

Chapter 7: The Ecology of Foraging

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The Ecology of Foraging Interactions

Animals forage for resources in the face of ecological constraints (Mangel and Clark 1986). Foraging often occurs under the watchful eye of a predator. The risk of predation is an ever-present danger and an animal's foraging behavior reflects this risk even in the physical absence of an actual predator. Vigilance is the state of arousal required for an alert animal to detect predators (Lima and Dill 1990). Animals pay a price of decreased intake as a cost for the increased vigilance required under the risk of predation. The nature of the risk is entirely analogous to the way theft can structure human society. How many of us have seen a thief stealing something of ours? Even though the actual frequency with which we have something stolen is low, the threat of theft leads us to certain preventative behaviors. Because theft is a reality, we pay a penalty that is staggering to comprehend. Think of a society without theft. No locks on cars, no lock downs for computers, no car alarms, and no theft insurance. On a slightly grander scale, no countries would attempt to steal land, and thus, perhaps no money would need to be spent on defense, therefore there would be no war. Animals pay similar penalties for their vigilance. Because the actual occurrence of predation is rare (an individual is only killed by a predator once), most studies of predation and foraging involve placing animals under the baleful eye of a stuffed predator. Foragers face risks from predators who are themselves foraging in the environment for their own prey. A spider forages for flies, while a bird forages for spiders. All of these factors reflect the **social and ecological constraints** on foraging.

In chapter 6, we considered animals foraging in isolation. In reality animals forage in complex ecosystems and social interactions. The view that animals forage on uniform patches of land is overly simplistic. This view ignores variation in patch quality and competition among animals for the best territory. Life is lot more interesting when predation risk or competition pressure alter the behavior of foraging animals. It is easy to see how competitors might interfere with resource acquisition. A concentrated resource can be defended, thus an individual might form a territory around the resource and exclude all others from the territory. Territory defense is not without its attendant costs, and the economically minded territory holder must balance the benefits of territoriality against the cost of defending their precious patch.

Territory defense is not the only way animals exploit their competitors. Information is also a precious commodity. Any knowledge gained regarding the location of a resource benefits the collector of information because they can return to exploit that patch in the future. However, competitors that are watching the forager might gain information that allows the competitor to exploit the patch. Humans have enacted elaborate conventions to circumvent the exploitation of information. We have copyright laws and patent laws that span the globe. Encryption laws are intended to make sure that terrorists and spies cannot pass top-secret information via computers. Each of these laws were developed to prevent the theft of ideas. Animals are not so fortunate in this regard, and they must forage with the risk that other individuals might usurp the information that they have acquired. In this chapter, we will explore how foraging behaviors are shaped by the presence of predators, and how foraging might be modified in the presence of competitors.

Foraging and Predation Risk

Stickleback Foraging under the Watchful Eye of a Kingfisher

Sticklebacks often face the threat of aerial predators as they forage for food among the weeds of their pond. The aerial predator is often a kingfisher, which hovers above ponds and charges headlong into the water when it detects prey (Milinski and Heller 1978). The sticklebacks are searching for small crustacea such as *Daphnia* spp., the water flea. At the same time, sticklebacks, must be vigilant to an attack from predatory of kingfishers.

In the absence of predators, the feeding efficiency (number of *Daphnia*/min) of the stickleback is far greater when feeding on a dense swarm of prey compared to a less dense swarm. However, when predators are present (or at least possibly present) the stickleback faces a perceptual dilemma. When feeding on dense swarms the sticklebacks' ability to attend to other visual stimuli, such as an approaching predator, is reduced. To feed on a dense swarm, the stickleback has to contend with the **confusion effect** generated by its prey (Welty 1934; Curio 1976). When a forager faces multiple moving targets, they experience difficulty feeding on any one prey. Under such conditions, the stickleback might actually prefer to feed on the less dense swarm so that

it is able to divide its attention between foraging and **predator vigilance** (Lima and Dill 1990).

Manfred Milinski and Rolf Heller (1978) tested sticklebacks for the trade-off between energy maximization and predator vigilance. They predicted that the preference of sticklebacks for dense prey swarms would be altered by the presence or absence of a predator. They used the silhouette of a European kingfisher, *Alcedo atthis*, gliding on two nylon threads as a predatory threat. Some sticklebacks experienced predation threat at the start of the trial, while others did not. After the initial period of holding in the start compartment with and without the threat predation, sticklebacks were released to forage in the tank (Fig. 7.1).

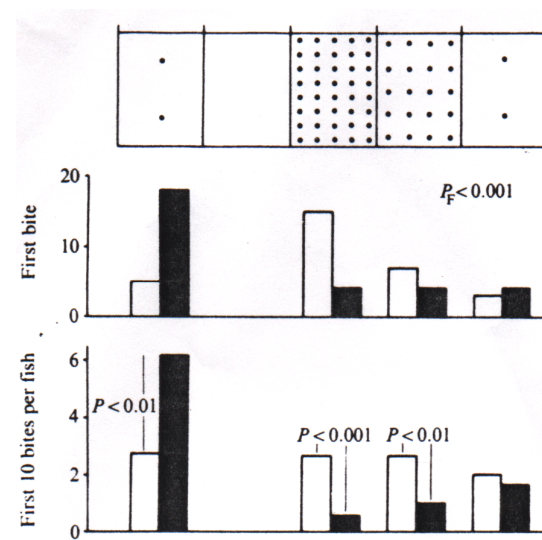


Figure 7.1. (top panel) The feeding side of an experimental aquarium used by Milinski and Heller (1978) in the foraging experiment on sticklebacks, *Gasterosteus aculeatus*, feeding on *Daphnia magna*. Density of *Daphnia* on the feeding tank is shown by dots. In the absence of a predator (white bars), the fish prefer to feed on dense swarms of *Daphnia* as judged by frequency of first bite and first ten bites on each of the *Daphnia* density treatment. Presence of a predator (kingfisher silhouette) reverses preference to the low-density sides of the feeding tank (black bars) (Milinski 1978).

The feeding tank for the foraging stickleback was divided into a start compartment at the front and a feeding compartment at the back of the tank. The feeding compartment was further divided into cells that contained the prey items at different densities. Sticklebacks had a choice of feeding on low, medium, and high densities. The sticklebacks could not actually feed on the *Daphnia* because Plexiglas enclosed them. As sticklebacks attempted to bite the *Daphnia*, the researchers recorded the

number of bites directed towards each density of prey. The number of attempts is used as an index of the sticklebacks' preference for prey density. As predicted, sticklebacks had a higher preference for feeding on low-density swarms of *Daphnia* after exposure to the predator than those that were not exposed to a predator (Fig. 7.1). It appears that sticklebacks are sensitive to the presence of a predator when balancing the conflicting needs of foraging and vigilance.

Foraging and Predation Risk in a central place forager

The example of a parental starling presented in Chapter 6, is an example of a central place forager. The foraging honeybee or bumblebee that returns to a hive is also a central place forager. The concept of **central place foraging** is a special case of the marginal value theorem (Stephens and Krebs 1986). Animals that forage around a retreat site such as beavers at a lodge (Holder and Polis 1987; Fryxell and Doucet 1991), gophers around the edge of a colony, pack rats around their packrat middens, or ants around a colony (Holder and Polis 1987), all face conceptually similar distance or time constraints that arise as they travel to and from a central location after visiting food resources located at some distance from the central place. The question is, how many items should an individual collect before returning to the retreat, storehouse, or larder? Another question arises regarding how best to exploit the resource around the central retreat before perhaps moving on to the next site. A central place forager can minimize risk of predation by staying close to their burrow or retreat site.

Chipmunks are also central place foragers (Giraldeau and Kramer 1982) that search the soil around their burrow for seeds. The loading curve for chipmunks relates to the size of their chubby cheeks. When a chipmunk finds a patch of seeds, it begins stuffing its cheek pouches. The more it stuffs in its cheeks, the slower it stuffs. There should be a load size that provides an optimal gain of energy, given the loading curve, and the round trip back to the burrow where the load of seeds is dumped. Giraldeau and Kramer (1982) provided chipmunks with patches of sunflower seeds at varying distances from their burrows.

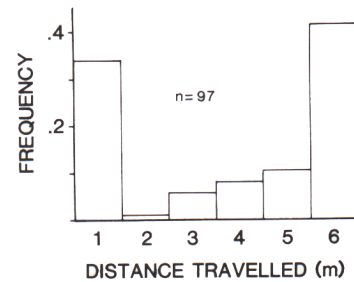
As the chipmunks stuffed their cheek pouches, the rate of seed collection declined in a fashion that was similar to the theoretical gain

curve. In addition, the chipmunks spent longer in each patch and took larger loads when visiting more distant patches from their burrow.

