + TP'(\tau)) / (TP'(\tau)\sigma_P(\tau))]$ , then expression (2) is positive at  $s=0$ , negative at  $s=t^*$  and strictly decreasing over the interval  $0 < s < t^*$ . Thus, if we restrict consideration to the range  $\gamma_1^* < \gamma_2 < \bar{\gamma}_2$ , then there is a unique value  $0 < s^* < t^*$  at which the expression is zero. If  $\gamma_2 = \gamma_1^*$ , then expression (2) is zero at  $t^*$  so that  $s^* = t^*$ . If  $\gamma_2 \geq \bar{\gamma}_2$ , then expression (2) is never positive, so  $s^* = 0$ . In each case, there is a unique optimal foraging time  $s^*$  under the model;  $s^*$  can be 0, but it cannot be larger than  $t^*$ .

Restriction of the reward rate at source 2 to the range  $\gamma_1^* < \gamma_2 < \bar{\gamma}_2$  makes intuitive sense. If the reward rate on source 2 was no better than the best overall reward rate on source 1 ( $\gamma_2 \leq \gamma_1^*$ ), there would be no reason ever to forage on source 2. Conversely, if  $\gamma_2 \geq \bar{\gamma}_2$ , then the value of information about source 2 is so large that the forager would be better off not foraging at source 1 at all. In that case, we would predict that the forager should just wait at the nest for source 2 to open (under the assumptions of the model, the forager would return immediately from source 1 at each visit without spending any foraging time there).

The analysis for the Constant-unlimited Model is similar, but takes into account the fact that  $r(s) = r_0$  is now constant. Here  $(\gamma_2 - r(s)) TP'(s + \tau) \sigma_P(s + \tau) / (1 + TP'(s + \tau))$  is positive and strictly increasing with limiting value  $(\gamma - r_0)T$ . If  $\gamma_1^* < \gamma_2 \leq r_0(T + \tau)/T$  then  $(\gamma_2 - r_0)T \leq r_0\tau$ , so expression (2) is always positive and  $I(s)$  is strictly increasing for all  $s \geq 0$ . Full details of the model and analysis are given in Collins et al. (2006).

In summary, we conclude the following.

Constant-unlimited model

The time the forager should spend at the food source depends crucially on the reward rate at the potentially opening source 2,  $\gamma_2$ . For  $\gamma_2 > r_0(T + \tau)/T$ , there is an optimal (finite) time the forager should spend at the food source ( $s^*$ ):  $I(s)$  is maximised over  $s \geq 0$  at a unique finite value  $s^*$ . This foraging time  $s^*$  can be 0 if and only if  $\gamma_2 \geq \bar{\gamma}_2$ : this means that the forager never forages for a positive amount of time at source 1 if the reward rate of source 2 is higher than a particular value ( $\bar{\gamma}_2$ ).

For smaller reward rates at source 2 (but still higher than reward rate at source 1), i.e.  $\gamma_1^* \leq \gamma_2 \leq r_0(T + \tau)/T$ , the delivery rate  $I(s)$  is strictly increasing for all  $s \geq 0$ , so the optimal

overall delivery rate is  $r_0$  and  $s^*=t^*=\infty$ . This means that the longer the forager stays at the food source, the higher its delivery rate will be, similar to the case with just a single source.

### Diminishing returns model

Given diminishing returns at the food source, there is always an optimal time the forager should spend at the food source:  $I(s)$  is maximised over  $s \geq 0$  at a unique finite value  $s^*$ . This  $s^*=0$  if and only if  $\gamma_2 \geq \bar{\gamma}_2$ , which is the same as above. If the reward rate at source 2 is equal to the maximal reward rate achieved at source 1,  $\gamma_2 = \gamma_1^*$ , then the forager should not reduce its foraging time (and thus load) compared to the situation with only one food source (or with no information):  $s^*=t^*$ . On the other hand, if the reward rate is between these two values ( $\gamma_1^* < \gamma_2 < \bar{\gamma}_2$ ), then the forager should forage at source 1 with a reduced foraging time ( $0 < s^* < t^*$ ), and thus carry reduced loads and have a reduced delivery rate at source 1 in response to the potential gain of information.

