attached to a shrub that was moved to different locations (an unfamiliar foraging site and handling behavior). Even pigeons and rats pressing keys in a psychologist's operant chamber can come quite close to the predictions of models developed for foraging in the field.

It is likely that the published literature is biased by the difficulty of publishing negative results and a tendency for researchers who obtain negative results to continue searching for additional relevant variables or invalid assumptions. Nevertheless, it is clear that the optimality approach has predictive power. Evaluation of this power would be improved if it could be quantified on a common scale. A promising approach comes from the mathematical technique of dimensional analysis (Stephens and Dunbar 1991), which transforms the mathematical relationships of a model into a reduced set of unit-free variables. This unit-free statement of the decision rule permits different studies to be compared within the same framework and reveals the relative magnitude of discrepancies between observation and prediction. Using this approach, a preliminary analysis of patch exploitation studies by Kramer and Giraldeau (unpublished) confirmed the overall positive relationship between proportional patch use and search or travel between patches when scaled to patch “half-life.”

**Foraging Games**

An important part of the foraging environment for many species is the presence of other foragers, of the same and sometimes other species, which can increase or decrease foraging success (table 18.3). Such effects are most evident when animals forage in groups, but even “solitary” foragers can affect each other, for example, by reducing prey abundance, alerting prey to the presence of predators, or revealing new food sources by their foraging activity. Many processes involving interactions with other foragers show density dependence because their occurrence, magnitude, and sometimes direction depends on the number of other individuals present. Density dependence is often negative, in that some currency of foraging declines with the number of other individuals, but it may also be positive (also known as an Allee effect) over at least part of the density range. Sometimes, social effects may be affected by the proportion of individuals making different alternative decisions. This frequency dependence is an important consequence of social foraging, often in combination with density dependence.

Optimality theory can be used to predict foraging decisions in relation to the abundance or tactics of other foragers as well as other environmental conditions. However, a major difficulty in testing such predictions is that the other foragers may also change their behavior in relation to the change in their foraging environment. Thus, to predict foraging behavior in a social context, the results of this series of mutual interactions must be predicted. Game theory provides the mathematical tools for this prediction. See Dugatkin and Reeve (1998) and Roff (this volume) for summaries of game theory in evolutionary ecology. Giraldeau and Caraco (2000) provide a detailed recent review along with new applications of game theory to social foraging.

The basic approach of game theory is to find, from a given set of decision rules, the rule or mix of rules among the interacting individuals such that no individual using an alternative rule would have greater success than the individuals using the established rule or rules. From the perspective of evolutionary genetics, this situation prevents genes for alternative rules from invading the population and is therefore called an *evolutionarily stable strategy* (ESS). *Evolutionarily stable state* is a more appropriate term to account for situations in which no single rule is unbeatable but a mix of rules is. The “strategies” in most models tend to be rather simple fixed responses or simple switches between two responses based on a single environmental factor. However, as with applications of optimality theory, in foraging game situations that have actually been studied, the decisions are typically flexible individual responses.

Game theory is so important because the outcome of games is often strikingly different from simple optimal solutions. The selection of foraging sites offers a simple illustration. Consider a choice of potential foraging sites that differ only in their food availability and consequently in the foraging success they offer. For a single forager, the optimal solution is to forage at the site with the highest food availability, and the model does not change the prediction if several individuals are considered. If foraging rate is negatively density-dependent, however, and there are many foragers using the same set of sites, the foraging rate in the patch with the highest food availability may drop below that of other unoccupied patches if all go to the site.
Table 18.3 Social influences on foraging.

1. Changes in food availability.
   - Exploitation—removal of food from the foraging area.
   - Passive interference (also called prey depression)—reducing foraging rates by making prey less available, for example, by inducing its antipredator defenses.
   + Facilitation—making prey more available, for example, by confusing them or making them more visible while fleeing another forager.
   + Risk reduction—lowering the variance of foraging success by sharing food discoveries among individuals.

2. Changes in costs or benefits of search, pursuit, and handling.
   + Cooperative hunting—improved pursuit and handling success or decreased pursuit and handling time by groups.
   + Increased rate of discovery of shareable prey or patches by foragers in groups.
   - Scramble competition—animals foraging in groups may have search areas that overlap with those of other foragers and therefore require more search time to discover the same number of prey; they may have to increase their rate of movement or change other foraging tactics to avoid having other foragers discover or capture the prey first.

