

# Resource geometry and provisioning routines

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Provisioners capture items both for delivery and for self-feeding. In doing so, they may travel directly to and from a single

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

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

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

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.,  $t$

provisioning with processing and multipatch foraging can be

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,

0.2(h)8ng441r3nc268.3(me-297.4(co)2n,(es)-242.(ed)14.5(i)15.4(ng)-380.8Tva(441r3o)-29ta09.3(pa)18.7

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.

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, behav-



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