Thus, our two-source model leads to a clear and surprising prediction about optimal foraging behaviour: under most conditions, the optimal time at source 1,  $s^*$ , is finite and smaller than  $t^*$ , i.e. a forager behaving optimally should return to the nest with what might seem to be a suboptimal load (less than optimal if there was no information exchange) to check for new information. Also, the possibility that information might be present at the nest ensures that  $s^*$  is finite for most parameter values even in the Constant-unlimited Model where  $r(t)$  is constant. For the Constant-unlimited Model, this contrasts sharply with the situation without potential information transfer where the optimal time at the food source is  $t^*=\infty$ .

### Effect of parameters

The two-source model also makes clear predictions about the dependence of the optimal foraging time  $s^*$  and the optimal overall delivery rate  $I(s^*)$  on the parameters  $\gamma_2$ ,  $T$  and  $\lambda$ , all of which describe the behaviour of source 2. In all three models, the optimal foraging time  $s^*$  on source 1 is strictly decreasing with each of the parameters  $\gamma_2$ ,  $T$  and  $\lambda$ , and the optimal overall delivery rate is strictly increasing with these parameters (in each case for fixed values of the other two parameters), except at values where  $s^*=0$  (in this case  $s^*$  remains 0 as  $\gamma_2$ ,  $T$  or  $\lambda$  increase). For the Constant-unlimited Model, if  $s^*=\infty$ , the optimal foraging time remains unbounded and the optimal overall delivery rate remains constant at  $r_0$  for increases in  $\gamma_2$ ,  $T$  or  $\lambda$ . Thus, in all cases where the forager forages at source 1 at all ( $s^*>0$ , and for a finite time), a forager acting optimally will spend strictly less time per trip on source 1 and will do strictly better overall, as each parameter increases.

These results make intuitive sense. As its reward rate  $\gamma_2$  increases, source 2 becomes more attractive; as  $T$  increases, source 2 effectively becomes more valuable as it is available for longer; as  $\lambda$  increases, the frequency of availability of source 2 increases. In each case, information indicating the availability of source 2 becomes more valuable or is more likely to be present, and foraging on source 1 is terminated as a result ( $s^*$  is smaller). Note that in the cases  $T=0$  and/or  $\lambda=0$ , the duration and/or the frequency of availability of source 2 is zero, and the model predicts that the forager behaves as if only source 1 was available. Similarly, if  $\gamma_2 = \gamma_1^*$ , so the rate of reward on source 2 is exactly equal to the maximum rate of reward on source 1, then again the model predicts that  $s^*=t^*$  and  $I^*=\gamma_1^*$  so that the forager's optimal behaviour is the same as under the single source model and the optimal delivery rate is also the same.

Finally, we note that although the optimal foraging time also depends on the travel time  $\tau$ , we cannot universally characterise this dependence in the same clear way we characterised the dependence on  $\gamma_2$ ,  $T$  and  $\lambda$ . Sometimes the dependence is straightforward; for example, for the parameter values used in the Constant-unlimited case in the numerical illustration in the next section, the optimal foraging time  $s^*$  increases monotonically from zero to infinity as  $\tau$  increases from zero to 120 min. However, quantities of interest, such as the bound  $\bar{\gamma}_2$  determining conditions under which the forager should return immediately, do not necessarily change monotonically with increasing  $\tau$ . Thus, even for the Constant-unlimited Model, it is not hard to construct parameter combinations for which  $s^*$  first increases with  $\tau$ , then decreases to zero, before finally increasing to infinity as  $r_0(T+\tau)/T$  increases to  $\gamma_2$ . (More details on the derivation of the parameter effects can be found in the [Appendix](#) and in Collins et al. 2006).

### Numerical illustration

We have shown analytically that, under our model, central-place foragers should depart earlier from a food source when they have the possibility of receiving information. To determine *how much* earlier the forager should depart, and which parameters have a biologically relevant effect, we computed specific values for  $s^*$  under various conditions appropriate to foraging in honeybees. The parameter values, as well as their ranges, were estimated from the honeybee literature (Seeley 1985, 1995) (Table 1). Similar computations could be made for other systems; we chose honeybees because they are well studied (thus, we can estimate the relevant parameters with some confidence) and because reasons for their 'partial loads' have been debated previously.