3. Kleptoparasitism—exploiting the search, pursuit, and handling of others.
   + For the kleptoparasite, more potential victims decrease search, pursuit, or handling time by allowing exploitation of prey or patches in which another individual has already invested.
   - For the kleptoparasite, more kleptoparasites may change food availability and change costs and benefits of foraging as in sections 1 and 2.
   - For the victim, more kleptoparasites result in increased effort in search, pursuit, or handling as a result of losing prey or part of patches, or additional effort to avoid or defend against kleptoparasites, or reduced success as a result of choosing prey less vulnerable to kleptoparasitism.
   + For the victim, more victims can improve defense or dilute the impact of kleptoparasites.

4. Food defense (also called active interference or interference competition)—use of aggressive behavior to reduce the foraging of other individuals on particular prey (food guarding) or specific locations (territoriality).
   + For the defender, increased prey availability as a result of reduced exploitation and passive interference by other individuals.
   + For the defender, effectiveness of defense may be increased by cooperative defense.
   - For the defender, costs of defense increase with the number of potential intruders.
   + For intruders, foraging in groups can increase access to defended areas or prey by overcoming the defense.
   - For intruders, decreased access to particular prey or defending sites as a result of effective defense by other individuals.
   - For intruders, increased effort or risk of injury to obtain resources by intruding in locations defended by others.

5. Changes in foraging time availability and risk of attack from predators or conspecifics.
   + Grouping can reduce predation risk during foraging; this may permit less time to be spent on vigilance during the foraging period or the use of sites that would be too dangerous for a solitary individual.
   - Foraging in groups may attract more predators, increasing predation risk or reducing the areas that are safe to use.
   +/- When attacks from conspecifics are a threat, groups may either increase or decrease the risk, depending on the situation.

6. Foraging information.
   + Other individuals can be used to obtain information about beneficial foraging locations, food types, and foraging techniques.
   - Information scavenging may reduce the number of accurately informed individuals and provide wrong information.

Note: Minus and plus signs indicate how each process will affect the foraging success of a focal individual as the number of other foragers increases.

with highest food availability. The game theory solution, known as the ideal free distribution, is for individuals to distribute themselves among sites so that the combination of forager density and food availability results in similar foraging rates in all sites, a very different result from the prediction of simple optimality. This is an example of frequency dependence in that the best site for any one forager depends on the distribution of the foragers among the other sites. The ideal free distribution is clearly too simple to apply in many real-world situations, but it has been repeatedly observed in controlled laboratory studies, where foragers often show an impressive capacity to adjust quickly to deviations
in foraging success. Furthermore, it has formed the basis for a series of more complex models that have strongly affected how behavioral ecologists think of foraging distributions and habitat selection.

Group size presents a similar problem. For certain foraging tasks such as the hunting of large prey by carnivores, it is possible to calculate an optimal group size that yields the highest rate of foraging success per individual. However, group formation constitutes a game: depending on how groups are formed and how access to groups is controlled, groups may form that are much larger than optimal size with foraging success much lower than the optimum. This is representative of a widespread finding in game theory models that individual success will be lower than that predicted by simple optimality.

A fundamental characteristic of social foraging is that the effort of individual foragers creates an opportunity for parasitism of that effort by other foragers. Kleptoparasitism, however, is not a viable foraging strategy if all foragers are attempting to do it and none are looking for their own food. This is another case where frequency dependence is clearly involved in the success of alternative forager decisions, such as searching for food patches independently or watching other foragers and attempting to join patches that they discover. "Producer-scrounger" models predict the occurrence and frequency of these alternative foraging decisions.

Game theory is also relevant to interactions between predators and prey and between plants and their pollinators and seed dispersal agents. A review of such coevolutionary interactions is beyond the scope of this chapter (see section "Interspecific Interactions," this volume). However, recent models of forager distribution are beginning to take into account distribution games between predators and prey as well as among foragers (e.g., the chapter by Sih in Dugatkin and Reeve (1998)).

Case Study

The Load Size Decisions of Chipmunks

Theory For central place foragers that carry more than one prey per trip, one foraging decision is when to stop loading and return to the central place. This decision determines the load size carried and is part of the foraging process for seed-hoarding rodents, for parental birds provisioning their young, and for nectar- and pollen-collecting bees and wasps. In this section, I will illustrate the interplay between foraging theory and experimental tests using the load size decision of eastern chipmunks, Tamias striatus. These small (100-g), terrestrial, forest-dwelling sciurid rodents feed primarily on the seeds of deciduous trees, though a wide range of plant and animal material is sometimes consumed. Food is carried to a burrow for both short-term consumption and long-term storage. In the winter, animals hibernate without accumulating significant fat reserves, waking periodically to feed on stored food. Except for females with young, each animal occupies its own burrow, which is vigorously defended against conspecifics. Although animals chase other individuals near food sources and in the vicinity of their burrows, home ranges overlap extensively. Chipmunks exposed to human presence and provisioning become very tame. At our study site, in the public portion of a university nature reserve, many animals can be observed from a few meters or less without evident disturbance.

