

Resource geometry and provisioning routines

Ronald C. Ydenberg and W. Eric Davies

Centre for Wildlife Ecology, Department of Biological Sciences, 8888 University Drive, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6

Provisioners capture items both for delivery and for self-feeding. In doing so, they may travel directly to and from a single location, visit several patches on each excursion from a delivery point, or alternate excursions to different destinations. Prey suitable for self-feeding versus delivery have differing attributes, which means that they are often best sought in different places. Visiting separate patches to self-feed and to load prey for delivery requires more travel time than foraging for both types of prey at a single location, but both self-feeding and loading are faster if carried out in the most suitable patches. Here, we investigate how the distribution of different types of food resources around a central delivery point affects the routine with which a provisioner visits patches to forage. Our results show that each of several basic travel routines is best in some broad region of a parameter space that considers the loading time saved in relation to the extra travel time required. This framework provides a simple explanation for the variety of routines observed in nature and can additionally account for the circumstances under which provisioners concentrate loads for delivery by internal processing, known in some seabirds. *Key words:* central place foraging, delivery, provisioning, seabirds, self-feeding, solitary bees. *[Behav Ecol 21:1170–1178 (2010)]*

Provisioners collect prey or other resources for delivery to offspring, to mates, to a cache, or to a nest site (Ydenberg 2007) and are known to use a variety of travel routines to do so. Some seabirds, for example, make a direct trip to and from specific locations where food is collected (e.g., Weimerskirsch and Robertson 1994), whereas others alternate short and long excursions to different destinations (Baduini and Hyrenbach 2003; Terauds and Gales 2006; Steen et al. 2007). The solitary mason bees *Osmia lignaria* studied by Williams and Tepedino (2003) traveled to widely separated patches of 2 different flower types on each excursion. Here, we investigate how the distribution of patches with different types of food resources around a central delivery point affects the routine or itinerary with which a provisioner visits patches to forage.

The diagnostic feature of provisioning is that items are collected both for delivery (these are not consumed by the provisioner) and for consumption (provisioners must also feed themselves). The process of searching for and consuming items is called “self-feeding,” whereas the process of finding and capturing items for delivery is called “loading.” Delivered food resources may differ from those that are consumed (e.g., Tierney et al. 2008). For example, parents may deliver smaller or more manageable prey than they themselves ingest (e.g., Elgar and Jebb 1999) because some items are too large or tough for offspring to consume. Furthermore, because provisioning often involves strenuous exercise, foods high in carbohydrates are valuable for self-feeding. Those being provisioned are often growing (offspring) or forming clutches of eggs (mates), making food high in protein valuable for delivery. Solitary bees and wasps (Ydenberg and Schmid-Hempel 1994) and Palestine sunbirds (*Nectarinia osea*; Markman et al. 2004) thus feed themselves on nectar but deliver pollen or insects to offspring.

Even in the absence of these considerations, however, foraging theory shows that the prey items best for delivery and those

best for self-feeding will often differ. The basic diet model of foraging theory (Stephens and Krebs 1986) shows that the rate of (self-)feeding is maximized by selecting prey items with sufficiently high profitability (energy per unit handling time). But when items must be transported for delivery, this prey choice criterion is altered—this is the key result of the seminal central place foraging paper by Orians and Pearson (1979). Handling time is unimportant when prey items are transported to a central place, either because it is short relative to travel time or because the provisioner does little of the handling required or both. When a single prey item is loaded for delivery, the selection criterion becomes sufficiently large size rather than profitability. When multiple items are loaded for delivery, energy density and “packing” considerations become important. These differing criteria mean that different kinds or sizes of prey are often best for self-feeding and loading, even if the nutritional requirements and the ability of provisioners and those provisioned to handle prey are identical.

A provisioner could presumably forage in a single patch, self-feeding on and delivering the same prey type. But if different patches have different prey types, an alternative is to visit 2 or more patches to take advantage of the superior characteristics of different prey types for loading and self-feeding. “Multi-patch provisioning” has the advantage that the rates of loading and/or self-feeding are higher than they would be using less-suitable prey, but it requires extra travel time. Here, we present a simple model that asks how much extra travel a provisioner should be willing to undertake in order to exploit different patches good for self-feeding and delivery, as opposed to using a single patch for both.

THE MODEL

Around any central place lies an array of patches containing different types and densities of prey. The patches lie at different distances from the central place and thus require different amounts of travel time. One of the patches in this array has the property that it offers a particular forager the highest self-feeding rate. There will be another patch, likely in a different location, in which can be found the prey most suitable for delivery. Yet other patches are located closer to the delivery

Address correspondence to R.C. Ydenberg. E-mail: ydenberg@sfsu.ca

Received 18 January 2010; revised 25 May 2010; accepted 16 June 2010.

© The Author 2010. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oxfordjournals.org

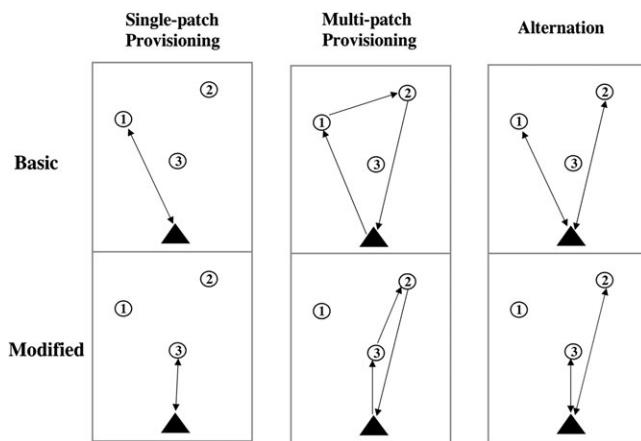


Figure 1

Categorization of basic provisioning routines on a generalized resource geometry. Patch 1 is best for self-feeding, whereas patch 2 is best for capturing prey for delivery. Patch 3 is a self-feeding patch located closer to the central place than patch 1 but is not as rich. The provisioner may exploit the patches using any of the provisioning routines shown. In single-patch provisioning, both self-feeding and delivery prey are collected in patch 1. In multi-patch provisioning, self-feeding is conducted in patch 1, and delivery prey are loaded in patch 2. When “alternating” the provisioner self-feeds and loads in patch 1 and then delivers the load before making a trip to patch 2 where prey are loaded for delivery, and no self-feeding takes place. In modified routines, the provisioner replaces use of patch 1 with patch 3. Patch 3 is inferior to patch 1 but is located closer to the delivery point.

point than either of these patches, but the prey there are scarcer and/or less suitable. The essential feature is that the self-feeding and delivery opportunities and travel costs vary between patches so that no single patch is best in every regard. We refer to this as the “resource geometry.” The simplest and most general situations are diagrammed in Figure 1.