**Table 1** Parameters used in the model

Parameter description	Values	
Source 1		
Travel time	$\tau$	(6 min)
Quality of the food source	$r_0$	(1 $\mu\text{l}/\text{min}$ )
Constant-unlimited		
Reward rate on source 1	$r(t)$	$=r_0$
Gain at source 1	$G(t)$	$=r_0 t$
Diminishing returns		
Reward rate on source 1	$r(t)$	$= r_0 \alpha t^{(\alpha-1)}$
Parameter that determines shape of $r(t)$	$\alpha$	$=5/6$
Gain at source 1	$G(t)$	$= r_0 t^\alpha$
Capacity-limited		
Reward rate on source 1	$r(t)$	$= r_0 / (1 + e^{(t-\mu)})$
Threshold at which rate of gain decreases	$G(\mu)$	(80 $\mu\text{l}$ )
Source 2		
Total availability of source 2 (during this time multiple trips can be made)	$T$	(120 min)
Reward rate on source 2	$\gamma_2$	( $2\gamma_1^*$ )
1/(expected time to next source 2 becoming available)	$\lambda$	( $1/60 \text{ min}^{-1}$ )
Probability that information on an active source 2 is available when the forager returns	$P(s)$	$= 1 - e^{(-\lambda s)}$

The numbers in brackets indicate which values were used to find numerical results; they are estimated from the literature on nectar foraging honey bees (Frisch 1967; Seeley 1985, 1995).

**Effects on honeybee foraging**

Should honeybees load their crop to capacity at a food source or return home early if they may receive information about a better food source from nestmates? All three models of reward dynamics predict that honeybees should

reduce their foraging time at source 1, and thus their load, to a remarkable degree (Table 2). With standard decreasing returns (Diminishing Returns Model), the optimal load is even smaller than with constant reward rate up to a maximal load (Capacity-limited Model). However, the values shown in Table 2 apply only to a specific situation in which a better source can be expected to become available every 60 min ( $1/\lambda$ ), last for 120 min ( $T$ ), and supply reward at twice the maximal delivery rate achieved under a model with only one source (i.e. relative reward rate  $\gamma_2/\gamma_1^*=2$ ). In Fig. 3 we show how the optimal time at the food source will change if these parameters are modified.

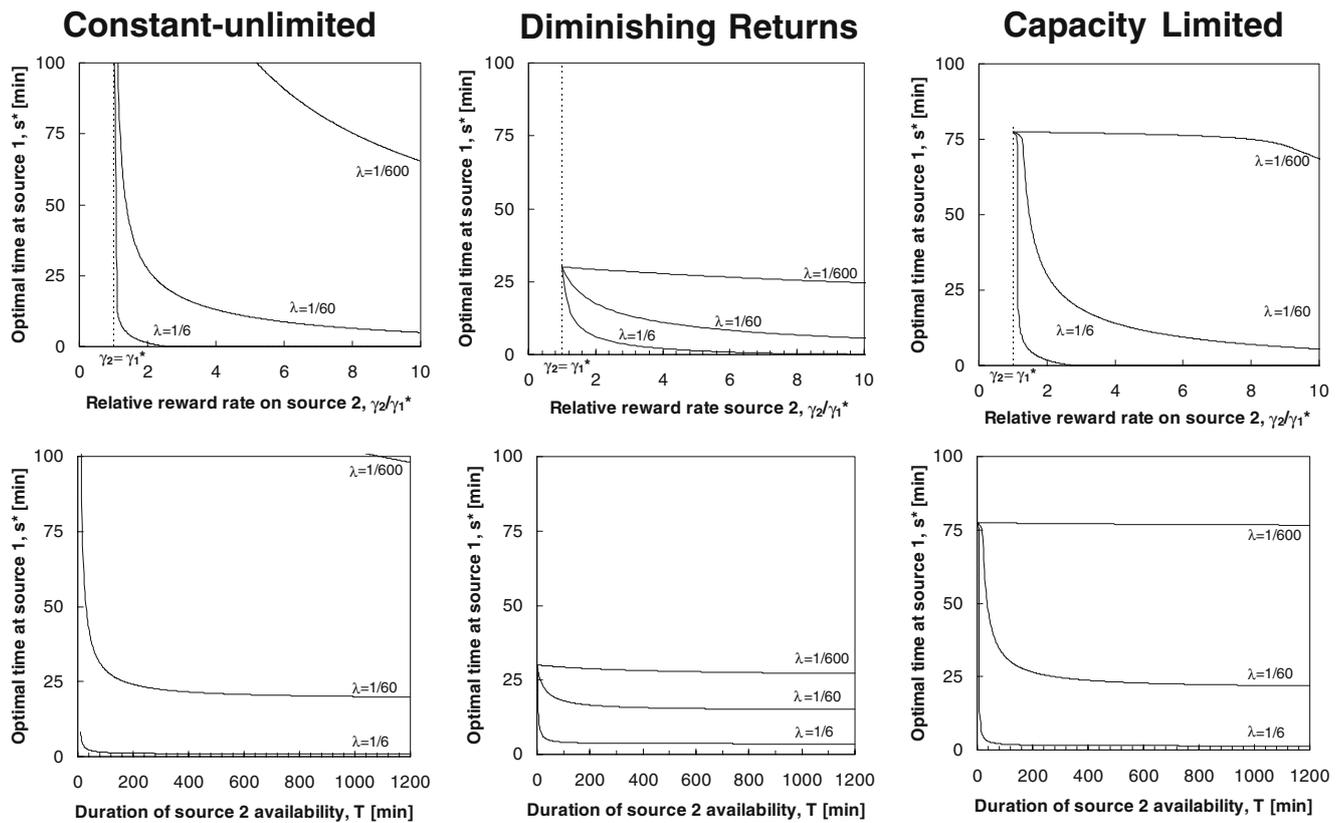
All three models predict a substantial decrease in foraging time  $s^*$ , and thus load,  $G(s^*)$ , with increasing quality  $\gamma_2$  of source 2. They also predict a reduction in foraging time with the duration  $T$  for which source 2 is available, although there is not much more change in  $s^*$  once  $T$  exceeds 120 min. Low values for  $1/\lambda$ , i.e. new sources becoming available frequently, lead to a decrease in optimal foraging time. However, natural food sources may often become available at lower frequencies than every hour, in which case we would expect foragers to adopt higher loads. Indeed, if a new food source was on average only expected every day ( $\lambda=1/600 \text{ min}$ ), then foragers should not reduce their foraging time much at all ( $s^*$  becomes similar to  $t^*$ ).