Our interest in load size decisions arose from one of a set of models of central place foraging published by Orians and Pearson (1979). This model is conceptually derived from an influential model of patch use known as the marginal value theorem (Charnov 1976). It predicts that, if loading rate decreases as the size of the load increases, the optimal load size should increase with distance to the central place and with food density. The derivation of this prediction is shown in a step-by-step analysis in figure 18.1, but an elegant graphical solution (figure 18.2) improves the intuitive understanding of the predictions. A decline in loading rate with size of the load already accumulated seems likely because holding prey could reduce the success or rate of search, pursuit, and handling of additional prey, depending on the morphology of the forager and the type of prey. The trade-off here is between the gain per trip, which is maximized by taking the largest load possible, and the number of trips per unit of foraging time, which is maximized by taking the smallest load. The rate of food delivery to the central place is the product of these components and is maximized at an intermediate load size (figure 18.1C). Note that if the declining loading-rate constraint is removed so that load size in-
Figure 18.1 Orians and Pearson's (1979) load-size/loading-time decision model for a central place forager. The model assumes a currency of gross rate of food delivery to the central place with constraints as follows: (1) The food density and distance from the central place are fixed by the environment. (2) Loading rate decreases with decreased food density and with the amount of load already acquired; therefore, the total load increases with loading time, but at a decreasing rate, and approaches the maximum load more slowly when food is scarce. Panel A illustrates loading functions for patches of high \[ W = 6(1 - \exp(-0.04L - 0.02)) \] and low \[ W = 6(1 - \exp(-0.02L - 0.02)) \] density. (3) Round-trip travel time includes the outward and return trip plus unloading time and is a fixed cost for any particular distance; it has a positive value at zero distance because of unloading time and increases linearly with distance. (4) Gross rate of food delivery is the product of food gained per trip (load size) and trips per unit time \((1/(loading + travel time))\). Panel B shows these values for a high-food-density patch 20 m from the burrow, assuming that \( T = 50 + 1.6D \), where \( T \) is travel time (s) and \( D \) is distance (m). The animal is free to cease loading at any time, and the decision rules to be determined relate loading time to travel time and loading time to food density. For any travel time and food density, food delivery rate can be calculated for all possible loading times. The loading time that provides the maximum delivery rate is predicted to be the one used by the animal. Panel C compares gain curves for high- and low-density patches 20 m from the burrow; panel D compares gain curves for high-density patches at 20 and 80 m. Optimal load sizes are indicated by arrows. The predicted decision rules in panel E relate optimal loading time to travel time for high- and low-density patches. In panel F, these are converted to optimal load sizes, using the loading functions. These show that optimal load sizes are larger in high-density patches and increase in a curvilinear fashion with travel time.
Figure 18.2 A graphical formulation of the optimal solution to the load size decision model based on Orians and Pearson (1979) and using the values for the high-density patch presented in figure 18.1. Load size in relation to loading time increases to the right and travel time increases to the left of the origin. For any travel time, the optimal loading time and load size are indicated by the tangent to the loading curve. This is because the slope of the loading curve equals the rate of food delivery (load divided by loading time + travel time). Any point along the curve represents a possible decision, but the tangent represents the greatest slope and hence the highest possible food delivery rate. This is illustrated for a short and a long travel time. Dotted lines drawn from the points of tangency to the axes indicate the optimal loading time and load size.

creases linearly, the optimal load is always the maximum (Kramer and Nowell 1980).

Tests We chose to make a quantitative, observational test of the predictive power of the decision rule relating load size to travel time, under field conditions (Giraldeau and Kramer 1982). If Orians and Pearson’s model is correct and if chipmunks show a curvilinear loading function, these animals could have been selected to take a species-characteristic, fixed load size corresponding to the average distance and seed density at which they forage. Our design assumed, however, that individuals can adjust their load size to recent experience of distance and loading characteristics, including evolutionarily novel food types and foraging situations. To determine the average loading curve for our study population, we recorded the weight of seeds taken in 738 uninterrupted loads and 113 loads in which the experimenter interrupted the chipmunk early in the loading process. We used a fixed quantity of sunflower seeds (10 g) on a bare tray (23 x 24 cm) placed at different distances (0.2-135 m) from the burrows of 21 different adult animals. By using data from some animals at long distances, we were able to estimate the consequences of taking large loads, even if the animals only took small loads when near their burrows. In addition, we determined the round-trip travel time and distance to the burrow for the same trials.