While these trends were present, there wasn't an exact match between the theoretical and predicted values, suggesting that other factors might have played a role in the chipmunks decision to return to its burrow. A striking mismatch between the expected and predicted pattern of foraging was that the chipmunks spent much less time in the patch than predicted under a model of optimal foraging. If chipmunks were paying attention to something intangible that could not be reconciled in the same currency as foraging efficiency, we might expect their observed behavior to be quite different from the behavior predicted from an optimal foraging model that only considered energy. Chipmunks may be foraging against competitors, and they may also be alert to predators. Without competition, the chipmunk would have less of a need to hoard items in a food cache (Lair et al. 1994). Without predation, the chipmunk could relax peacefully at the foraging site and perhaps eat the seed there. Subsequent experiments on central-place foraging by the chipmunk have revealed that the amount of time they are willing to spend in a patch is dependent on how much cover there is around the patch (Bowers and Ellis 1993; Bowers 1995), which tends to minimize the chipmunks perceived risk of predation. More cover means more time spent in the patch. A poor chipmunk has so much to think about; so many decisions to make.

Steve Lima and colleagues (1985) designed a set of experiments to test foraging in the grey squirrel, *Sciurus carolinensis*. Lima et al. (1985) were specifically interested in how a foraging squirrel trades off the risk between foraging efficiency and minimizing the risk of predation. They chose to study squirrels that forage on seeds in open areas where exposure to predators was high. They did not in fact, ever observe a predation event, but nevertheless they observed behavior that is consistent with predator avoidance. A grey squirrel, unlike a chipmunk, is not interested in caching much of its food. Instead squirrels pack on extra body fat for hibernation. A squirrel prefers to eat items where they are found. The basic discrepancy that led Lima and his team to infer predator avoidance is that squirrels used two different foraging behaviors: some would eat seeds where they found them, while others would scurry to cover to eat the seeds and then return for more.

Figure 7.2. Frequency distribution of seeds carried before consumption by foraging grey squirrels, *Sciurus carolinensis*. Seeds consumed where they were found (1 m) were out in the open, whereas seeds that were consumed under the protection of cover were carried 6 m (from Lima et al. 1985).



A simple model of the conflict between predation risk and energy acquisition can explain the behavior of squirrels. Let's take two extreme perspectives. Assume: 1) the squirrel minimizes risk of predation or 2) the squirrel maximizes intake. A squirrel interested in minimizing predation risk would take each seed to cover, regardless of distance to cover. However, the squirrel spends time traveling to cover to avoid predation risk. Travel time limits energy intake, and travel is energetically expensive in terms of locomotion. A squirrel interested in maximizing gain would avoid any travel costs and eat the seeds where they are found. The observation of two kinds of behaviors (eat seeds on the spot or retreat to cover to eat) in the squirrels suggests that they are torn between the two constraints: minimize risk and maximize gain.

Consider the likelihood of risk avoidance (retreat) versus energy maximization (stay) if the size of the seed is varied. If seeds are small, there is far less to be gained from traveling to cover. A small seed can be consumed rapidly. However, consuming a large seed takes time, and the energy spent to travel back to cover is minimal compared to the risk of consuming large seeds in an open area. Lima et al reasoned from their model that a squirrel is presented with a conflict if the time taken to travel to cover is similar to the time taken to consume a seed. As seed size increases, squirrels should travel back to cover with a higher frequency. However, as the distance to cover increases, the squirrel should be less likely to travel the distance. If the distance to cover is great, there really is no gain from retreating. Too much back and forth motion between cover and open areas could alert a predator. If the distance between seed to cover is large, the squirrel should eat the seed rather than travel back to cover. Lima et al. (1985) varied the size of the seeds and the distance to cover to test these ideas.

The qualitative behavior of the squirrels fit their model fairly well. As distance to cover increased, the squirrels were less likely to carry the seed back to cover. As seed size increased, squirrels were more likely to carry the seed to cover. An unexpected finding of this study was a difference between solitary squirrels and squirrels feeding in groups. Many of the squirrels feeding in groups opted to retreat to cover at a higher rate. The retreat was usually associated with agonistic interactions at the feeding site, suggesting that social interactions as well as the size of the seed, distance to cover, and relative risk of predation modify foraging decisions by squirrels.

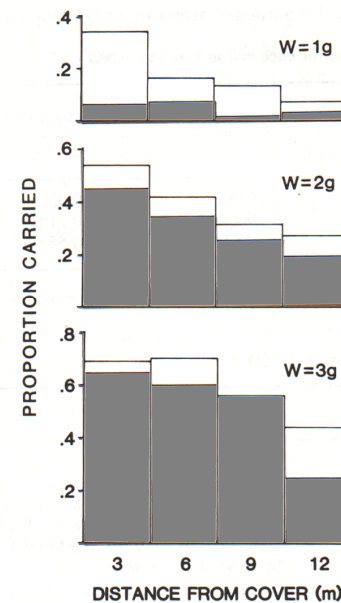


Figure 7.3. The effect of varying seed size (g) and distance of seed piles from cover (m) on the probability that a grey squirrel, *Sciurus carolinensis*, will carry the seed to cover before eating. The dark areas represent the probability that solitary squirrels return to cover, while the additional light areas represent the increased likelihood that squirrels feeding in groups return to cover. In the context of group feeding, retreat is usually preceded by an agonistic interaction between dominant and subordinate squirrels (from Lima et al 1985).

Equating Currencies of Predation Risk with Energy Maximization

One of the challenges raised by Lima and his colleagues (1985; Lima and Valone 1986) is the difficulty of reconciling the currency of energy maximization with the currency of predation risk. There is no practical way to equate the two currencies because energy is measured in calories, while predation is measured in terms of decreased survival. This would also be true for the sticklebacks studied by Milinski and Heller (1978). Because we cannot find a common currency that allows us to compare maximization of energy to minimization of predation risk, it is challenging to generate quantitative predictions for animals in nature.

Early in the development of foraging theory, a few situations were identified where the two currencies might be reconciled. Gilliam (1982) suggested that there might be specific situations where it would be possible to equate the maximization of energy gain and the minimization of predation risk. If body size was related to risk of predation, then foraging could be tied to body size and energy maximization through a growth rate trade-off. Energy maximization would affect growth and likewise growth may be related to escaping a risk of predation. The only challenge that remained is developing a theory, which relates behavior to foraging, foraging to growth, and growth to mortality. The complexity of the problem led to the development of a new theoretical approach referred to as **dynamic optimization**. The optimal solution an animal tracks is dynamic, in that it changes with time and as the animal grows. The approach is quite powerful and has been applied to diverse problems of behavioral optimization. The details of the modeling can be found in Stephens and Krebs (1986) and Mangel and Clarke (1986).

We can look at the choices faced by bluegill sunfish, *Lepomis macrochirus*, when it forages as a small juvenile compared to a large adult (Gilliam 1982). Mortality is always greater for small fish because they are slower and easier to eat. The faster a fish grows, the sooner it lowers its risk of predation. To avoid predation, small bluegill sunfish seek the safety of the weedy shoreline. There are abundant small prey in the weeds, which can sustain a small fish's needs. However, at a certain size, the bluegill can only maximize its energy intake in the open water when feeding on plankton. Bluegills face a dilemma as their size changes. They should stay in the weeds until they reach a certain size. Once they have reached this critical size threshold, they should begin to

forage in the open water. While foraging in the open water is riskier, a bluegill sunfish that is large enough can escape being eaten by its predator, a large-mouth bass that doesn't have a large enough mouth.

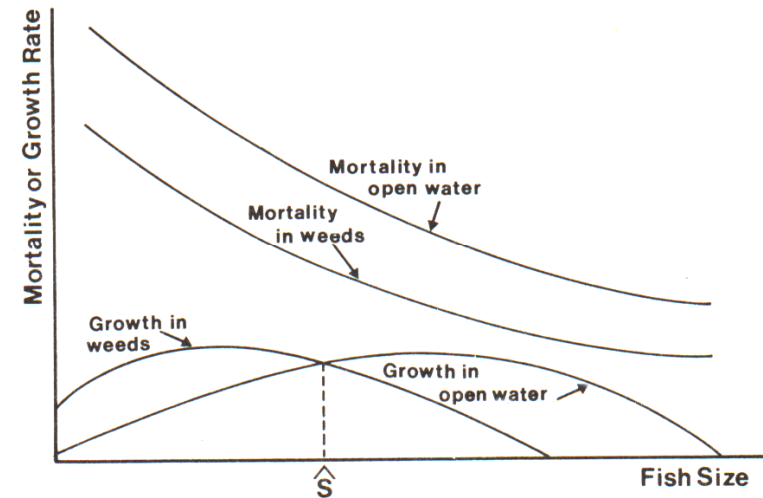


Figure 7.4. The relevant tradeoffs between foraging in weeds, and open water as a function of bluegill sunfish (*Lepomis macrochirus*) size. Mortality is expected to change as the fish's size changes. As they grow, the risk of mortality is reduced. At some point, the fish should opt to switch from foraging in weeds to foraging in the open water (\hat{S}) because it can grow faster and escape predation due to its newly gained larger size (from Stephens and Krebs, 1986 after Gilliam 1982).