Finally, travel time to the food source also has an effect on optimal foraging time. If travel time is longer, foragers should generally stay longer at the food source to achieve larger loads (with both the Diminishing Returns and the Capacity-limited models and with or without information transfer). As the Diminishing Returns model assumes a decreasing reward rate as the forager spends more time foraging, optimal loads are low with short travel times even without information

**Table 2** Numerical predictions of the different models using the default values of  $T$ ,  $\gamma_2$ ,  $\lambda$ ,  $r_0$  and  $\tau$  that were estimated for honeybees

		Constant-unlimited	Diminishing returns	Capacity-limited
Without information transfer				
Optimal time at source 1	$t^*$	$\infty$	30 min	77 min
Overall delivery rate	$\gamma_1^*$	1 $\mu\text{l min}^{-1}$	0.47 $\mu\text{l min}^{-1}$	0.93 $\mu\text{l min}^{-1}$
Resulting load	$G(t^*)$	$\infty$	17 $\mu\text{l}$	77 $\mu\text{l}$
With information transfer				
Optimal time at source 1	$s^*$	27 min	18 min	30 min
Resulting load	$G(s^*)$	27 $\mu\text{l}$	11 $\mu\text{l}$	30 $\mu\text{l}$
Overall delivery rate	$I(s^*)$	1.53 $\mu\text{l min}^{-1}$	0.76 $\mu\text{l min}^{-1}$	1.45 $\mu\text{l min}^{-1}$
Percentage decrease in load per trip	$G(t^*)-G(s^*)/G(t^*)$		35%	61%
Percentage increase in delivery rate by reducing load per trip	$I(s^*)-I(t^*)/I(t^*)$	53%	1%	3%

Overall delivery rates [ $\gamma_1^*$  and  $I(s^*)$ ] include travel time;  $I(s^*)$  is computed over a whole cycle including several trips to source 1 and one period of source 2 being available (may also include several trips).



**Fig. 3** Numerical results for  $s^*$  (the optimal foraging time on source 1) as it depends on  $T$  (the duration that source 2 is available),  $\lambda$  (the rate at which it becomes available), and  $\gamma_2/\gamma_1^*$  (the relative reward rate on source 2 compared to the maximum delivery rate on source 1).