The data showed clearly that load size increased at a decreasing rate with loading time (figure 18.3A) and that travel time increased linearly with distance. The optimal load size for each travel time was calculated with the equation \( T = \frac{f(P^*)}{f'(P^*)} - P^* \) where \( f(P^*) \) and \( f'(P^*) \) are the loading function and its derivative evaluated at \( P^* \), the optimal loading time. (See Giraldeau and Kramer 1982 for details.) The result was a prediction for a strong increase in load size with increases in travel time over the range of travel times observed (figure 18.3B).

Data from the 738 uninterrupted loads showed that chipmunks did take larger loads when they were farther from their burrows, a finding providing qualitative support for the predictive capacity of the model (figure 18.3B). However, load sizes were considerably smaller than predicted. In addi-
Figure 18.3 (A) The relationship between load size and loading time for eastern chipmunks hoarding sunflower seeds at different distances from their burrows. Each point represents a different load. The line shows the best fitting exponential equation, \( W = 6.0 \left( 1 - \exp \left( -0.018 - 0.023 \right) \right) \), \( r^2 = 0.56 \); other curvilinear functions gave a similar fit. (B) The relationship between travel time and load size. The solid circles show observed mean load sizes ±1 SD, and the dashed line shows the load size predicted to maximize the rate of food delivery. (Modified from Giraldeau and Kramer 1982, figures 1 and 3.)
tion, instead of a relatively sharp increase in load size with increasing distance, chipmunks showed little change in load size over the first 50 m, with a sharper increase at greater distances. In a subsequent study, using a uniform spatial array that allowed us to determine the loading time for each seed, we also found curvilinearity of the loading function and an increase of load size with distance (Giraldeau et al. 1994). However, this study also found highly significant individual differences, as well as effects of distance and the presence of competitors, on the loading functions. Travel time was also affected by the presence of competitors. Unfortunately, this prevents the generalization of loading curves to predict what animals would have obtained if they had taken larger loads than the ones observed. Nevertheless, the data clearly showed that the chipmunks would have had lower rates of food delivery if they had used loads smaller than those observed, and an extrapolation strongly suggested that they would have done better by taking larger loads. In other words, chipmunks in this different test situation were also very likely to be taking smaller loads than predicted by the Orians and Pearson model.

Other researchers have confirmed the qualitative increase of load size with distance (Bowers and Ellis 1993) and have shown that load sizes also increase as a result of delayed access to the food source, even when distance does not change (Lair et al. 1994). The predicted increase of load size with food density was confirmed qualitatively (Kramer and Weary 1991). A decrease in load size from patches with less canopy cover and presumably more risk of aerial predation has been found in some situations (Bowers and Ellis 1993), but not in others (Otter 1994). Furthermore, three studies found a strong, but unpredicted, decrease in load size with increasing trip number (Giraldeau and Kramer 1982; Bowers and Adams-Manson 1993; Lair et al. 1994). Because these tests did not measure the loading curves, it is not clear whether the patterns arise through differences in loading and travel rates that changed the delivery rate optimum or as independent variables that produce deviations from the delivery rate optimum.

Implications The load size decision seems relatively minor in that animals ought to be able to get by quite satisfactorily by simply filling their cheek pouches to some constant level on each trip. However, chipmunks showed rapid short-term flexibil-

ity not only to distance but also to several other environmental conditions. These patterns would not have been discovered without the a priori theory. Optimality models provide a framework for the discovery of natural patterns even when they fail to predict accurately. To illustrate, I will discuss some hypotheses to explain why chipmunks take loads smaller than the predicted optimum. These suggest future studies and ultimately stronger predictions.

First, consider possible limitations in the model resulting from potentially relevant variables that were ignored. When an animal takes smaller loads than predicted, it makes more trips per unit of foraging time than predicted and thus spends more time traveling and less time in the patch than it would if it took the predicted load sizes. Thus, we should consider alternative currencies that would recognize the benefit of more trips or more traveling relative to more time loading. Note that small loads require more of an explanation than large loads. Consider the rate of gain curves in figure 18.1D and E. An animal taking too large a load suffers less of a reduction in gain rate than an animal taking too small a load. Hence, we might expect less of a cost in responding to variables that require an increase than a decrease in load.