Werner and Hall (1988) applied the dynamic optimization model to predict the optimal size threshold for switching between habitats of weeds and habitats of open water. Werner and Hall verified several assumptions of Gilliam's model. First, bluegills can indeed grow much faster in the open water because this area is a much more profitable feeding area. However, the risk of predation by largemouth bass, *Micropterus salmoides*, in the open water for a small fish is elevated 40-80 times compared to the shoreline habitat of weeds. Werner and Hall found that the sunfish were sensitive to the population density of the large-mouth bass. The optimal body size when bluegills shift from the

weeds to the open water varied from 50 mm in low-predation lakes, to as high as 83 mm in high predation lakes. While using foraging currencies based on growth rate is not possible in all situations, the optimal foraging solution appears to be used by bluegills. In addition, bluegills appear to be able to adjust the costs and benefits according to the level of risk they face in a given lake.

Foraging and Competition

Competition poses a similar challenge to the development of predictive models. Fortunately, a relatively simple **null model** was developed to explain the distribution of competitors around a resource. Null models are useful in biology as they predict what kinds of patterns we might expect if certain simple conditions are met. Fretwell and Lucas developed the concept of **the ideal free distribution** to explore how competitors and patch quality affect foraging behavior (Fretwell and Lucas 1969; Fretwell and Lucas 1970; Fretwell 1972). Variations on the ideal free distribution in foraging ecology were also developed by Brown to explain territories (1964) and by Orians (1969) to explain the mating systems of birds (see Chapter 11). The ideal free distribution answers a minor paradox of animal behavior. If animals are free to choose among patches that vary in quality, why aren't all animals clamoring for the best patches? The poorest patches should be empty of foragers, but this is rarely the case. Poor patches are often occupied by many animals.

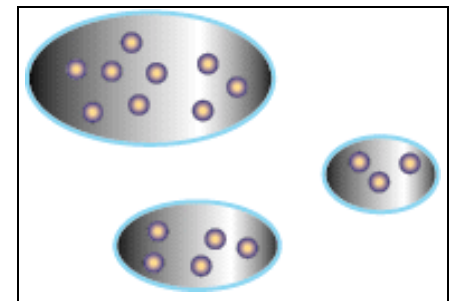
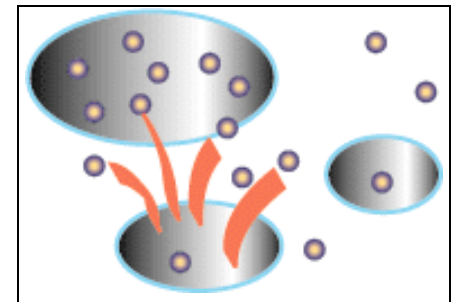
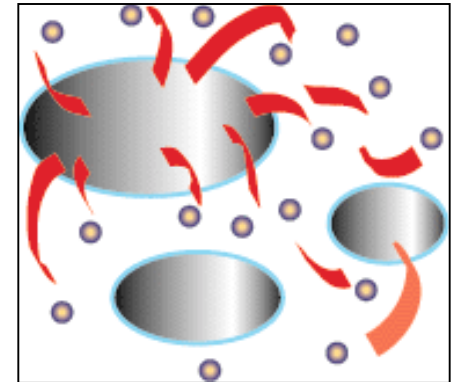
The ideal free distribution posits that animals that are **free** to sample the environment will **distribute** themselves among patches in proportion to the quality of each patch. These are the two premises of the null model. After a period of sampling, the animals begin to settle into patches as a function of the payoff that they experience in a patch (see Side Box 7.1). As competitors flood the best patches, they depress the quality of the patch to the point where the poorer patches now appear to be better. Animals should be distributed among patches in densities proportional to the ability of a patch to support the animals.

Side Box 7.1. Competitors and the Ideal Free Distribution

Ideal free refers to an animal that is **free** to move between patches under **ideal** conditions with no constraints on movement. Animals should **distribute** themselves in areas with the highest gains. Consider patch size as a measure of quality. Animals exploit high quality patches first and avoid low quality patches.

A problem arises for the individuals as more and competitors move into high quality patches. If too many competitors move into high quality patches, then it actually pays for some to move to the patch of next highest quality. Gains from these patches are higher. Animals move among patches until they find the highest gains, and those with low gain move.

At equilibrium, all patches are filled in proportion to patch quality. Every competitor does equally well, and it does not pay to move among patches. The ideal free distribution is a simple concept, but it can explain foraging behavior in the lab and nature.



Ideal Free Fish

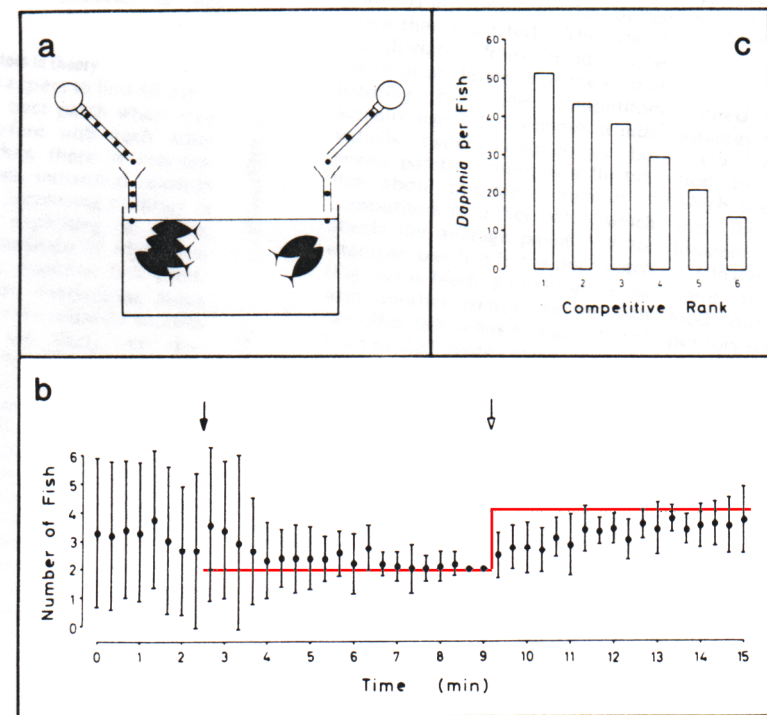
Do animals follow an ideal free distribution? The key is to pick the right time-scale to observe animals making such ideal free decisions, and allow the animals time to arrive at an equilibrium. A test of the ideal free distribution requires that animals are capable of some freedom of movement, and sampling of the environment must take place in a short enough period of time so that the animals can adjust their density among patches.

It is for these reasons that Manfred Milinski (1988) used sticklebacks, *Gasterosteus aculeatus*, feeding on patches of *Daphnia magna*, to test the principles of the ideal free distribution. Many aquatic animals appear to adhere to ideal free principles when foraging. The ideal free distribution has been shown from experiments conducted on the guppy, *Poecilia reticulata* (Dill 1987), the zebrafish, *Brachydanio rerio* (Gillis and Kramer 1987), the minnow, *Phoxinus phoxinus* (Pitcher et al. 1988), the goldfish, *Carassius auratus* (Sutherland et al. 1988), the water flea, *Daphnia pulex* (Jakobsen and Johnsen 1987) and aquatic birds such as the duck, *Ana platyrhynchos* (Spencer et al. 1995) and the swan (Milinski et al. 1995).

As we will see in upcoming chapters, the concepts of ideal free distributions extend beyond theory developed for foraging on food to foraging for mates (Orians 1969). The ideal free distribution is a simple but extremely powerful concept that operates across many behavioral contexts.

Figure 7.5. a) Sticklebacks are nearly ideal free fish when feeding at food patches. b) Equal food is delivered at both sides of the aquarium at the start of the trial. At two minutes, twice as much food is delivered on one side relative to the other. At nine minutes, the patch quality is reversed between the two sides of the aquarium. Fish redistribute themselves at the two patches in a ratio that corresponds to the patch quality (number of *Daphnia* delivered). If fish were ideal free, they should track the horizontal line. c) Discrepancies between truly ideal free fish were caused by slight differences in the competitive rank of the fish. Lower ranking fish that fed on less *Daphnia* tended to be found in the low quality patch while more competitive fish were found in the high quality patch. (from Milinski 1989).