$T$  has practically no influence at all from 120 to 1,200 min; with increasing  $\lambda$ ,  $s^*$  decreases; and with a higher reward rate at source 2,  $s^*$  decreases as well. With high  $\lambda$  and high relative reward rate at source 2, the forager quickly stops visiting source 1 at all ( $s^*=0$ )

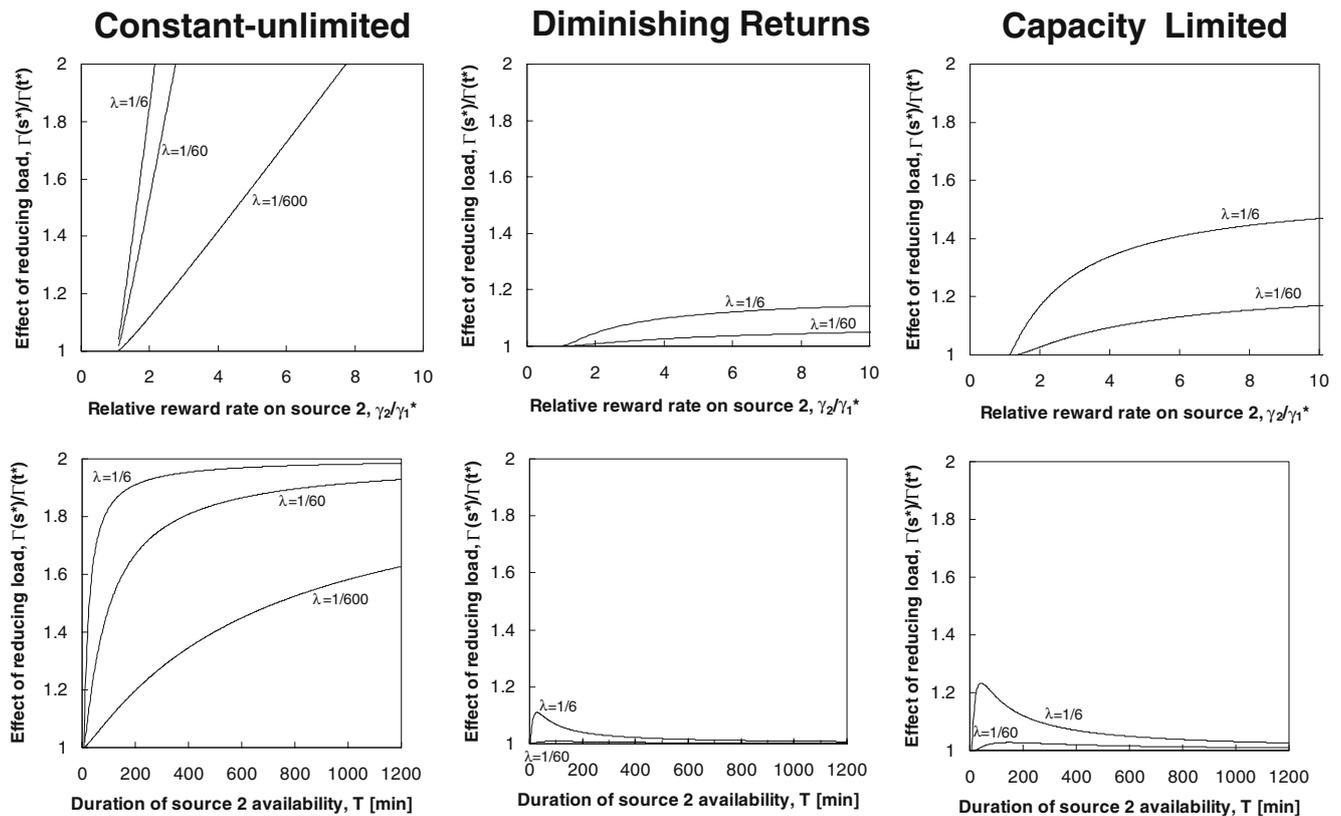
transfer. For example, if travel time is increased from 3 to 30 min, the optimal load,  $G(t^*)$ , increases from 10 to 65  $\mu\text{l}$ . With information about a superior food source potentially becoming available, loads increase even more slowly with travel time: from 7  $\mu\text{l}$  at  $\tau=3$  min to 26  $\mu\text{l}$  at  $\tau=30$  min. In the Capacity-limited model, however, reward rate initially stays constant, and thus travel time has no great effect on time spent foraging per trip if there is no potential information transfer:  $G(t^*)$  only changes from 77 to 79  $\mu\text{l}$  over the same range of travel times. With information transfer, loads increase rapidly with travel time:  $G(s^*)$  increases from 21 to 77  $\mu\text{l}$ .