The most obvious simplification in this model is its currency of gross rate of food delivery. Net rate of energy gain might seem to be more appropriate. However, a 3-g load of sunflower seeds contains about 12 kcal of energy, while loading requires about 0.02 kcal/min and running requires about 0.035 kcal/min (M. Humphries, personal communication), so net rate will not differ much from gross rate in our study. Furthermore, the energy cost of running is higher than the energy cost of loading, so including energy costs will increase the discrepancy. Predation risk could be a factor if loading is more dangerous than traveling or if predation risk increases disproportionately with larger loads. Intraspecific competition might also be a factor. Small loads reduce the rate of food delivery, making an animal less effective in scramble competition for a short-lived patch. They also reduce time at the foraging site, where a dominant animal might gain an additional guarding advantage. On the other hand, if the main threat from conspecifics is pilferage from the burrow while the owner is away, taking smaller loads could improve the guarding of the hoard by increasing the frequency with which the burrow is visited. Ydenberg et al. (1986) developed several models indicating
how animals could use active and passive interference as competitive tactics to increase their share of a limited ephemeral resource. This suggests that a game theory model of load size taking intraspecific competition into account might have greater predictive power.

Having considered possible limitations of the model, we should now consider possible limitations of the animal. To match the predictions of the model using behavioral flexibility, an animal has to have information about travel time, loading rate, and how they are to be integrated. Determining these from recent experience involves complex issues such as how many trips to include, how to weight more recent versus less recent trips, and how to deal with interruptions such as time vigilant, hiding from predators, grooming, or engaged in aggressive interactions with conspecifics. Furthermore, animals may measure time and mass on a different scale from scientists (Kacelnik and Bateson 1996). If a chipmunk underestimated loading rate or travel time, its loads would be too small. Most chipmunks' prior experience would involve far lower food densities than what we offered, and optimal loads, therefore, almost always would be smaller. If the animal used a simple rule of thumb, it is likely that the food type, location, or mode of presentation did not match the evolutionary or developmental environment in which the rule of thumb had been established. Models that take into account specific mechanisms by which animals determine and integrate the foraging parameters might be able to improve the precision of predictions at a considerable loss of generality.

Future Directions

Foraging studies have a long history of providing conceptual and methodological advances in behavioral ecology. This field provides an excellent example of the advantages of integrating quantitative theory with rigorous empirical testing. The number of variables influencing the "simple" load size decision suggests that there are numerous other decision rules to be discovered, possibly for load size, and certainly for the large number of other decisions involved in foraging. In fact, a few elegant models such as prey choice, patch departure (marginal value theorem), and spatial distribution (ideal free distribution) have received disproportionate research attention. For many other decisions of equal importance, clear general models remain to be discovered. Furthermore, many interesting models proposed over the last two decades have received little or no testing. This is true even for situations where simple optimality approaches apply; the investigation of social impacts on these decisions adds new challenges and should receive a strong impetus with Giraldeau and Caraco's (2000) book.

Extending the scope of foraging studies will yield fascinating insights into the links between behavior and the neuroscience of information acquisition and processing. The field of risk-sensitive foraging illustrates these connections. While there was not space in this chapter to discuss how animals deal with variance in foraging and other fitness benefits, this is currently a lively area (see Kacelnik and Bateson 1996 and other papers in the same symposium). Foraging studies can provide valuable insights for other areas of physiology. The conceptual framework of foraging is closely related to that of the acquisition of water, minerals, and oxygen, and these processes can be studied with similar approaches, even though different physiological systems are involved.

Optimal foraging arose from questions raised by community ecologists but developed with a focus on individual behavior. Our understanding of foraging is now such that the field can make a real contribution at the levels of population and community. Although ecological situations are often too complex for predictions based on simple behavioral theories, the theory and empirical base provided by foraging studies provide important insights into processes of linking behavior and populations.

Acknowledgments I thank the many undergraduates and graduate students and postdoctoral scholars who have worked with me on chipmunk behavior at McGill over the past 25 years as well as colleagues at many other institutions who have offered feedback and made constructive suggestions. D. Gidley, L.-A. Giraldeau, C. Hall, M. Humphries, P. McDougall, C. Schiffer, and H. Young provided helpful feedback on an earlier draft. M. Humphries and D. Roff provided timely help with the figures. Our research has been funded by NSERC Canada and FCAR Quebec and has been greatly aided by the staff and facilities of the Gault Nature Reserve in St. Hilaire.