How should a provisioner exploit the resource geometry? It could in principle self-feed or capture resources for delivery (or both) in any patch, but it might be advantageous to self-feed in the patch best for this and then to travel the patch with the most suitable prey for delivery to capture the delivered resource. We analyze this problem, assuming that the internal mechanisms that control this decision evolved under natural selection for maximization of the rate of delivery of the resource to the central place. A further assumption is that the provisioner must balance its own energy budget by spending enough self-feeding time to capture and consume the prey necessary to provide the metabolic energy necessary to power its activities. This approach was first applied by Norberg (1981) and further developed by Houston (1987; see also Ydenberg 2007).

Initially, we require that the provisioner spend some time on each trip to capture and ingest enough prey to power the entire trip. We later relax this requirement. Generally, foragers self-feed prior to loading for delivery, because prey held for delivery interfere with self-feeding, and increase the energetic costs of transport (Brooke 1981; Kacelnik 1984; Krebs and Avery 1985), but this assumption is not essential to the model developed here.

A few remarks on terminology will be helpful at this stage. Baduini and Hyrenbach (2003) review the literature on the provisioning routines of seabirds and give names to the main routines described. These names are based on the duration of provisioning excursions, as measured at breeding colonies. In “unimodal” foraging, the duration of provisioning excursions shows a distribution with a single mode. In “bimodal” or “dual”

foraging, the length of provisioning excursions shows a distribution with 2 distinct modes. The terminology we develop below is based on the locations visited during a provisioning excursion. The correspondence between these names is discussed further below.

In our schematized resource geometry, we denote the patch best for self-feeding as patch 1 (see Figure 1). One-way travel to this patch requires time t_1 (round trip travel requires $2t_1$). The patch best for delivery is denoted as patch 2. One-way travel to this patch requires time t_2 (round trip travel requires $2t_2$). The travel time between patch 1 and patch 2 is Δt . The loading rate of prey for delivery in patch 1 is r_1 , the loading rate of prey for delivery in patch 2 is r_2 (by definition $r_2 > r_1$). All delivered loads are of size L , so loading in patch 1 requires time L/r_1 or time L/r_2 in patch 2. The resultant delivery rate is measured in energy per time unit. The energy expenditure rate while foraging and while traveling is c . The energetic expenditure of travel to patch 1 is $2t_1 c$, and the energetic cost of loading there is cL/r_1 . The net self-feeding rate in patch 1 is s .

Single- and multipatch provisioning

The simplest provisioning routine is “single-patch provisioning,” in which the forager visits a single patch for both self-feeding and for delivery. The forager travels to patch 1, self-feeds, collects a load of size L and then returns to the central place to deliver it. (We treat the question of whether the forager could better self-feed and provision from patch 2 below under “Modified Provisioning.”) The rate of delivery is found by dividing the size of the delivery by the total time required, including round-trip travel time, loading time, and self-feeding time. Self-feeding requires time $2t_1 c/s$ to recover the costs of travel and time cL/sr_1 to recover the loading cost. The rate of delivery D_S is

$$D_S = \frac{L}{L/r_1 + 2t_1 + cL/sr_1 + c2t_1/s},$$

which is conveniently written as

$$D_S = \frac{L}{(1 + c/s)(L/r_1 + 2t_1)}. \quad (1)$$

The factor c/s is the self-feeding time required per unit energy expenditure while loading and traveling. The term $(1 + c/s)$ increases the time required for the travel and loading portions of the trip by that required for self-feeding. We use the general form of (1) in the equations derived below.

When multipatch provisioning, the forager travels first to patch 1 (travel time t_1), where it self-feeds to finance the energetic expense of the entire trip, then travels to patch 2 (travel time Δt) to collect a load of size L (time L/r_2) before returning to the delivery point (travel time t_2). The self-feeding time recovers the energetic costs of each of these components of the round trip. The rate of delivery is

$$D_M = \frac{L}{(1 + c/s)(L/r_2 + t_1 + \Delta t + t_2)}. \quad (2)$$

Single-patch and multipatch provisioning have different characteristics. By assumption, prey for delivery can be loaded more quickly in patch 2 than in patch 1. The extra time that loading in patch 1 requires compared with patch 2 ($L/r_1 - L/r_2$) is called the “loading penalty” and plays a central role in our analysis. Multipatch provisioning avoids the loading penalty, but the round-trip travel time is greater, and the self-feeding time required to power the trip also differs. For single-patch provisioning, the required self-feeding time

is $(c/s)(L/r_1 + 2t_1)$; for multipatch foraging, the required self-feeding time is $(c/s)(L/r_2 + t_1 + \Delta t + t_2)$.

To find the conditions under which multipatch foraging yields a higher delivery rate than single-patch foraging, we solve $D_M > D_S$, which gives

$$\frac{L}{r_1} - \frac{L}{r_2} > \Delta t + t_2 - t_1. \quad (3)$$

The left-hand side (LHS) of (3) is the loading penalty, whereas the right-hand side (RHS) represents the extra travel time required for multipatch provisioning. The inequality confirms that multipatch provisioning performs better (i.e., yields higher delivery rate) when the time saved by loading prey in patch 2 rather than in patch 1 outweighs the extra travel time required.

Alternation

We now relax the assumption that the provisioner must balance its energy budget on every trip. It may self-feed only on every other trip, or even less frequently, by traveling to the self-feeding patch only on every n th excursion from the central place. There it both self-feeds and collects a load of size L for delivery. On the next $n-1$ trips, it travels to the delivery patch where a load is collected and delivered without any self-feeding. We call this " n -alternation," where n is the number of trips in a complete cycle (i.e., 2-alternation means every other trip is made to the self-feeding patch, 3-alternation means every third trip, and so on).