Our two-source model thus predicts a significant reduction in optimal loads and foraging times for many conditions. However, it is important also to quantify the effect of such load reduction on foraging success. The optimal overall delivery rate (i.e. the maximal reward that can be collected per unit time),  $\Gamma(s^*)$ , increases on the single source value  $\Gamma(t^*)$  only by 1% (Diminishing Returns Model) or 3% (Capacity-limited Model) if foraging time at source 1, and thus load, is reduced (Table 2). The benefit of reducing load is much higher in the Constant-unlimited

Model, but this is under the condition that an infinite load can be collected, which will not be met in a real biological system. Even with a substantial reduction in load, the benefits in terms of increased delivery rate, which reflects foraging success, are thus not very high in these numerical examples. They are highest when new food sources are available for intermediate durations (about 100–200 min, Fig. 4). They also increase with higher food source variability (if the new source has a reward rate many times higher than the current one). Benefits of load reduction also increase with higher probability of new food sources becoming available.

### Other numerical results

Load sizes and recruitment have also been studied in social foragers other than honeybees. One example for which some of the relevant parameters can be estimated is foraging by leafcutter ants. These ants cut leaves into fragments which they then transport to their nest. They also use communication by pheromone trails and substrate



**Fig. 4** Numerical results on how the effect of reducing load on overall delivery rate (reward collected from both sources per unit time) changes with  $\lambda$ ,  $\gamma_2/\gamma_1^*$  and  $T$ . Y-axes show  $I(s^*)/I(t^*)$ , i.e. the ratio of delivery rate with reduced load (foraging time  $s^*$ ) to delivery rate with

load optimised for foraging just on source 1 (foraging time  $t^*$ ). High  $I(s^*)/I(t^*)$  thus denote situations where reducing load has high benefits in terms of long-term delivery rate

vibration to recruit nestmates to high-quality food sources (Roces 2002).

Should leafcutter ant foragers reduce load sizes to gain information more quickly? Essentially, our model predicts that they should not. It predicts a trivial decrease in optimal load by 0.05% and thereby an increase in delivery rate of 0.000002%. This is based on using the following rough estimates in the model:  $\tau=12$  min (walking 200 m to a food source with a speed of  $\sim 17$  m/min; a longer travel time is likely to lead to an even smaller reduction in optimal load),  $r_0=15$  mg/min,  $T=600$  min,  $\lambda=1/14,400$  min (if new food sources appear on average every 10 days) and otherwise using the same values as before and the Diminishing Returns Model as the reward function (parameters estimated from Rocés and Núñez 1993; Howard 2001; Rocés 2002).

## Discussion

We have shown that central place foragers may well do better by trading material goods for valuable information. More specifically, they can profit by reducing the time they

spend at a food source, and collecting less forage, to gain information about new profitable food sources from other foragers at their common central place. Our model applies with only minimal assumptions on the shape of the reward function  $r(t)$ . The assumption that source 2 becomes available at constant rate  $\lambda$  can also be relaxed. All animals that forage from a central place that also allows information transfer may, therefore, benefit from a reduction in foraging time at a patch.

We do not address in this paper any costs of information transfer, or any implications these different load patterns may have on mortality rates, and hence on optimal behaviour in a broader context (Houston et al. 1988). Our model has some similarity to a model by Stephens 1987 (see also Stephens and Krebs 1986), in which an animal can forage in one of two locations. In the Stephens Model, one location offers food at a constant probability. The other location switches between two states. The location that switches states is sometimes better and sometimes worse than the location characterised by a constant reward probability. Stephens considers an animal that makes choices at discrete times and shows how the number of consecutive choices of the constant option depends on

environmental parameters. In contrast to our model, in the Stephens Model there is no depletion and the forager consumes food as it finds it rather than bringing it back to a central place. In these respects, his model is not directly comparable to ours. Houston and McNamara (1985) consider a central place forager that brings back at most a single item and incurs a cost by being away from the central place. They show that the effect of the cost is to make the animal less selective about its choice of item the longer it has been away from the central place. This could result in the forager returning to the central place with an item that is smaller than would be optimal in the absence of a cost. This result is similar to ours in general, but our present model addresses more specifically the consequences of food source parameters and specifies how the cost of being away changes through information transfer.