Manfred Milinski's test of the ideal free distribution entailed a tank of six fish with two feeding stations located on either end. At the outset of the experiment, the feeding rate at the two stations was the same. Under these conditions patch quality was identical, and the six fish distributed themselves equally between the two stations. At the two-minute time point, the number of *Daphnia* supplied at one station doubled relative to the delivery rate at the other station. Under the predictions of the ideal free distribution, the fish should rapidly redistribute themselves between stations in the same proportion as the difference in food delivery: four at the high food station, two at the low food station. Sticklebacks appear to think ideal free; as predicted, they moved towards the station within 1.5 minutes of the change in patch quality. Finally, Milinski switched the rate of delivery between the two sides of the tank at 9 minutes, and again the fish adjusted according to a predicted ideal free distribution, but it took longer on the second manipulation of food delivery. Because the sticklebacks matched their distribution to the input of food into a patch,

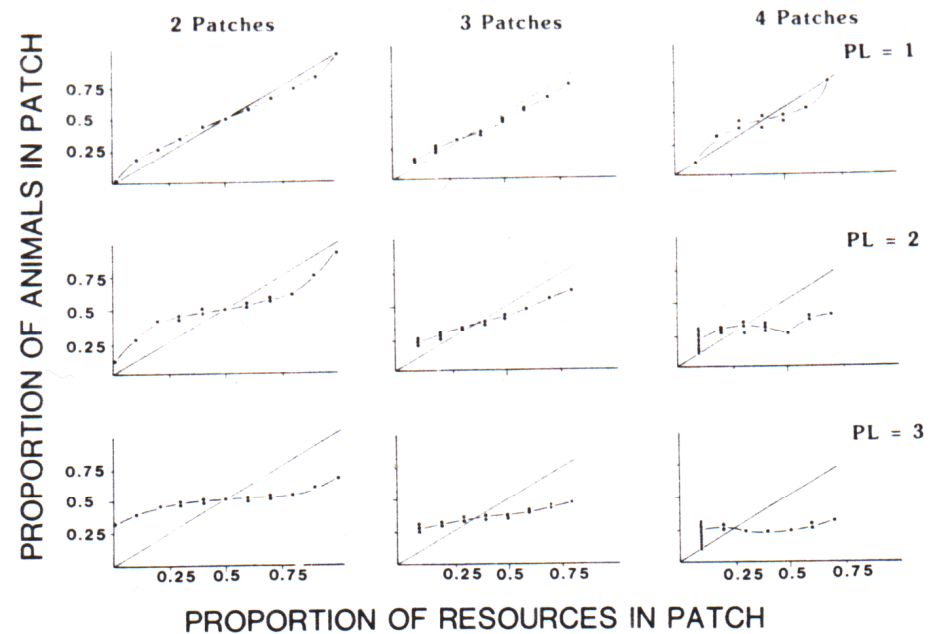


their behavior under the ideal free distribution is referred to as **input matching**. A group of foraging animals match their own distribution in proportion to the rate of food delivery into a patch or the patch's productivity. However, Milinski's fish were not quite ideal free. Fish that were judged to have higher competitive ability based on the number of *Daphnia* they consumed, tended to be found in the high quality patch. Less competitive fish tended to favor the low quality patch. Nevertheless, these fish fit key aspects of the ideal free distribution in that they maximized their food intake by distributing themselves in an ideal free manner between the two patches. However, some fish did not seem quite as free as others in their choice of feeding stations.

One of the key assumptions of the ideal free distribution is the notion that animals have perfect knowledge regarding the distribution of resources. As we have seen in Chapter 6, time constraints on sampling, perceptual constraints, and an imperfect memory serve to limit the acquisition of information, and thus the ability to achieve an ideal free distribution. While the list of animals that appear to conform to an ideal free distribution is lengthy, other research shows that many animals exhibit striking departures from the ideal free distribution. Abrahams developed a model of perceptual constraints that can be explicitly tested in organisms to provide a more critical test of the ideal free distribution (Abrahams 1986). If animals are capable of detecting all differences in resource quality between sites, then animals should distribute in an ideal free pattern based on relative difference in resource distributions, regardless of the absolute of difference in resource distributions (e.g., 1:12 should be perceived the same as 10:120).

If perception of resource value varies among animals (e.g., some have poorer perceptive abilities), then a small difference in resource distribution would be perceived of as equivalent by some animals, and they would distribute themselves randomly between sites. In contrast, animals that possess superior perceptive abilities may be able to perceive the differences among patches and distribute themselves in an ideal free distribution, and thereby maximize energy return. A model of perceptual constraints predicts that departures of ideal free distribution (i.e., a random distribution between patches) will be seen when the *absolute difference* between patches is small.

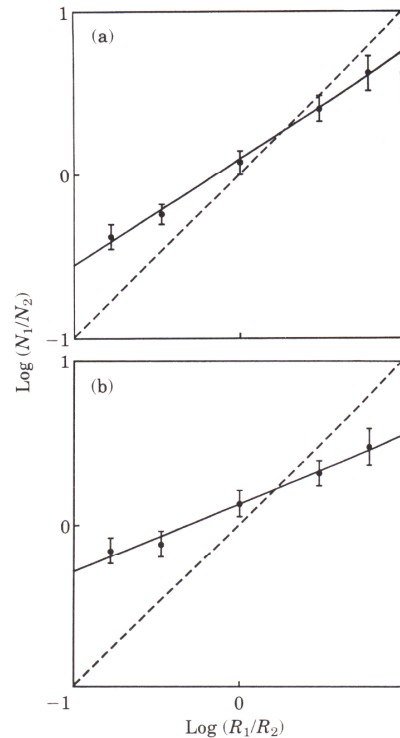
Figure 7.6. Theoretical effects of perceptual constraints and number of patches to search on the expectation of an ideal free distribution. If animals were distributed ideal free, the proportion of animals in a patch should equal the proportion of resources in a patch and the points would fall on the 1:1 line. However, increasing the number of patches, or decreasing the perceptive ability of animals causes fewer animals to be found in the rich patches and correspondingly more in the poor patches than would be expected under ideal free distribution. A higher perceptual limit (PL) implies that a difference between good and bad patches must be large before foragers can detect the difference. PL is a threshold value of perception analogous to the concept of resolving power of a microscope (ability to see 2 things as distinct). A completely flat response from the simulated foragers would imply no preference or random choice (from Abrahams 1986), which occurs when PL is high.



Gray and Kennedy (1994) applied a version of Abrahams perceptual constraints model (Spencer et al. 1995; Spencer et al. 1996) to foraging ducks and found that the ducks were nearly ideal free in their distribution among food patches, but only when absolute variation

among patches was large. A simulation of the duck's perception of resource value demonstrated that only a small ability at perceptual resolution was required to explain a large departure in the distribution of ducks from ideal free expectations.

Figure 7.8. The discrepancy between the expected ideal free distribution (dashed line, no perceptual constraints) and observed distribution (points, solid line) for mallard ducks, *Anas platyrhynchos*, feeding on two resource levels. Ducks had a choice among five feeding stations, which varied in resource input. The same relative input ratios of food at the five patches (6:1, 3:1, 1:1, 1:3, 1:6) was used in both the case of high and low levels of overall food delivery to the five patches. a) Under the conditions of the high food treatment the ducks received 20 pieces of bread per min spread out over all 5 patches in the ratios given above. b) In contrast, under conditions of the low food treatment the ducks received 3.3 pieces of bread per min spread out over all 5 patches in the ratios given above. Even though the relative input ratios were similar among high versus low resource treatments, the departure from IFD (1:1 line) is greater under the low food resource. A model of perceptual constraints would predict that the ducks would be less able to discern the differences among stations if the absolute differences are small (e.g., low overall resource input to the 5 stations) compared to large (e.g., high overall resource input to the 5 stations) (from Gray and Kennedy, 1994).



The density of competitors among foragers for resources at patches will have a similar effect on ideal free expectations as the effect of perceptual constraints. As the competitors begin to interfere with each other in utilizing the resource, the number of animals in the dense patch interfere with each other a bit more than at the low quality patches (Sutherland 1983). There are more absolute numbers of animals at the high quality patch scurrying around furiously trying to get food. The effect of this 'scramble competition' for resources is to depress the

number of animals in rich patches compared to the numbers expected under ideal free, and correspondingly more animals are found in the poor patches than would be expected under ideal free. The high quality patches have too many animals trying to get at the resource and they interfere with each other's feeding rate (Gillis and Kramer 1987).

The ideal free distribution was used in an interesting experiment to titrate how guppies, *Poecilia reticulata*, equate a risk of predation with energy maximization. Abrahams and Dill (1989) used two feeding stations, one of which had a risk of predation; a predator was visible in an adjoining tank. Naturally, if rewards were equal between the two stations the fish would tend to avoid the predator side of the tank. However, as Abrahams and Dill increased the input of food at the predator station, the number of fish opting for the risky station increased until it equaled the number of fish at the less-risky but low-food-input station. The exact food level at which fish equilibrated between high and low risk stations is of minor importance. Rather, the difference in the response between the sexes is quite telling. Males were much less likely than females to approach the risky station. The sex difference is easy to reconcile in terms of a difference in energy needs between the sexes; female guppies require large amounts of energy for reproduction and thus are much more willing to elevate risk.