When alternating, the provisioner does enough self-feeding on the visit to patch 1 to finance all the trips in a cycle, which in the case of 2-alternation requires time $2t_1c/s + 2t_2c/s$ to recover the costs of travel and time $cL/sr_1 + cL/sr_2$ to recover the loading costs. The consequent rate of delivery is

$$D_{A2} = \frac{2L}{(1 + c/s)(L/r_1 + L/r_2 + 2t_1 + 2t_2)}. \quad (4)$$

To delineate conditions under which 2-alternation performs best, we compare it with single-patch provisioning and with multipatch provisioning. To find conditions under which 2-alternation yields higher delivery rate than single-patch provisioning, we set $D_{A2} > D_S$, which gives

$$\frac{L}{r_1} - \frac{L}{r_2} > 2(t_2 - t_1), \quad (5)$$

meaning that 2-alternation is favored over single-patch provisioning when the loading penalty is greater than $2(t_2 - t_1)$, which is the difference in total travel time between 2-alternation and 2 successive single-patch trips. Note that alternation always attains higher delivery rate than single-patch provisioning if patch 1 (the self-feeding patch) is more distant (because then RHS < 0, whereas LHS is by definition >0).

To find when 2-alternation yields higher delivery rate than multipatch provisioning, we solve $D_{A2} > D_M$, which gives the condition

$$\frac{L}{r_1} - \frac{L}{r_2} < 2\Delta t, \quad (6)$$

meaning that 2-alternation is favored when the loading penalty is less than $2\Delta t$, which is the difference in total travel time between 2-alternation and 2 successive multipatch trips. Figure 2 gives a graphical representation, showing regions of the parameter space in which single-patch provisioning, multipatch provisioning, and 2-alternation maximize the delivery rate.

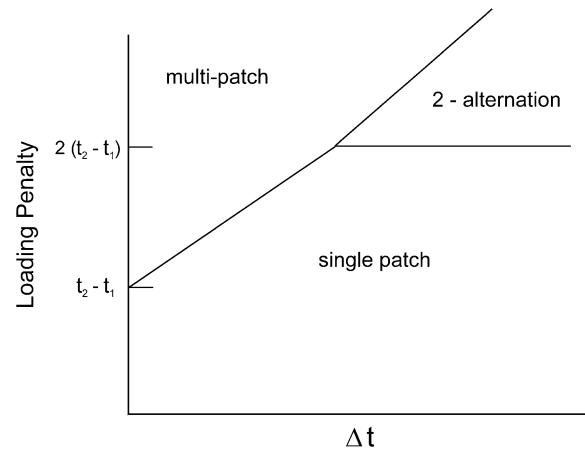


Figure 2

When provisioners should use single-patch provisioning, multipatch provisioning, or 2-alternation. Single-patch provisioning is used when the loading penalty is small relative to the extra travel involved. Multipatch provisioning is favored when the loading penalty is large relative to the extra travel involved. Two-alternation is favored in between the 2 in a region that expands with Δt . In the case pictured here $t_2 - t_1 > 0$ (i.e., the self-feeding patch is less distant than the delivery patch).

The lower boundary of the 2-alternation space is defined by inequality (5), formed by a horizontal line with height $2(t_2 - t_1)$; whereas the upper boundary of the 2-alternation region is defined by inequality (6), formed by a line from the origin with slope 2.

A provisioner may travel to the self-feeding patch less frequently than on alternate trips. For example, in 3-alternation (i.e., a self-feeding excursion is made only on every third trip), the rate of delivery is

$$D_{A3} = \frac{3L}{(1 + c/s)(L/r_1 + 2L/r_2 + 2t_1 + 4t_2)}. \quad (7)$$

In general, the rate of delivery attained by n -alternation is

$$D_{An} = \frac{nL}{(1 + c/s)(L/r_1 + (n-1)L/r_2 + 2t_1 + 2(n-1)t_2)}. \quad (8)$$

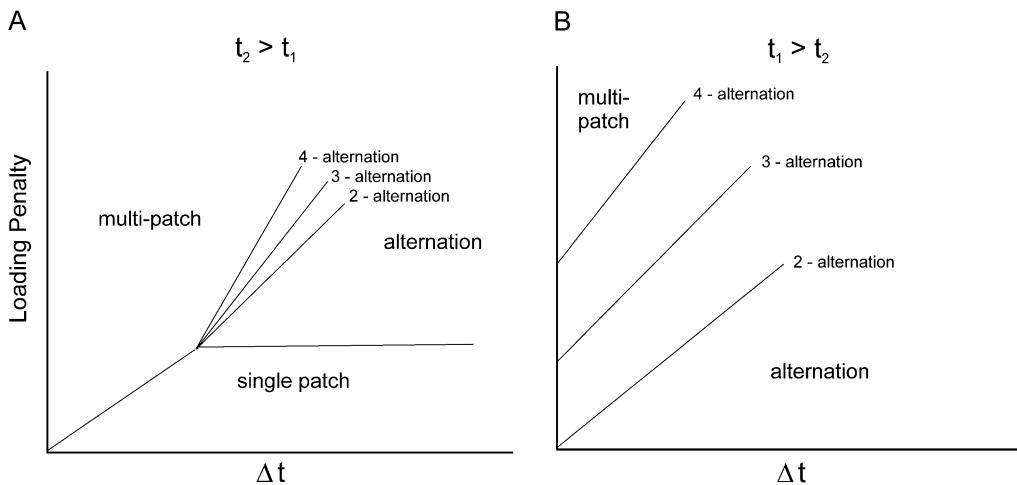
The boundary separating the n -alternation and single-patch provisioning regions is found by setting $D_{An} > D_S$, which gives

$$\frac{L}{r_1} - \frac{L}{r_2} > 2(t_2 - t_1) \quad (9)$$

The position of this boundary is therefore independent of the value of n . The position of the boundary between the alternation and multipatch regions is found by setting $D_{An} > D_M$, which yields

$$\frac{L}{r_1} - \frac{L}{r_2} < n\Delta t + (n-2)(t_1 - t_2) \quad (10)$$

Both the slope (equal to n) and intercept (given by $[n-2](t_1 - t_2)$) of the boundary are affected by the value of n . For example, the upper boundary for 3-alternation is $3\Delta t + (t_1 - t_2)$, whereas the boundary between 4-alternation and multipatch foraging is $4\Delta t + 2(t_1 - t_2)$. The basic effect is

**Figure 3**

The effect of n on the n -alternation region, for cases when $t_2 > t_1$ (i.e., the self-feeding patch is less distant than the delivery patch; Panel A) and $t_1 > t_2$ (i.e., the self-feeding patch more distant; Panel B). Note that single-patch provisioning does not occur in the latter case (see inequalities 5 and 9). In both cases, n increases the size of the region and the region expands with Δt .

that as n increases the size of the region in which alternation is preferred over multipatch provisioning enlarges. The reason is that less-frequent trips to the self-feeding patch make a larger loading penalty acceptable. Note also that the effect of n on the alternation region differs somewhat when patch 1 is less distant than patch 2 (i.e., $t_1 - t_2$ is negative) than when patch 1 is more distant (i.e., $t_1 - t_2$ positive; see Figure 3).

