Central Place Foraging



Joseph L. Woodgate and Lars Chittka School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

Definition

A foraging strategy in which prey or resources are transported to a nest or other habitual base rather than being consumed in situ.

Introduction

Many animals use one or more habitual locations as nests, shelters, or storage caches during all or part of their lives and transport resources to this central place. Examples include birds bringing food to their nests to feed their chicks, bees storing honey at their nest to feed brood and provide food during periods when no flowers are available, male terns bringing food to females during courtship, chipmunks stockpiling seed for the winter, or eastern woodrats collecting nesting materials. A central place can also function as a store of information, as in ant colonies where pheromone trails radiating from the nest encode the sum of the colony's knowledge about available food sources or honeybees which dance inside the nest to communicate the position of flowers. Humans, too, are central place foragers, transporting everything

from food to fuel, building materials and even status symbols or the spoils of war to their homes, often over great distances.

Modeling Optimal Strategies

Central place foraging theory is an offshoot of optimal foraging theory, making quantitative predictions about foraging behavior by assuming that animals attempt to optimize their net gain per unit of time or energy invested. The requirement to return to a central location imposes time and energy costs in addition to those incurred by searching for, capturing, and handling prey items. These additional costs can alter the optimal strategy, which also depends on whether animals are single-prey loaders, which catch and transport a single item at a time, or multiple-prey loaders, which can acquire many items on a single trip (Orians and Pearson 1979).

To optimize foraging performance, multipleprey loaders ought to spend longer searching for (and collecting) food, and carry larger loads, when foraging at distant locations than at those closer to the nest. Single-prey loaders, unable to increase their load by collecting more items, are predicted to prefer larger prey items further from the nest and to accept a smaller range of prey sizes. The logic underlying these predictions is illuminated by an analogy to human shopping: it can be worthwhile to visit a local shop to pick up a few items only. Conversely, if a shop is time-

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consuming to reach, it is only worthwhile if the produce is particularly good and if you stock up on everything you are likely to need for some time to come.

Choice of prey gives animals an opportunity to adjust the profitability of a trip. Foragers should be choosier and more likely to specialize on the most profitable food sources when foraging further from their central place, although the optimal prey choice strategy varies in complex ways depending on the relative profitability and abundance of different items and on the time taken to handle different types of prey (Houston 1985). Smaller or less profitable items are more likely to be harvested when the best items are rarely encountered or require time-consuming handling, as well as when the round-trip time is lower. In some species, foragers will consume small prey in the field but transport larger items to the nest.

Foragers should become less selective as costs associated with foraging increase. Within a foraging trip, animals should become progressively less choosy as time spent foraging increases. Thus, single-prey loaders may return from a long foraging trip with items less profitable than they rejected at the start of the trip (Houston and McNamara 1985).

Many animals process their food before eating it. Processing prey at the point of capture will result in lighter loads to carry back to the nest, resulting in time and energy savings. Beyond a certain distance, these savings result in a lower round-trip time, and a forager should switch from processing at the central place to the point of capture. If processing can be done in stages, progressively greater levels of processing are expected at increasing distances from the central place (Rands et al. 2000).

A further prediction is that animals should choose nesting sites at the centers of profitable foraging areas, particularly when food supplies are unpredictable. Nest-searching bumblebee queens, for example, will spend weeks searching for suitable sites and in the process may first sample foraging resources before deciding where to settle.

Empirical Tests

Empirical tests show broad qualitative support for the major predictions of the theory. For example, animals from birds to honeybees have been found to take larger loads when foraging further from their central place. Quantitatively, however, animals' behavior often departs significantly from models' predictions. Chipmunks collecting sunflower seeds spend longer filling their cheek pouches and carry heavier loads when foraging at patches further from their nests, as predicted, but neither the actual sizes of the loads nor the function describing the relationship between travel distance and load size is accurately explained by theory (Giraldeau and Kramer 1982). Although merlins switch from processing their prey at the nest to the point of capture as the distance to the nest increases, they do so at around 1/50 of the distance predicted by a model (Rands et al. 2000), suggesting that either the model used unrealistic inputs or that other factors influence the birds' decision, such as ectoparasite removal or strategies to avoid kleptoparasitism.