Laboratory tests of the departures from the ideal free distribution that are expected under perceptual constraints, interference from competition, and predation risk are really only in their infancy. Milinski's experiments (1989) on fish suggest that movement may be restricted under most situation. Gray and Kennedy's (1994) experiments on ducks suggests that animal perception is likely to be constrained. Variation in perception among individuals is likely to lead to a substantial deviation from the ideal free distribution (Abrahams 1986; Wetterer 1989; Spencer et al. 1995; Spencer et al. 1996) as will the effects of long-term memory (Milinski 1994). Even though the assumptions of the ideal free distribution are likely to be violated in most situations in nature, the idea is still a very useful "null hypothesis" for testing the distribution of animals among resource patches. The challenge for the future is devise tests of ideal free distribution in the wild to see whether foraging animals face similar constraints due to perception, competition, and predation risk that limit movement decisions among patches.

Ideal Despotic Distribution

A critical premise of the ideal free distribution is that all competitors are equally matched in competitive ability. Even under the best of circumstances, individuals vary in the ability to exclude competitors. Milinski's fish only behaved according to ideal free principles when the theory for competitive ability was adjusted. The ideal free distribution can be contrasted with its *döppelgänger* or evil twin, the **ideal despotic distribution**. If individuals that settle in an area are capable of excluding newcomers, than an ideal despotic distribution can result in a situation in which only a few individuals control the best resources. All of the other assumptions underlying the ideal free and ideal despotic distribution remain the same. Both kinds of distributions are ideal in that individuals have perfect knowledge, and the resulting distribution maximizes the fitness of the individuals. Unfortunately, under the ideal despotic distribution there is a large difference in fitness between the 'haves' and the 'have-nots'. The have-nots cannot get anything better. We will reserve discussion of the actual mechanics of conflict between territorial contestants to Chapter 8.

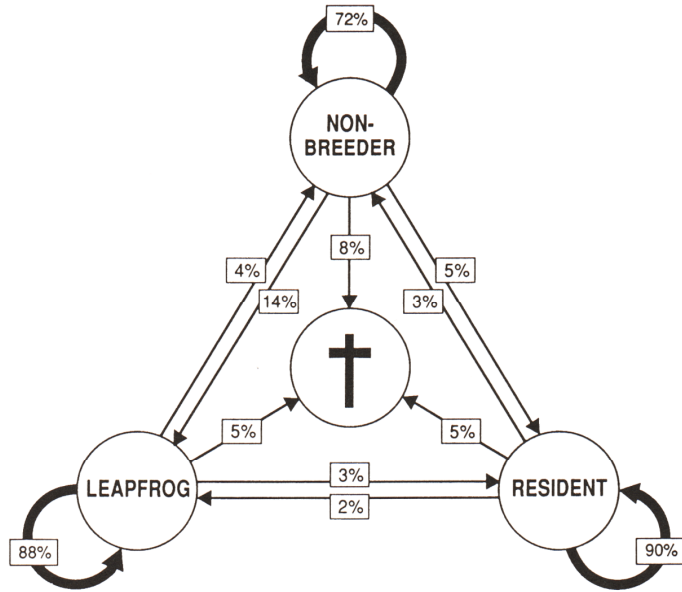
Figure 7.10. Ideal despotic distribution of breeding oystercatchers on a mudflat in the Netherlands. Small circles at the center of breeding territories denote breeding nests. 1) Residents acquire access to prime beachfront real estate (dark shading) and enjoy high reproductive success. 2) Leapfroggers still breed (clear territories to the right of residents), but must fly over the breeding and feeding territories of residents to gain access to their feeding territory on the mudflat (clear areas to right of residents). 3) Non-breeders have no breeding territory, but congregate at the 'CLUB' during high tide. With nowhere else to hang out, the CLUB serves as a refuge from high tide for non-breeders. Non-breeders vigorously defend a feeding territory in the mudflat. Non-breeders also engage in a hovering ceremony (top of figure), which are aggressive displays usually directed at other non-breeders, and occasionally at residents (from Ens et al 1995).



In chapter 6, we saw oystercatchers foraging optimally on the Dutch mussel mudflats. Bruno Ens and his colleagues (1995) have carried out detailed observations on the territories defended by pairs of oystercatchers. Oystercatchers spend a lot of time near the mudflats because their nesting sites are nearby. Of course, a mudflat is not a suitable site for a nest. Getting close to the mudflat is desirable because the nesting territory provides oystercatchers easy access to food for their developing young. In addition, once young are ready to learn the tricks of the oystercatcher trade (hammering or stabbing mussels, see Chapter

6) from their parents, they can simply wander off their territory into the mudflats without the need of flight. Not all oystercatchers are so lucky as to hold prime beachfront properties. The lucky few are referred to as 'residents'. Many oystercatchers nest a bit further inland, gaining access to food by 'leapfrogging' over resident's territories and then feeding at some distance into the mudflat. A third class of oystercatchers does not even gain access to a beachfront or interior breeding territory. These 'non-breeders' defend a feeding territory on the mudflat, but their reproductive success is zero because they do not hold a nesting territory. In contrast, reproductive success of residents is 0.67 chicks per year (Ens 1995), while reproductive success of leapfroggers is a mere 0.19. There is clearly a despotic distribution of resources for fledging young.

Figure 7.9. The probability that a pair of oystercatchers will change status from year to year. The central circle represents the state-of-no-return or death. Death is quite likely compared to the probability of upward mobility between the classes. The most likely outcome is no change in status (from Ens et al 1995).



Oystercatchers can live up to 35 years. The leapfroggers may eventually acquire beachfront property and enjoy higher reproductive success. Non-breeders must also wait to be a territory holder. The less fortunate non-breeders defer maturation while waiting in the queue in the hopes of securing prime real estate. It is far more likely for a non-breeder to inherit a low quality leapfrogger breeding territory (14%) than to inherit a high quality territory from a resident (5%). In fact, non-breeders are more likely to die (8%) than inherit the high quality territory. A ‘hopeful’ non-breeder is then faced with a dilemma, should it wait for the more likely leapfrogger territory or the less likely residents territory? Because these birds have such a long lifespan, we are not yet able to answer this question, but data collection continues. Ens and colleagues

who have studied oystercatchers for 10 years, have not found an obvious difference in competitive ability between the three classes of oystercatchers. Simple ownership of a quality site results in **site dominance** (e.g., see Chapter 8), which is enough to keep access to feeding and breeding territories strongly despotic and stable among pairs year after year. As we will see in Chapter 11, pairs of female oystercatchers cooperatively defend both their territories and young, so part of the despotic distribution may be due to social alliances.

Beavers, *Castor fiber*, illustrate the point that a despotic distribution can arise simply from the order in which a habitat is colonized. Beavers were extensively trapped out during the fur trade, but beavers are now making a comeback in many areas of North America. Nolet and Rossell (1994) capitalized on the emptiness of prime beaver habitat by reintroducing beavers to these areas. As the animals settled into the habitat, the distribution of the beavers approximated an ideal despotic distribution. The earliest settling beavers obtained the best territories.

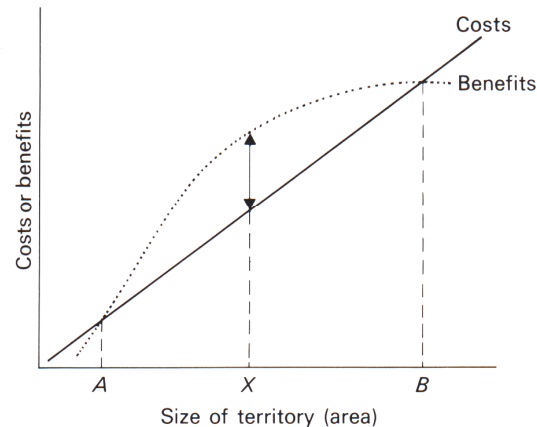
Like most rodents, beavers are central place foragers. Beavers are optimal central place foragers. For example, we can predict that beavers would opt to collect larger branches when foraging at a distance because increased travel costs make it more profitable to return with larger items; experiments and field observations show this to be the case (Mcginley and Whitman 1985). Given that beavers are sensitive to travel costs, the costs in winter are much higher compared to summer owing to a change in water temperature. In winter, the optimal territory size is smaller than in summer (Fryxell and Doucet 1991; Nolet and Rosell 1994), because swimming long distances in cold water is very expensive.

The ideal territory would allow a beaver to contract its territory in the winter to sustain its needs, and expand in the summer (Nolet and Rosell 1994) during energetically demanding periods of increased activity. Early settling beavers were able to set up such optimal-sized territories. In contrast, late settling beavers had to settle for sub-optimal territories that required them to travel longer distances from the lodge during winter-time foraging bouts. The early settling beavers appeared to have an ideal despotic distribution, largely achieved by the priority of occupancy. In Chapter 8, we will consider additional factors such as individual fighting ability that lead to success in territory establishment.