Two conditions combine to create the circumstances under which alternation performs best as a provisioning strategy. First, the loading penalty must be of moderate magnitude. If it is small single-patch provisioning is favored, and if it is large multipatch provisioning is favored. Secondly, the self-feeding and delivery patches must be widely separated; if they are close together, multi-patch provisioning is favored because it avoids the loading penalty.

The value of n that maximizes the rate of delivery can be investigated by finding the circumstances under which $D_{An+1} > D_{An}$. We solve this first of all for $n = 2$ and find

$$\frac{L}{r_1} - \frac{L}{r_2} > 2(t_2 - t_1) \quad (11)$$

The solution is identical for $n = 2, 3, 4 \dots$ meaning that if 2-alternation performs better than single-patch foraging then $n + 1$ -alternation performs better than n -alternation. Thus, when alternating, provisioners should make as many successive visits to the delivery patch as possible. Considerations not included in the model, likely the extra energetic cost of transporting the fuel for several excursions, may restrict the number of delivery patch visits that can be made between visits to the self-feeding patch. The energetic cost of carrying the fuel as well as of the load to be delivered point are likely important factors for any provisioner (see Houston 1993; Rands et al. 2000).

Processing prey for delivery

Some provisioners prepare or process prey before delivery by removing nonessential or less valuable portions of prey items (Kaspari 1991; Rands et al. 2000). The effect is to concentrate the energy and nutrients of the delivered load. The type of processing modeled by Kaspari (1991) and Rands et al. (2000)

requires extra handling time. Here, we consider the case in which processing proceeds internally while foraging, by biochemical alteration of ingested prey to concentrate energy, as in some seabirds (Roby et al. 1997). This process concentrates the energy and nutrients of the delivered load, and we assume that there are no extra time costs. Processing concentrates the load for delivery by a factor f , resulting in eventual delivery of a load with energy fL (see Ydenberg 1994).

Internal processing of prey for delivery requires ingestion and is therefore best fulfilled by profitable (self-feeding) prey. This means that prey for processing are best captured on trips to patch 1 rather than on trips to patch 2 as the self-feeding rate is by definition highest in patch 1. When processing, a single-patch provisioner travels to patch 1, where it both self-feeds and loads prey for delivery, concentrating the latter by a factor f . The load requires time fL/s to collect and time $2t_1$ for round trip travel to the patch. Self-feeding to finance the trip requires time $2t_1 c/s$ to recover the costs of travel and time $c f L/s^2$ to recover the loading costs. The rate of delivery is

$$D_{SP} = \frac{fL}{(1 + c/s)(fL/s + 2t_1)}. \quad (12)$$

By comparing Equation 12 with Equation 1, we find that (when single-patch provisioning) processing prey yields higher delivery rate than the delivery of unprocessed prey when

$$\frac{L}{s} - \frac{L}{r_2} < \frac{(f-1)}{f} 2t_1. \quad (13)$$

In this case, the loading penalty (LHS of 12) is the extra time required to collect a load of size L in patch 1 by ingesting rather than loading prey. The RHS of Equation 12 is the (per excursion) travel time saving over that required to collect f loads without processing. This inequality suggests that distant self-feeding patches (i.e., long travel time to patch 1) favor the delivery of processed prey, as do large concentration factors (i.e., high f). This result is basically identical to that reached previously by Ydenberg (1994; though notation differs somewhat).

This analysis considers processing in the context of single-patch provisioning. What about other routines? Single-patch

provisioning with processing and multipatch foraging can be compared using Equation 12 and Equation 2. Processing gives higher delivery when $D_{SP} > D_M$, which is true when

$$\frac{L}{s} - \frac{L}{r_2} < \Delta t + t_2 + \frac{(f-2)}{f} t_1. \quad (14)$$

Note that when $f = 1$ (i.e., no processing), inequality (14) is identical to inequality (3). As f increases in value, the intercept of the boundary separating the single-patch and multipatch regions rises from $(t_2 - t_1)$ when $f = 1$, to t_2 (when $f = 2$), to $(t_2 + t_1/3)$ (when $f = 3$), to $(t_2 + t_1/2)$ (when $f = 4$) and so on, converging on $(t_2 + t_1)$.

We next consider processing in association with 2-alternation, as recorded in some seabirds (Baduini and Hyrenbach 2003; Terauds and Gales 2006). The provisioner travels to patch 1, where it self-feeds and collects prey for delivery, processing them as before. The load in patch 1 requires time fL/s to collect, and time $2t_1$ for round trip travel to the patch. The provisioner does enough self-feeding to finance the trip, as well as the subsequent excursion to patch 2, which requires time $2t_1c/s + 2t_2c/s$ to recover the costs of travel, and time $cL/s^2 + cL/sr_2$ to recover the loading costs. The provisioner then makes a round trip to patch 2 where a load is collected without any self-feeding or processing. The consequent rate of delivery rate of alternation with processing is

$$D_{AP} = \frac{fL + L}{(1 + c/s)(fL/s + L/r_2 + 2t_1 + 2t_2)}. \quad (15)$$

To discover when processing is advantageous, we compare this to the delivery rate of alternation without processing (Equation 4); $D_{AP} > D_{A2}$ when

$$\frac{L}{s} - \frac{L}{r_2} > 2(t_2 + t_1). \quad (16)$$

Note that there is no dependence on f . We also compare 2-alternation with processing to multipatch foraging by setting $D_{AP} > D_M$, which yields the condition

$$\frac{L}{s} - \frac{L}{r_2} < \frac{(f+1)}{f} \Delta t + \frac{(f-1)}{f} (t_1 + t_2). \quad (17)$$

Results are shown in Figure 4. Inequality (16) reveals that processing should occur in combination with 2-alternation when the loading penalty exceeds the sum of the round-trip travel times. Inequality (17) defines the boundary with the multipatch provisioning region, which changes with the concentration factor f . To understand its influence, we note first of all that when $f = 1$ (i.e., no processing of prey), inequality (17) is identical to inequality (6). As f increases in value (i.e., prey are increasingly concentrated for delivery), the slope of the boundary falls from 2 and approaches 1; the intercept rises from 0 when $f = 1$, to $(t_1 + t_2)/2$ when $f = 2$, to $(2/3)(t_1 + t_2)$ when $f = 3$, to $(3/4)(t_1 + t_2)$ when $f = 4$, and so on, converging on $(t_1 + t_2)$. Inequalities (16) and (17) are easily generalized to the case of n -alternation.