Criticisms of Central Place Foraging Models

Models of central place foraging are vulnerable to the same criticisms that have been directed at optimal foraging models in general (Pyke 1984), namely, that they do not account for constraints on the ability of natural selection to optimize any particular function; that they require unrealistic simplifications of natural situations; that they ignore environmental stochasticity; that their proponents cannot determine what "currency" foraging animals ought to optimize; and that, because very different predictions can be arrived at by varying the model parameters, they can be used to explain any empirical result and so, by explaining too much, they fail to explain anything at all.

The real world is more complex and variable than that of simplified mathematical models, and it is unlikely that natural selection could equip any organism with the optimal response to every possible scenario. Instead, evolution is likely to favor general behavioral rules that perform well on average, in the natural environment typically faced by a given species (McNamara and Houston 2009). Two conclusions follow: perfectly optimized behavior may not occur under any specific set of conditions; and the optimal behavioral rules for a given species will depend on its biology and ecology. Understanding the needs of animals within their environment and the mechanisms by which they fulfill these needs is the key to a fuller understanding of how foraging strategies evolve.

What to Optimize

The optimal behavior in a given situation depends on what you hope to optimize. Most models use the currency of net rate of energetic gain and zebra finches, for example, forage in ways consistent with such currency; but honeybees aim to maximize energy efficiency, the ratio of energy gained to energy spent. The choice of currency may depend on the biology of the species in question. For example, social species like ants share information on the location and quality of food sources. It can be beneficial for foragers discovering a highquality source to cut short their foraging trip to disseminate information, raising the long-term rate of energetic return of the colony at the expense of their individual short-term profitability (Dornhaus et al. 2006). Constraints, such as the need for small birds to acquire enough energy to survive the night, may mean that under certain conditions optimizing foraging efficiency is less important than simply getting enough to eat.

Spatial Cognition and Foraging

Many models assume an animal has perfect knowledge of the distribution of resources and how to reach them. In fact, organisms start their foraging career with no specific knowledge of their environment. This is significant because the mechanisms by which they acquire and use spatial information, along with constraints and limitations on those mechanisms, determine where and how they forage. The need to balance learning about the environment with the exploitation of known resources is an important factor in explaining why predictions of optimal foraging behavior seldom provide a perfect fit to empirical data.

Central place foragers must learn to navigate their environment and return successfully to their starting point. They must explore in search of food and develop efficient routes to get to and from foraging patches. A variety of navigational strategies are employed by central place foragers (Collett et al. 2013). Path integration involves keeping a constantly updated memory of one's position relative to a central location and can operate independently of the features of the environment. Other strategies involve learning and recognizing environmental features and include matching a visual scene to a memorized snapshot or following an olfactory or chemical gradient. In rats, grid cells and place cells provide a neural architecture for the animal to keep track of its position in space (Moser et al. 2008).

Species from insects to primates visit multiple destinations on a single foraging trip. Multidestination routes reveal several ways in which foraging behavior is richer than previous models have accounted for. One is that foraging decisions involve more than just determining when to leave a patch: visiting many patches in turn is efficient if no single patch is rich enough to gather a full load in a reasonable time frame and can also reduce the costs of competition. Another is that the length and geometry of an entire route are likely to be more important than simple distance from the nest in determining the optimal strategy. Bumblebees visit locations in repeatable sequences that often converge on the most efficient route (Lihoreau et al. 2012), although experiments in which they do not find an optimal route have revealed that they use heuristic strategies that lead to good results over a range of situations. In addition to

multiple destinations, primates like spider monkeys also use multiple sleeping sites, allowing reduced travel distances in large home ranges while retaining the benefits of a central place.

Conclusion

The features of the environment an animal attends to, and the navigational strategies it employs, are tailored to its habitat and lifestyle. These mechanisms determine what information is available for foraging, which will influence the optimal strategy. The animal's ability to remember and follow routes will affect which patches are best to exploit, while the mechanisms by which it finds and captures prey will influence the optimal choice of food. Such information must be integrated with central place foraging models to improve success in predicting real behavior.

Cross-References

- Caching
- Cognitive Map
- Food Patch
- Foraging
- Home Range
- Marginal Value Theorem
- Movement/Locomotion
- ► Navigation
- Neural Mechanisms of Navigation
- Optimal Foraging Theory
- Path Integration
- Risk-Sensitive Foraging
- Spatial Memory
- ► View-Based Homing

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