The costs and benefits of territorial behavior

Brown (1964) was the first to introduce the concept of economic defendability, in which the benefits of territoriality are balanced against the costs of defending that territory. Territory defense only occurs if the net benefits exceed the costs of defense. The costs of territoriality are generally thought to increase as the area of the territory increases. The benefits of territoriality should increase rapidly with small gains in territory size, but as resources become superabundant on the territory the benefits from increased territory size should level off because the rich resources exceed the individual's processing capacity.

Figure 7.11. The costs and benefits of a territory determine the economic defendability of a territory (Brown 1964). A territory size of **A** would be the minimum size of territory in which the cost of defense equals the benefit from territoriality. Conversely, a territory size of **B** would be the maximum size territory at which the benefit still exceeds the cost. A territory of size **X** would maximize energy gain because net gain = benefits-costs is the greatest possible (double-headed arrow) (from Davies and Houston (1978).

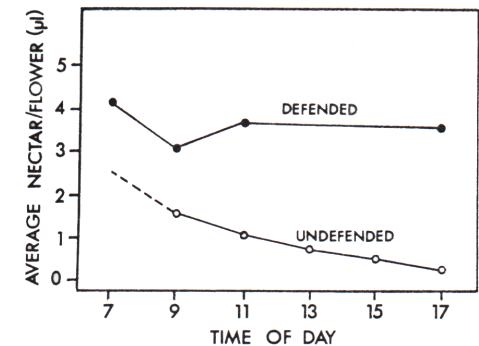


Energetic costs and benefits of territoriality are readily addressed with an organism that defends a static resource like flowers. Golden-wing sunbirds, *Nectarinia reichenowi*, are nectivores that are common in mountainous areas of Eastern Africa. Nectivores such as sunbirds (Pyke 1979), Hawaiian honeycreepers (Carpenter and MacMillen 1976), and hummingbirds (Montogomerie et al. 1984) derive much of their energy for metabolism from nectar that is provided by flowers. The flowers provide the nectar to attract the birds and insects, and the birds and insects serve as pollinators for the flower and transport pollen from flower to flower. The amount of nectar in a flower is relatively easy to

quantify by using a capillary tube and drawing the nectar out of the flower to measure its volume and sugar concentration or quality.

The amount of floral nectar found in undefended areas is generally lower than the amount of floral nectar found on a sunbird's territory. This pattern has at least two possible explanations. Flowers that are defended by sunbirds are less likely to be depleted during the course of the day by many different sunbirds and they retain a high value of floral nectar for the territory holder (Gill and Wolf 1975). Alternatively, sunbirds only defend the highest quality flowers, leaving the flowers that are poor producers of nectar undefended. These two alternative hypotheses can only be addressed with an experiment in which the resident sunbird is removed from a patch of flowers for several successive days. In addition, other sunbirds would be allowed to feed in the undefended area. The nectar volumes on the experimentally altered undefended flower patch (but previously defended) should drop to levels seen in flower patches that are naturally undefended. Such territory-holder removal experiments would have been useful but they were not conducted. However, Gill and Wolf (1975) did collect data that has been used extensively by others to test sophisticated models of the currency used in defense.

Figure 7.12. More nectar is present in flowers defended by golden-wing sunbirds, *Nectarinia reichenowi*, compared to undefended flowers. (Gill and Wolf 1975).



Pyke (1979) used Gill and Wolf's (1975) data to test a model of optimal territory defense based on energy maximization or cost minimization. Pyke computed the optimal number of flowers that should be on a sunbird's territory given that sunbirds maximize total daily intake of energy. Alternatively, sunbirds might minimize an alternative currency such as the costs of foraging. A key constraint on minimizing the cost of foraging is that they end up with a zero net energy balance during the

day (costs = gains). We can consider these two hypotheses in terms of Brown's ideas of economic defendability. The optimum territory size that maximizes energy intake would correspond to point **X** in Figure 7.11. In contrast, the territory size that minimizes costs while maintaining a net energy balance of zero would correspond to point **A** in Figure 7.11.

The predicted number of flowers for the energy maximization hypothesis was 9,628. In contrast, the predicted number of flowers under the cost minimization hypothesis was 1,576. In actuality, sunbirds defend a territory that consists of a relatively consistent 1,600 flowers which is remarkably close to the number predicted by the cost minimization hypothesis. This observation leads to the conclusion that sunbirds defend a group of flowers that is sufficient to supply their daily needs, but small enough to minimize total costs of defense, costs of foraging, baseline metabolic costs of sitting during the day, and fasting through the night. Similar studies indicate that hummingbirds defend a territory to obtain sufficient energy reserves to balance their daily energy needs, with enough energy leftover to make it through the night (Montogomerie et al. 1984). Sunbirds and hummingbirds, like the energy-conserving bees of Chapter 6, are efficiency freaks rather than workaholics.

Interestingly, the territorial behavior of sunbirds can be abandoned completely if it becomes uneconomical to defend flowers. When resources in flowers are plentiful, sunbirds have no need for hoarding them (Gill and Wolf 1975; Gill and Wolf 1977). Similar results have been reported for a variety of nectar feeding birds. Hawaiian honeycreepers, *Vestiaria coccinea*, will abandon territoriality when there is abundant food (Carpenter and MacMillen 1976). Conversely, when food availability declines to low levels, honeycreepers are no longer territorial because the costs of defense exceed the gains from a large territory. North American hummingbirds appear to adjust their territory size to include the enough flowers to sustain their energy needs (Kodric-Brown and Brown 1978). If several flower species are available and flowers vary in quality, hummingbirds adjust their territories to provide the same total amount of energy regardless of density and species of flower providing the nectar (Gass et al. 1976; Gass 1979; Gass and Montogomerie 1981). Experimental removal of flowers from a

hummingbirds territory causes the birds to expand their territory to include enough flowers so that the total energy from nectar remains constant (Kodric-Brown and Brown 1978).

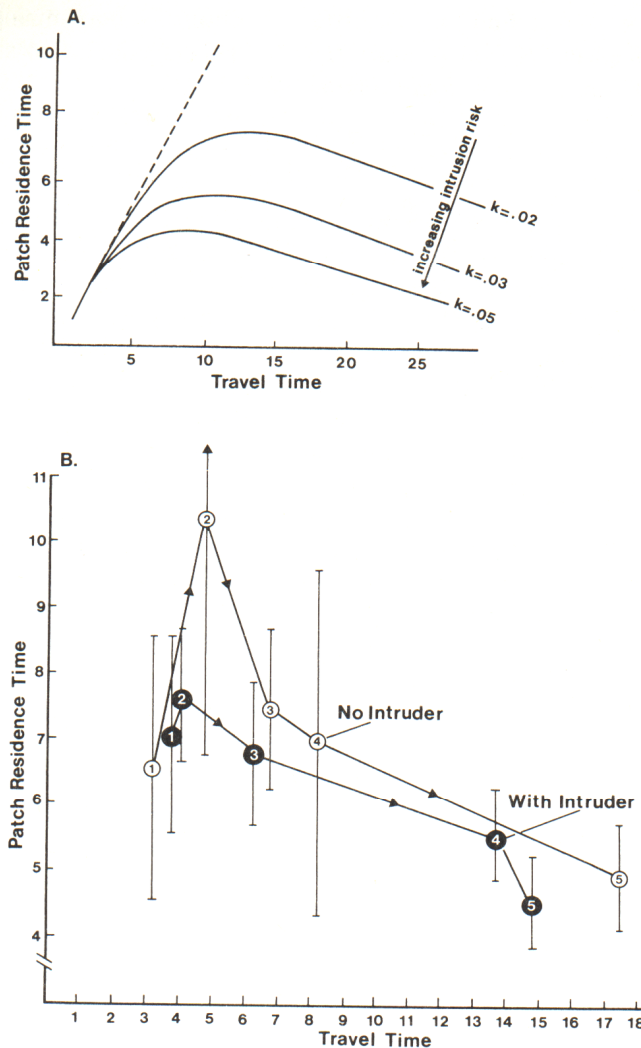
The Trade-off between Vigilance in Territory Defense and Foraging

The simple model of territory economics (Fig. 7.7) and the tests in nectivorous birds do not provide us with an explicit test of potential time conflicts between territory defense and foraging behavior. Does territorial defense reduce feeding rate? Ydenberg (1984), and Ydenberg and Houston (1986) tested this trade-off by training great tits to collect food rewards from a feeder. In a manner similar to Kacelnik's experiment on parental starlings (Chapter 6), they adjusted the food delivered at the platform by increasing the release rate of food during each feeding bout by the territory holders. This simulates the decrease in energy gain a bird would receive under the **marginal value theorem** (MVT). They also varied the distance of the feeder relative to the male's perch, which experimentally altered travel time to and from a patch.