The value of f that maximizes the rate of delivery is found by comparing 2-alternation with $f+1$ processing (i.e., concentrating the load delivered from patch 1 by a factor of $f+1$) and 2-alternation with f processing. The solution to this inequality is identical to (13), meaning that if processing is favored at all then greater concentration of prey is favored.

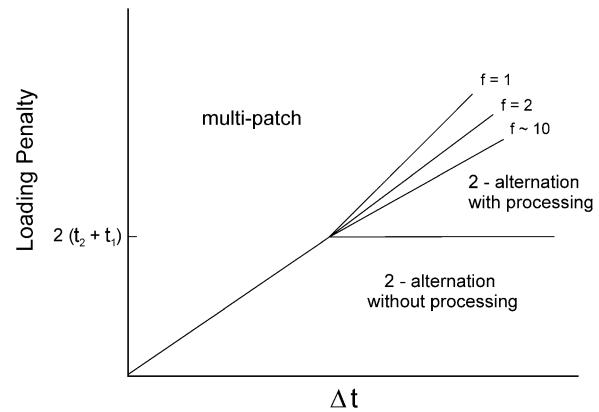


Figure 4

When a provisioning seabird should process loads for delivery. Processing with 2-alternation occurs in a region with the lower boundary given by inequality (13) and the upper boundary by inequality (14). The effect of the concentration factor f on the position of the upper boundary is indicated.

“Modified” provisioning routines

The analysis so far requires the provisioner to self-feed at patch 1 and asks when it should add extra travel to capture prey for delivery at patch 2. We can also ask if there are circumstances under which the provisioner should forego self-feeding at patch 1 if the total travel time could be reduced by self-feeding at a less suitable but closer patch elsewhere. In the generalized resource geometry shown in Figure 1 this option is created by the existence of patch 3. Patch 3 lies closer to the delivery point than patch 1 but is of poorer quality. The use of patch 3 for self-feeding in place of patch 1 reduces the total travel time, but as patch 3 is of poorer quality the self-feeding rate is lower and hence more self-feeding time is necessary. We term routines that incorporate patch 3 in place of patch 1 modified provisioning.

We develop only the basic equation here, asking whether a provisioner should single-patch provision from a near or distant patch (cf. Figure 1a,d). Call the one-way travel time to patch 3 t_3 ($t_3 < t_1$), the loading rate attainable there r_3 ($r_3 < r_2$) and the self-feeding rate s_3 . By definition, $s_3 < s$, the self-feeding rate in patch 1. The delivery rate attainable by single-patch provisioning in patch 1 (D_S) is given by Equation 1 and that attainable by modified single-patch provisioning is

$$D_{Sm} = \frac{L}{(1 + c/s_3)(L/r_3 + 2t_3)}. \quad (18)$$

Modified single-patch provisioning performs better when $D_{Sm} > D_S$, the routines compared in Figure 1a,d. This comparison yields

$$(1 + c/s_3 - c/s) < \frac{(L/r_1 + 2t_1)}{(L/r_3 + 2t_3)}. \quad (19)$$

Note that $(1 + c/s_3 - c/s) = (1 + c/s_3)/(1 + c/s)$. Inequality (19) says that modified single-patch provisioning is preferred when the relative increase in self-feeding time is less than the relative decrease in the travel plus loading time of the 2 routines being compared.

The same logic can be applied to find when multi-patch provisioning should be modified (cf. Figure 1b,e) and when 2-alternation should be modified (cf. Figure 1c,f). By substituting s_2 (self-feeding rate in patch 2; by definition $s_2 < s$) for s_3 and t_2 for t_3 in inequality (19), this logic also

applies to the question of whether the forager could better self-feed and provision from patch 2 than from patch 1. In all cases, the result is analogous to inequality (19): the modified routine is preferred when the relative increase in self-feeding time is less than the relative decrease in the travel plus loading time of the routines being compared.

DISCUSSION

The differing attributes of prey suitable for self-feeding and delivery mean that they often are best sought in different places. Doing so requires more travel time of a provisioner than foraging for both types of prey at a single location, but the necessary loading time is shorter. It is worth visiting separate patches for loading and self-feeding when the loading penalty (the extra time required to load prey in the self-feeding patch compared with that required in the patch best for loading) is greater than the extra travel time. Our results show that each of several basic provisioning routines (single, multi, alternation, with variations introduced by processing and by modification) is best in some broad region of a parameter space that considers the loading penalty in relation to the extra travel time contingent on the resource geometry. The conditions defining these regions are summarized in Table 1. Properties of the routines are listed in Table 2. A numerical example is shown in Figure 5. In general, single-patch provisioning is preferred when the loading penalty is small and multipatch provisioning when the loading penalty is sufficiently large. Alternation is preferred when the loading penalty is intermediate, and the travel time between the patches is sufficiently large. A larger loading penalty and longer travel time between the patches creates the conditions under which alternation with processing is preferred.

Our model was motivated by data on 5 seabird species on Triangle Island, British Columbia (Davies et al. 2009) showing that in some species, the diets of adults and nestlings are similar and caught at the same location but sharply different and caught at different locations in others (see also Tierney et al. 2008, and references therein). We hypothesize that this arises because the species face differing resource geometries that favor either single-patch or multipatch provisioning. We further anticipate that many provisioning species are able to assess the resource geometry and to shift facultatively between the basic routines. For example, Cory's shearwater *Calonectris diomedea* on one breeding colony did not alternate, whereas those on another alternated in 1 of 2 years

Table 2
Characteristics of basic provisioning routines

Routine	Duration	Diets	Deliveries
Single-patch	Unimodal	Same	1
Multipatch	Unimodal	Different	1
Alternation	Bimodal	Same on long trips Differs on short trips	2

The names of the routines are those used here. The column "Duration" describes the shape of the distribution of trip durations and corresponds to the terminology of Baduini and Hyrenbach (2003). The column "Diets" identifies whether the prey delivered (e.g., fed to offspring) are the same as those self-fed on (e.g., eaten by parents). The column "Deliveries" identifies how many kinds of deliveries are made.