For each particular case, our model makes precise predictions about load size and time spent at food patches. In the example of nectar foraging in honeybees, our model predicts a substantial reduction in optimal loads per foraging trip in some situations, particularly at times when good quality food sources are likely to become available frequently. The reduction in load size (compared to optimal load with just one source) is compensated for by an increase in overall delivery rate after switching to a better food source, which is made possible using information received at the colony. This implies that an important function of communication should be the redirection of foragers to the best available sources; this has been shown to be the case in honeybees (Seeley and Visscher 1988).

Our results also imply that if honeybees are found to return from food sources with submaximal loads, a reason for this may be that they can potentially receive information about better food sources at the colony. Such submaximal loads have indeed been shown to occur in honeybees (e.g. Núñez 1970). Submaximal loads have also been observed in leafcutter ants (in the species *Acromyrmex lundii*: Roces and Núñez 1993). The reduction in load observed in ants is, however, larger than what is predicted by our model; so this cannot be explained only by foragers expecting to receive information at the colony.

Various explanations for partial loads observed in social insect foragers have been proposed in the literature (see Introduction). Schmid-Hempel et al. (1985) showed that load size could be predicted on the assumption that bees maximise energetic efficiency instead of delivery rate. For a solitary forager, a lifetime energy budget that cannot be exceeded, i.e. a lifespan limited by energy expenditure, means that maximising energetic efficiency maximises lifetime energetic gain. For a social forager, however, it is not clear why energetic efficiency should be maximised, as maximising lifetime energetic gain does not necessarily maximise colony fitness. Moreover, it has not been shown that the lifespan of

honeybees is limited by energy expenditure (Wolf and Schmid-Hempel 1989). In contrast, the advantages of rapid delivery of food are clear. Núñez (1970) suggests that submaximal loads arise because of the advantages of distributing (rather than receiving) information at the hive. Until now, there have been very few quantitative predictions derived about the effect of information transfer (either by giving or receiving information; see, however, Dechaume-Moncharmont et al. 2005 and below). None of these explanations are mutually exclusive, and all may contribute to a reduction of load size from the maximum.

However, our model also makes predictions about how load size should vary with food source parameters such as reward rate. This can be used to distinguish between hypotheses explaining load size reduction, in particular between the effects of potentially giving information vs potentially receiving information. Our model analyses how much load is reduced to take advantage of receiving information, and predicts that foragers should collect higher loads when they visit better food sources. This is because at an already high-quality food source, a potential new source is not likely to be much better ( $\gamma_2/\gamma_1^*$  small). On the other hand, although a theoretical analysis of information giving would require a more complex model than that presented in this paper, intuition suggests that if load is reduced to recruit nestmates more quickly (giving information), load sizes may be reduced even further at high-quality food sources, because of the higher benefits for the recruits, and thus the colony as a whole. Such a reduction in load size has been demonstrated experimentally in honeybees (Varju and Núñez 1993).

Similarly, submaximal loads in leafcutter ants have been observed particularly at very high-quality food sources (Roces and Núñez 1993), consistent with the hypothesis that foragers may recruit other nestmates (Roces and Núñez 1993; Roces 1994, 2002). This explanation has not been studied in a formal model, and other hypotheses exist involving mass-dependent cost (Kacelnik 1993; Clark and Kacelnik 1994) or interactions with other members of the colony (Burd 1996b; Burd and Howard 2005). However, empirical data do not support mass-dependent costs for leafcutter ants (Roces and Núñez 1993; Roces 1994). It is also interesting that for a given reward rate function at source 1, our analysis predicts that similar overall delivery rates can be achieved with very different individual load patterns in the two scenarios, i.e. with or without adjusting load to the possibility of information about source 2. This may mean that the selection pressure on reducing load size in response to potentially available information is not very strong.

Therefore, at least under the conditions studied, receiving information does not explain the observed pattern of load size reduction in honeybees or leafcutter ants. The hypothesis most consistent with available data in these cases thus seems to be

colony-level, rather than individual-level, optimisation of delivery rate (and rate of processing, Burd and Howard 2005). If colony-level delivery rate is maximised, then foragers may change their behaviour to give information to others at a cost to their own delivery rate. The comparison of our model's predictions with empirical results thus indicates that in social insects, giving information may have a larger effect on load size than receiving information. In a sense, social insect foragers would be paying for information delivery to others, rather than paying for getting information themselves. This is an interesting avenue for further study.