Under the MVT a bird feeding at a distant patch should spend more time in the patch compared to a bird at a nearby patch (see Side Box 6.1, Chapter 6). Staying on a distant patch longer would increase the return rate and balance the costs of travel to the patch. There should be a simple linear increase between travel time to a patch and the amount of time a bird spends, provided the bird has no other concerns (Fig. 7.13). However, if a bird must split its time between feeding and territory defense, the amount of time a bird spends in more distant patches declines sharply as a function of increasing distance from the retreat site.

Ydenberg and Houston gave the trained males something to worry about back at their retreat site. When a male was on its retreat perch they could see another male in an adjoining cage. However, they could not see the male when foraging at the feeder. This simulates the conflict that a male experiences in nature (Stephens and Krebs 1986). When traveling or at rest a male can monitor his neighbors, but not when he is engaged in feeding. As predicted by a model of the trade-off between defense and feeding, male birds spent less time in a patch when the risk of intrusion was high and when another neighboring male was visible. When the neighboring male was removed, and the risk of intrusion risk was low, the birds increased the time spent feeding at a patch (Figure 7.13).

Figure 7.13. The dashed line provides the theoretical relationship between patch residence time and travel time based on the marginal value theorem (MVT). As travel time increases, a forager should stay in a patch longer (see Side Box 6.1 for the logic). The solid lines describe theoretical curves predicted for patch and residence time under the threat of territorial intrusion. Increased risk of intrusion causes a reduction in the time a territory holder stays on feeding patches (patch residence time), which are located away from the nest. Ydenberg and Houston (1986) tested the model with and without an intruder and found the predicted depression in patch residence time under threat of intrusion. From Stephens and Krebs (1986) after Ydenberg and Houston (1986).



However, territoriality *per se* appears to always depress the feeding rate relative to that possible under the MVT, because even when the intruder was not visible, the territory holder would spend less time in distant patches. The costs of vigilance for detecting predators is a constant force

faced by a territory holder. Territory defense is an energetically costly enterprise (e.g., sunbirds), and additional costs arise from lost feeding opportunity owing to the vigilance required to be alert to intruders (e.g., great tits). Other costs arise from the actual fighting that might occur on territories. If individuals do not have a territory, it may be necessary to take over a territory by force. In such cases, territory takeover entails the acquisition of a suite of information regarding the defensive and offensive capabilities of territorial holder before the decision to invade a territory is made. As was the case with foraging under the risk of predation, it is difficult to formulate these costs in terms of the currency that is used in optimal foraging decisions. However, in the case of competition, we can measure the costs that one individual imposes on another in terms of decreased fitness. The paradigm of evolutionary game theory is required to understand these ideas (Chapter 8).

Group Foraging

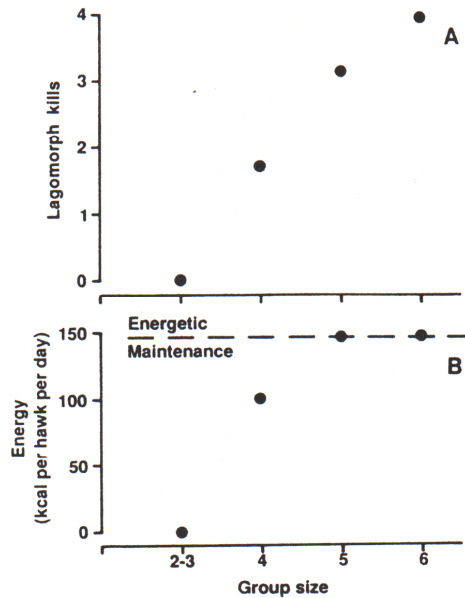
Optimal Foraging and Cooperative Hunting in Harris' Hawks

It seems intuitively appealing that teamwork during hunting should lead to higher success rate, particularly when hunting agile or unusually large prey. Raptors routinely hunt nimble-footed prey like rabbits. Group hunting has been reported for a number of raptors (Cade 1982) but good evidence for success as a function of group size is scant. Bednarz's work on Harris' Hawks, *Parabuteo unicinctus*, is exceptional in that data is available on success rate as a function of group size (Bednarz 1988).

Foraging success in Harris' Hawks is strongly related to group size. In addition, their quarry consists almost exclusively of large and speedy lagomorphs (e.g., jackrabbits, etc.) that are difficult to catch. Groups with fewer than 4 members were not successful on capturing the large lagomorphs, and they fed on smaller prey (e.g., rodents), which have a lower payoff. The optimal group size that would sustain an individual bird's daily energy needs was greater than or equal to 5 members.

Groups in Harris' Hawks consist of the breeding male and female in addition to zero to two adult "auxiliaries" that were raised on the breeding pair's territory, and zero to three immature hawks, reared the previous season (Bednarz 1988). Foraging groups of Harris' Hawks therefore have a high degree of kinship, and kin selection undoubtedly plays a major role in the benefits of cooperation.

Figure 7.14. A) Number of Lagomorph (e.g., jackrabbits) kills made per day for Harris' Hawks, *Parabuteo unicinctus*, that forage in various sized groups. B) Groups of Harris' Hawks must be greater than 5 or 6 in order to provide the minimum energy requirements for each group member on a per day basis, if the Hawks were only foraging on the wiley jackrabbits. (from Bednarz, 1988).



Optimal Group Size and Territoriality in Social Lions

Optimal foraging studies of lions illustrate how behaviorists refine ideas and how hypotheses are tested with new data. The following example shows how a comprehensive understanding of a problem may require entirely new solutions, which are beyond the current paradigm for explaining patterns. In the case of lions, the earliest paradigms only dealt with the economics of acquiring meat. When it was realized that there was a large discrepancy between the group sizes of lions predicted by theory and those observed in nature, additional solutions were sought. The solutions hit upon the conflicts and conflict resolution that occur in lion prides. New ideas of mutualism and kin selection were incorporated to explain discrepancies in foraging behavior.

Group foraging in lions, *Panthera leo*, has fascinated behavioral ecologists for decades ever since Schaller's (1972) classic observations suggested that lions hunting in large groups have a higher probability of success compared to small groups. Most of us are armchair natural historians when it comes to lions and other large beasts of the African savannahs, in that we have seen enough natural history documentaries to realize the basics of lion social structure but don't know much else about their complex social dynamic. Lions form prides or social groups of related females with a single male lion. Females do the 'lion's share' of

hunting. Given that females form kin groups, a complete consideration of the optimal group size in lions must consider the benefits arising from both individual fitness, and the inclusive fitness an individual female receives from cooperating with related members of the pride. Given this caveat, let's consider a simple foraging model of lion group size that ignores the benefits of kin associations.

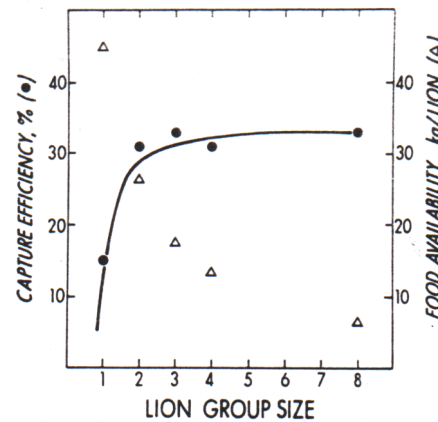


Figure 7.15 Capture efficiency (% prey captured) of lions rise with diminishing returns for larger groups (solid circles). However, amount of food available from a kill for each individual lion declines inversely with group size (triangles). (Caraco and Wolf 1975).

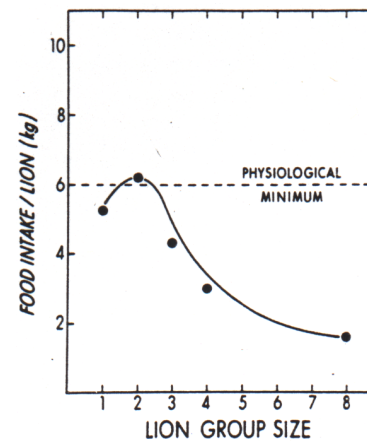


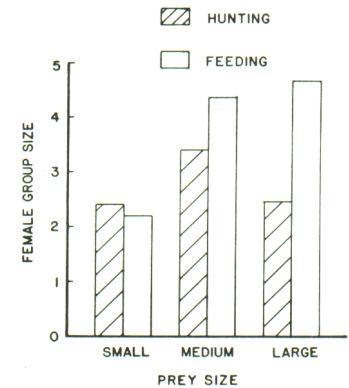
Figure 7.16. The optimum group size when feeding on gazelle reflects a tradeoff between an increase in efficiency of capture and a decrease in food per lion as a function of group size. The optimum group size is two lions. Two lions hunting and feeding on gazelle will just sustain the lion's energy needs (dashed line describing the minimum physiological requirements for a lion (Caraco and Wolf 1975)).