(Granadeiro et al. 1998). Tufted puffins (*Fratercula cirrhata*) on Triangle Island, British Columbia fed themselves and nestlings on the same diet (Davies et al. 2009), which suggests single-patch provisioning, whereas parents and nestlings on an Alaskan colony had different diets (Baird 1991), suggesting multipatch foraging.

No studies of seabirds published to date, including those of the previous paragraph, have enough information on the resource geometry to be able to test whether the observed provisioning routines match those predicted by the model developed here. All the basic routines considered here have been described, and the detailed descriptions of provisioning trips by seabirds (e.g., see Figure 6.3 in Williams 1995) that have now been published are suggestive. Alternation has been especially well documented (see Baduini and Hyrenbach 2003; Terauds and Gales 2006). For example, dovekies (*Alle alle*) breeding at Bjørndalen on Spitsbergen make on average 5 successive short (on average 89 min) provisioning trips within the fjord on which the colony is located before making a single long (average 11.5 h) trip out of the fjord to the edge of the continental shelf, 150 km distant (Steen et al. 2007; this would be termed "6-alternation" in the nomenclature developed here). A large energy-rich copepod species (*Calanus hyperboreus*) dominates delivered loads after long trips, whereas a smaller species (*C. glacialis*) dominates after short trips. Blue petrels (*Halobaena caerulea*) in the Southern Ocean alternate long and short trips, with self-feeding taking

Table 1
Logical relations defining which of 2 provisioning routines yields higher delivery rate

Comparison	Loading penalty	Inequality	Figures
$D_M > D_S$	$>\Delta t + t_2 - t_1$	(3)	3
$D_{A2} > D_S$	$>2(t_2 - t_1)$	(5)	3
$D_{A2} > D_M$	$<2\Delta t$	(6)	3
$D_{An} > D_S$	$>2(t_2 - t_1)$	(9)	4
$D_{An} > D_M$	$<n\Delta t + (n-2)(t_1 - t_2)$	(10)	4
$D_{SP} > D_M$	$<\Delta t + t_2 + \frac{(f-2)}{f}t_1$	(14)	/
$D_{AP} > D_{A2}$	$>2(t_2 + t_1)$	(16)	5
$D_{AP} > D_M$	$<\frac{(f+1)}{f}\Delta t + \frac{(f-1)}{f}(t_1 + t_2)$	(17)	5

D_M is the delivery rate of multipatch provisioning; D_S of single-patch provisioning; D_{A2} of 2-alternation; D_{An} of n -alternation; D_{AP} of 2-alternation with processing. The table is read as follows (taking the first line as an example): multipatch provisioning (D_M) yields higher delivery rate than single-patch provisioning (D_S) when the loading penalty is greater than $\Delta t + t_2 - t_1$. This result is given in inequality (3) in the text and shown in Figure 3.

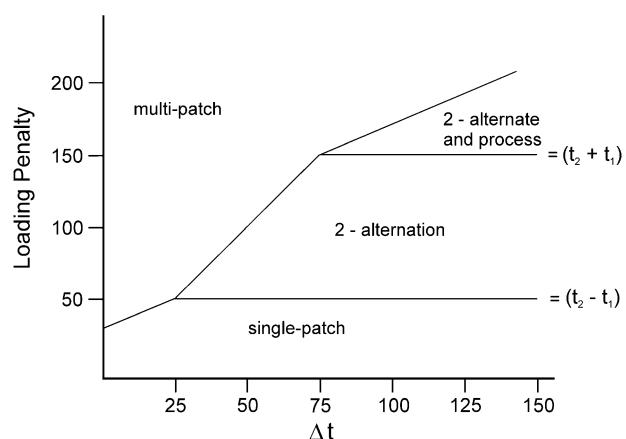


Figure 5

A numerical example, with $t_1 = 25$ and $t_2 = 50$. Two-alternation only considered. Boundaries between regions calculated from the logical relations in Table 1.

place solely on long trips (Weimerskirch et al. 2003). The type of prey delivered differs between short and long trips (Chaurand and Weimerskirch 1994), and the pattern is similar in other seabird species (see Cherel et al. 2005). Processed prey is associated with the long trips in all cases in which it has been recorded. All of these observations are consistent with the model developed here.

The literature on seabirds has generally interpreted alternation as a manifestation of the conflict parents face between feeding offspring and feeding themselves (Baduini and Hyrenbach 2003), with short trips used to boost delivery to needy offspring, at the expense of parental condition, which is recovered on long trips. The model developed here does not incorporate the concept of parent–offspring conflict: Alternation is favored on particular resource geometries because it achieves the highest delivery rate while allowing the parent to balance its energy budget. However, this does not mean that the approach here negates parent–offspring conflict. Conflict could be easily incorporated in a model structure that gives parents the option of deferring a self-feeding trip in order to make extra delivery excursions when offspring are hungry or in poor condition, so boosting delivery but at the expense of further lowering their body reserves. Beauchamp et al. (1991) model a closely related decision using a dynamic state variable model.

Our model also considers the circumstances under which the delivery of processed and concentrated prey is worthwhile, such as the stomach oil of species in the Procellariiformes (Roby et al. 1997). Figure 5 shows that the conditions favoring this tactic occur when long travel distances are involved, and the loading penalty is great. These conditions seem, qualitatively at least, to fit the ecology of some highly pelagic species adapted to foraging on the open ocean, such as albatrosses.

The model might be tested quantitatively by predicting attributes of prey and foraging behavior in natural situations. For example, the dovekies studied by Steen et al. (2007) on Spitsbergen were found to alternate successive short provisioning trips with a single long trip. As predicted by the model developed here, different types of prey are captured on these trips, but our model also makes more detailed predictions about the prey. In particular, it predicts that the prey collected on long trips (the energy-rich copepod *C. hyperboreus*) are better prey for self-feeding (i.e., more profitable) than the prey collected on short trips (the smaller copepod *C. glacialis*), while the latter can be loaded more rapidly. Based on information in Steen et al. (2007), we estimated broad ranges to encompass the possible loading penalty (16–216 min), round trip travel time to patch 1 (300–450 min), round trip travel time to patch 2 (20–80 min), and Δt (220–420 min), and used inequalities (3), (5), and (6) to determine that alternation indeed yields the highest delivery rate under almost all the geometries possible with these values. Better knowledge of flight speeds, foraging distances, trip times, prey size, and load size would enable a more exacting test.