As we have already indicated, our model does not assume cooperation between foragers. In non-cooperative foragers, we do not expect individuals to give information to others at a cost to their own delivery rate. But non-cooperative foragers may still be able to get information from others. This may occur, for example, in breeding colonies of birds (Brown et al. 1991), where foragers may return early to the colony to observe whether other birds return from superior food patches. It is necessary to estimate the relevant parameters of forager and food source behaviour to be able to judge the quantitative benefits of reducing load (and foraging time) in any particular case.

A relevant result of our model is the strong dependency of the benefits of information transfer on the reward schedules offered by food sources. With diminishing returns at food sources, foraging times per trip are short anyway, and any additional reductions due to information transfer are likely to be small. If, however, food sources offer an almost fixed reward rate up to a maximum time or load, then foragers are expected to load up to capacity without information transfer, but reduce their load per trip substantially if information may be available at the central place. Different central-place foragers are likely to differ in the way they exploit resources.

It is necessary, therefore, to study the reward schedules of resources to estimate the magnitude of the effects of information transfer in any particular system. Indeed, this may have implications for the evolution of reward production by flowers, for example. Plants will gain more, per unit of investment in nectar, from many short visits by pollinators than from fewer longer visits. Paying for information by sacrificing short-term foraging efficiency may thus be a common phenomenon in group-living animals.

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## Appendix

Effect of parameters on the optimal foraging time and optimal overall reward rate.

We start with the Diminishing Returns and Capacity-limited models. As the optimal foraging time  $s^*$  is the unique value at which expression (2) is zero, we need to determine how this changes with the parameter values. For fixed  $T$  and  $\lambda$ , the second term in expression (2) increases with  $\gamma_2$  for each fixed  $s$ , while the first term stays constant. Thus, if the expression was zero at  $s > 0$  for a given  $\gamma_2$ , then it will be negative at  $s$  for a small increase in the parameter to, say,  $\gamma' < \gamma_2$  and the new zero will be at  $0 < s' < s$ . Thus  $s^*$  decreases with increasing  $\gamma_2$ . The cases  $T$  increasing and  $\lambda$  increasing follow in similar fashion, the latter utilising the fact that  $P(s, \lambda) \sigma_P(s, \lambda) / (1 + T P(s, \lambda))$  increases with  $\lambda$ , where we write  $P(s, \lambda)$  and  $\sigma_P(s, \lambda)$  to explicitly indicate the dependence of these quantities on  $\lambda$ .

To see how the optimal overall reward varies, we consider first  $\gamma_2$  increasing. Write  $I(s, \gamma_2)$  for the overall delivery rate corresponding to foraging for time  $s$  on source 1 for the given value of  $\gamma_2$ , write  $s(\gamma_2)$  for the corresponding optimal foraging time on source 1, and write  $I^*(\gamma_2)$  for the corresponding optimal overall delivery rate. For fixed  $T$  and  $\lambda$ , the derivative of  $I(s, \gamma_2)$  with respect to  $\gamma_2$  is strictly positive, so for each fixed  $s$ ,  $I(s, \gamma_2)$  is strictly increasing in  $\gamma_2$ . Thus for, say,  $\beta > \gamma_2$ ,  $I(s(\gamma_2), \gamma_2) < I(s(\gamma_2), \beta)$ . Moreover,  $I(s(\gamma_2), \beta) < I(s(\beta), \beta)$  from above, as  $s(\beta) < s(\gamma_2)$  from above and  $s(\beta)$  is the unique maximising value for  $I(s, \beta)$ . Thus  $I(s(\gamma_2), \gamma_2) < I(s(\gamma_2), \beta) < I(s(\beta), \beta)$ , implying that the optimal overall delivery rate  $I^*(\gamma_2)$  is strictly increasing in  $\gamma_2$ . The cases  $T$  increasing and  $\lambda$  increasing follow in similar fashion.

Finally, the analysis for the Constant-unlimited Model is similar but slightly more complicated. In this paper,  $\gamma_2 = r_0(T + \tau) / T$  represents the borderline between the unbounded and the finite optimal foraging time cases. When  $s^* = t^* = \infty$  and  $\gamma_2 = r_0(T + \tau) / T$ , then as  $\lambda$  increases for fixed values of the other two parameters, the optimal foraging time remains constant and the optimal overall delivery rate remains constant at  $I^* = r_0$ . However, as each of  $\gamma_2$  and  $T$  increases for fixed values of the other two parameters, the optimal foraging time  $s^*$  becomes strictly decreasing and finite and the optimal overall delivery rate  $I(s^*)$  becomes strictly increasing.

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