Experimental approaches are also possible (though seabirds are unlikely candidates). Williams and Tepedino (2003) placed nest-boxes for solitary mason bees *O. lignaria* in the field, locating them between widely separated patches of 2 species of flowers. Mother bees provision pollen and nectar to the nest, building a “loaf” on which an egg is laid. The loaf is consumed by the developing larva. By examining the pollen loads delivered, Williams and Tepedino concluded that bees must have visited patches of both types on most provisioning trips (i.e., multipatch provisioning). They write “The most striking pattern remains the consistent pollen mixing . . . Female *O. lignaria* collected mixtures of pollen species from distantly separated patches, usually within single foraging trips. Such inveterate mixing behavior, with its attendant in-

crease in between-patch travel costs begs explanation. Why would females have traveled an extra 7.3–16 km, requiring up to 43 min per [loaf] . . . to collect pollen from both species on each foraging trip?”

The hypothesis that pollen loads were mixed to provide a balanced diet was not supported as experiments showed that larva grew as well on either species of pollen as on a mixture, and Williams and Tepedino (2003) proposed an explanation resembling that developed here. They found that flowers of one of the species (*Hydrophyllum capitatum*) had high nectar but little pollen (i.e., better for self-feeding), whereas the other (*Salix* spp.) was pollen rich but nectar poor (i.e., better for loading). We can apply inequality (3) to test the prediction of our model that the delivery rate of mason bees in this situation is enhanced by visiting both types of flower on every trip. In the most extreme situation created by Williams and Tepedino (2003; see their Figure 1), a bee would have had to fly an extra 850 m for multipatch foraging, requiring an extra 110 s (at a flight speed of 7.7 ms^{-1}). Williams and Tepedino (2003; see their Table 3) report that the pollen handling time per flower in *Salix* (5.52 s) was half that in *Hydrophyllum* (12.00 s). Assuming that 25 flowers were visited to collect a load (Williams and Tepedino report 25 inflorescences, so 25 flowers is a minimum), the loading penalty is 162 s ($=25 \times (12.00 - 5.52)$). Thus, in the most conservative comparison possible, the minimum loading penalty (i.e., LHS of inequality 3–162 s) exceeds the maximum extra travel time (RHS of inequality 3–110 s), which suggests that multipatch provisioning is strongly favored over single-patch provisioning in this situation.

Markman et al. (2004) studied Palestine sunbirds, which self-feed on floral nectar and arthropods but deliver only arthropods to nestlings. (Therefore nectar is used for self-feeding only.) Markman et al. placed artificial feeding patches on opposite sides of the nest. One patch offered a low concentration sucrose solution ($0.25 \text{ mol kg}^{-1} \text{ H}_2\text{O}$), as well as flightless flies that were delivered to offspring. The feeder on the other side offered a sucrose solution that was varied between 0.25 and 0.75 mol kg⁻¹ H₂O (i.e., self-feeding conditions there were usually better), but there were no flies for delivery.

The possible routines on this experimental resource geometry are to visit only the low concentration feeder to both self-feed and load flies for delivery; or to visit the higher concentration sucrose feeder for self-feeding and to collect flies at the low concentration feeder (Box 8.2 in Ydenberg 2007 considers this provisioning routine variant). Markman et al. (2004) did not directly measure provisioning routines, but they did find that as the sucrose concentration in the variable patch was experimentally increased, parent sunbirds 1) consumed more sucrose solution and spent more time feeding in this patch; 2) collected and delivered more flies from this patch; but 3) did not increase time or consumption at the low-quality sucrose solution. These findings show that they were sensitive to the relative qualities of the self-feeding and delivery patches and suggest that they adjusted their provisioning behavior accordingly.

Our model does not consider the many possibilities that might arise if load sizes could vary, if the rate of work could be adjusted, if the energetic costs of search and travel were different, if the provisioner did not have perfect knowledge of the environment, if it could respond to hunger of the offspring, or any of the many other tactical considerations. Some of these are considered by Ydenberg (2007), and all of these questions have been treated in other foraging contexts. Of these, uncertainty about the location or contents of patches is perhaps the most likely to be important, especially in some environments (e.g., seabirds in dynamic marine settings). In the cases

of multipatch provisioning and alternation, the uncertainty about both types of patch has to be considered.

Nevertheless, our results have a number of implications as well as possible applications. For example, many studies have relied on prey observed at delivery points (where they can be observed) to make inferences about their abundance in the environment or about environmental conditions. Seabird biologists, for example, have often suggested that the prey delivered to nestlings on seabird colonies may be used to monitor marine conditions (see Davoren and Montevecchi 2005 for a recent example and discussion). Our model (see also Houston 2000) shows that the relation between the prey delivered and the availability of those prey in the environment is not straightforward. The reason is that the choice by provisioners of the patch for delivery depends on the loading penalty, which is not easily measurable. A change in the type or availability of delivery prey in patch 1 that increases r_1 and reduces the loading penalty could induce provisioners to adopt single-patch foraging and change completely the type of prey delivered, even if the abundance or distribution of the prey in patch 2 were unchanged.

A second implication concerns inferences that may be made about self-feeding conditions. The model developed here assumes that provisioners balance their energy budgets on every (or every n) excursions, spending enough time self-feeding to pay the costs of the excursion(s). Thus, the rate of work a provisioner is able to sustain depends on the rate of self-feeding: better self-feeding opportunities enable harder work. With enough information, an investigator should be able to infer from the rate of work just what the self-feeding rate is. For example, Moore (2002; in Ydenberg 2007) showed that the flight speed of provisioning common terns (*Sterna hirundo*) was that at which the extra self-feeding time needed to fuel faster flight would have required the same amount of time as the increase in flight speed would have saved (as in Norberg's (1981) model). On this theory, behavioral attributes of provisioners such as their flight speed can inform us of the self-feeding rate available. An investigation of this idea would be very valuable.

Finally, provisioning also occurs in nonbiological situations. For example, robots are increasingly used to carry out tasks of all sorts, including the delivery of material to or from a depot. Such robots must be independent of power sources and hence must regularly travel somewhere to charge themselves (i.e., self-feed; Wawerla and Vaughan 2007). This may be viewed as a provisioning routine in the sense that "self-feeding" must be considered in order to be able to maximize the delivery rate.

FUNDING

National Sciences and Engineering Council (Canada) Discovery Grant to R.C.Y. The work of the Centre for Wildlife Ecology at Simon Fraser University, including that at Triangle Island, is supported by a Grants and Contribution Agreement with Environment Canada.

R.C.Y. thanks The Pacific Seabird Group for the opportunity to present some of these ideas at their 2007 meeting in Taiwan. David Stephens commented on the manuscript. Shai Markman also gave feedback on the manuscript and with his family hosted a most enjoyable visit to Sde Boqer to observe Palestine sunbirds firsthand. Richard Vaughan pointed out the possible application of these ideas to robots.

REFERENCES

Baduini C, Hyrenbach D. 2003. Biogeography of Procellariiform foraging strategies: does oceanography influence provisioning? *Mar Ornithol.* 31:101–112.

Baird PH. 1991. Optimal foraging and intraspecific competition in the tufted puffin. *Condor*. 93:503–515.

Beauchamp G, Ens BJ, Kacelnik A. 1991. A dynamic model of food allocation to starling (*Sturnus vulgaris*) nestlings. *Behav Ecol*. 2:21–37.

Brooke MD. 1981. How an adult wheatear (*Oenanthe oenanthe*) uses its territory when feeding nestlings. *J Anim Ecol*. 50:683–696.

Chaurand T, Weimerskirch H. 1994. Incubation routine, body-mass regulation, and egg neglect in the blue petrel *Halobaena caerulea*. *Ibis*. 136:285–290.

Cherel Y, Hobson KA, Weimerskirch H. 2005. Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. *Oecologia*. 145:533–540.

Davies WE, Hipfner JM, Hobson KA, Ydenberg RC. 2009. Seabird seasonal trophodynamics: isotopic patterns in a community of Pacific alcids. *Mar Ecol Prog Ser*. 382:211–219.

Davoren GK, Montevecchi WA. 2005. Did signals from seabirds indicate changes in capelin biology? Reply to Carscadden. 2004. *Mar Ecol Prog Ser*. 285:299–309.

Elgar MA, Jebb M. 1999. Nest provisioning in the mud-dauber wasp *Sceliphron laetum* (F. Smith): body mass and taxa specific prey selection. *Behaviour*. 136:147–159.

Granadeiro JP, Nunes M, Silva MC, Furness RW. 1998. Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Anim Behav*. 56:1169–1176.

Houston AI. 1987. Optimal foraging by parent birds feeding dependent young. *J Theor Biol*. 124:251–274.

Houston AI. 1993. The efficiency of mass loss in breeding birds. *Proc R Soc Ser B Biol Sci*. 254:221–225.

Houston AI. 2000. Prey size of single-prey loaders as an indicator of prey abundance. *Ecol Lett*. 3:5–6.

Kacelnik A. 1984. Central place foraging in starlings (*Sturnus vulgaris*). 1. Patch residence time. *J Anim Ecol*. 53:283–299.

Kaspari M. 1991. Central place foraging in grasshopper sparrows—opportunism or optimal foraging in a variable environment? *Oikos*. 60:307–312.

Krebs JR, Avery MA. 1985. Central place foraging in the European bee-eater. *J Anim Ecol*. 54:459–472.

Markman S, Pinshow B, Wright J, Kotler BP. 2004. Food patch use by parent birds: to gather food for themselves or for their chicks? *J Anim Ecol*. 73:747–755.

Moore D. 2002. The provisioning tactics of parent Common Terns (*Sterna hirundo*) in relation to brood energy requirement [PhD thesis]. [Burnaby (Canada)]: Simon Fraser University. 209 pp.

Norberg RA. 1981. Temporary weight decrease in breeding birds may result in more fledged young. *Am Nat*. 118:838–850.

Orians G, Pearson NE. 1979. On the theory of central place foraging. In: Horn DJ, Stairs GR, Mitchell RD, editors. *Analysis of ecological systems*. Columbus (OH): Ohio State University Press. p. 155–177.

Rands S, Houston AI, Gasson CE. 2000. Prey processing in central place foragers. *J Theor Biol*. 202:161–174.

Roby DD, Taylor JRE, Place A. 1997. Significance of stomach oil for reproduction in seabirds: an interspecies cross-fostering experiment. *Auk*. 114:725–736.

Steen H, Vogedes D, Broms F, Falk-Petersen S, Berge J. 2007. Little auks (*Alle alle*) breeding in a High Arctic fjord system: bimodal foraging strategies as a response to poor food quality? *Polar Res*. 26:118–125.

Stephens DW, Krebs JR. 1986. *Foraging theory*. Princeton (NJ): Princeton University Press.

Terauds A, Gales R. 2006. Provisioning strategies and growth patterns of light-mantled sooty albatrosses *Phoebetria palpebrata* on Macquarie Island. *Polar Biol*. 29:917–926.

Tierney M, Southwell C, Emmerson LM, Hindell M. 2008. Evaluating and using stable-isotope analysis to infer diet composition and foraging ecology of Adélie penguins *Pygoscelis adeliae*. *Mar Ecol Prog Ser*. 355:297–307.

Wawerla J, Vaughan RT. 2007. Near-optimal mobile robot recharging with the rate-maximizing forager. *Proceedings of the 9th European Conference on Artificial Life*. Lisbon, Portugal, 2007, Berlin, Heidelberg: Springer-Verlag p. 776–785.

Weimerskirch H, Robertson G. 1994. Satellite tracking of light-mantled sooty albatrosses. *Polar Biol*. 14:123–126.

Weimerskirch H, Ancel A, Caloin M, Zahariev A, Spagiari J, Kersten M, Chastel O. 2003. Foraging efficiency and adjustment of energy

expenditure in a pelagic seabird provisioning its chick. *J Anim Ecol.* 72:500–508.

Williams NM, Tepedino VJ. 2003. Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee *Osmia lignaria*. *Behav Ecol.* 14:141–149.

Williams TD. 1995. *The penguins*. Oxford: Oxford university Press.

Ydenberg RC. 1994. The behavioral ecology of provisioning in birds. *Ecoscience.* 1:1–14.

Ydenberg RC. 2007. Provisioning. In: Stephens DW, Brown J, Ydenberg RC, editors. *Foraging*. Chicago: University of Chicago Press. p. 273–303.

Ydenberg RC, Schmid-Hempel P. 1994. Modelling social insect foraging. *Trends Ecol Evol.* 9:491–493.