Caraco and Wolf (1975) analyzed Schaller's data in terms of the average daily food intake per individual as a function of foraging group size. Consider the optimal group size when feeding on a relatively small prey such as a Thomson's gazelle, *Gazella thomsoni*. Capture efficiency or the probability that a single lion takes down the prey is only 15%. The capture efficiency of two lions is more than doubled to 31%. Because capture efficiency levels off once two lions form a group (Figure 7.15), the predicted optimal hunting group size when stalking gazelle is two. Caraco and Wolf's explicit optimal foraging model weighed the marginal gains in capture probability against the reduced allotment per lion from sharing a single kill (Fig. 7.16). Similar computations for lions hunting the zebra, *Equus burchelli*, and the wildebeest, *Connochaetes taurinus*, indicate an optimal group size is two members. In contrast, the observed group sizes feeding on the kills ranged from 3.7 to 7 lions, far larger than the predicted group size, under simple optimal models.

The magnitude of discrepancy between theory and data begs alternative explanations for lion group size. Several studies during the ensuing decade provided intriguing solutions to optimal group size of lions. The discussion of these studies is meant to highlight the ways in which scientific inquiry leads to refinements of existing theory. In particular, while theory may adequately describe some phenomena, additional theory is required to fully understand a given pattern. The example of lions is useful because it illustrates the importance of understanding individual versus group interactions on fitness.

Packer (1986) pointed out that Schaller's (1972) data on number of lions feeding at a kill could not adequately test optimal group size of hunting lions. Many lions from the same pride would join a kill after the hunt to "share in the bounty". Both Caraco and Wolf (1975) and Packer (1986) advanced the view that a solitary lion could not possibly eat all of a kill. Estimates of a lion's gut capacity range from 30-50 kg (Clark 1987; Packer et al. 1990), and the modal weight of the prey is three times their gut capacity. In a waste-not-want-not fashion, the lions should share with the unsuccessful members of the pride, even if those members did not participate in the group's successful hunt. Packer's model predicted the number of lions to group sizes of 2.5 - 3.5, well within the observed group sizes of hunting lions, while the group size for feeding lions is always larger (e.g., Schaller [1972] observed 3-7.3 lions).

Figure 7.17. A comparison of hunting group sizes of lions and the number of lions observed feeding at the kill for small, medium, and large prey (from Packer 1986).



In parallel work, Colin Clark (1987) formalized observations on the discrepancy between hunting and feeding group sizes into a dynamic optimization model that predicted number of lions as a function of hunger level. Hungry lions should hunt and feed in small groups while nearly satiated lions should feed in larger groups. In theory, lions could increase their fitness by communally sharing kills, particularly if they were well fed.

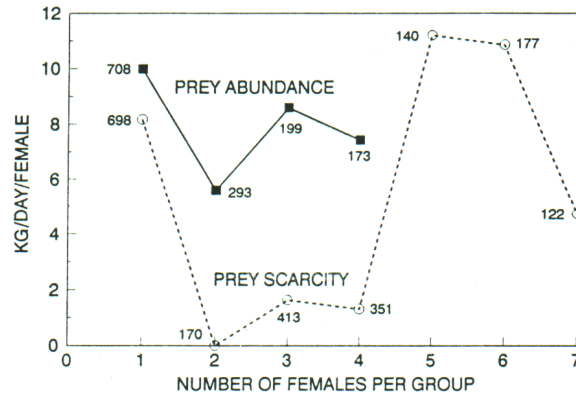
Another theory contends that what is optimal for the group is not necessarily the optimal strategy for the individual (Giraldeau and Gillis 1985). This issue contrasts selection on individuals versus selection on groups. The decision of whether or not a single lion should join a group is an individually based decision. An individual should only join a group when it will enhance the individual's fitness. In other words, an individual should join a group whenever the fitness of joining is greater than the fitness of remaining alone. There may be situations when it is advantageous for an individual to join a group that is already of optimal size, and thus the individual's fitness is enhanced. However, the act of an individual joining with an already optimal-sized group may cause the group's fitness to be reduced because the group becomes too large. Thus, the optimal group size is not necessarily stable in the evolutionary long run (Sibly 1983). Individuals that can gain fitness by joining a group may in turn reduce group fitness (see Group selection, Chapter 4).

The notion of an optimal group size in lions is also complicated by kin relationships among female lions, which on average have a coefficient of relatedness, $r = 0.2$ (see Chapter 4). Because of this relationship, we can predict that individuals would join groups if their fitness when solitary is less than their inclusive fitness in a group. Thus, a lioness should join a group when joining would yield a higher payoff from the

direct benefits for her in the group plus the indirect fitness gains through the help provided to related kin, compared to the fitness that she experiences alone. Groups should sometimes accept additional kin members to prevent close relatives from incurring a low-payoff solitary foraging strategy. Predicted group size with the calculations of inclusive fitness are 2 lions when hunting gazelle and 3 lions when hunting wildebeest and zebra. This reflects a better fit with Packer's estimates of observed group size of hunting lions, but a large discrepancy still remains for Schaller's (1972) group size of feeding lions.

The final component to optimal group size of lions was added when Packer and colleagues (1990) collected new data on the hunting efficiency of groups of lions. They made observations that allowed them to test specific predictions of kin selection and its impact on group size. A number of benefits from kin associations that are unrelated to hunting have a profound effect on group size. Previous data ignored the role of nighttime foraging on hunting success, or the contribution that scavenging makes to the diet of lion groups. Armed with radio-collar tracking equipment, and night-vision goggles, Packer et al (1990) made unprecedented observations on lion foraging and social structure, that would make the arm-chair animal behaviorist squeal with delight. This level of detail on the natural history of an organism is what it often takes to understand a problem in behavioral ecology.

Figure 7.18. Daily feeding rate of lion groups of various sizes. When prey is abundant groups of 2-4 lions do quite well compared to solitary lions. When prey is scarce groups of 2-4 lions do very poorly compared to solitary lions or groups of five to six lions. (from Packer et al 1990).



During periods in which there was abundant prey, the size of the group did not affect hunting success (Fig. 7.18). The situation is quite different

during seasons when prey is scarce and groups of hunting lions with five to six members had high success, as did the solitary lioness. Groups of four to five lions failed miserably at hunting compared to singletons or groups of five and six. These differences in foraging were largely because 62.5% of food in singletons and small groups was obtained from scavenging; large groups scavenged no food. Whereas, a lucky solo female could scavenge an entire carcass and be quite satiated, groups of 2-4 would be left hungry from a scavenged carcass. In addition, the largest groups added the large cape buffalo to their menu, a prey that is far too large for a group of less than four lions to capture. These revised conclusions from optimal foraging theory are quite robust; prides should hunt solo or in groups of five or six. Moreover, the pattern of selection on group size is disruptive such that one should often see very small groups or very large groups of lions.

Why do some lions still hunt in suboptimal groups of 2-4 rather than hunt as solitary females? The final piece of the puzzle is provided by other advantages afforded by large group size. Female lions form groups and stay in prides for other reasons besides just hunting. They rear their young communally in a **crèche** where females with cubs of the same age can mutually defend cubs against attack. Attack is most likely from nomadic males. Infanticide of cubs by a male that attempts to usurp control from the current pride holder accounts for 27% of all cub mortality (Bertram 1975; Packer et al. 1988). Nomadic males kill cubs that were sired by a previous pride holder, which brings females into oestrus. If the nomadic male is successful in ousting the pride holder, he may only have a limited amount of time to sire young before another rival ousts him, so it is essential to rapidly bring the females into oestrus.

Packer et al (1990) found that when a single female defended the crèche, five litters out of six were lost due to males trying to usurp control over the group. In contrast, when two or more females defended the crèche, five litters out of five had at least some cubs survive. A large pride can hunt in efficient groups and it is also of sufficiently large to allow females to defend crèches. However, females in small prides of less than 5 members are forced to band together in groups that are sub-optimal for hunting (e.g., 2-4 lionesses) to ensure that there are enough females to defend the crèche. The risk of litter loss brought about by infanticidal male lions drives some small prides to maladaptive hunting group sizes.

Finally, one of the most important advantages of lion groups may be their ability to defend their communal territory. Lion prides maintain a territory that is essential for reproduction. Larger lion prides periodically oust smaller prides from their territories (Packer et al 1990). Skirmishes between prides often take place near borders, and of the 15 encounters between groups observed by Packer and colleagues, 13 were won by the larger group. Optimal group size for foraging may be a singleton, but the safest size to defend a territory may be much larger. Thus, both crèche defense and territory defense may force prides to maintain group sizes that are sub-optimal from the viewpoint of hunting, but optimal when defense is factored into the equations.

Levels of conflict in lion prides and resource-holding power

Several levels of conflict and contest are observed within and between groups of lions. First, a nomadic male may attempt to usurp control from the pride holder. When a nomadic male enters the pride a conflict occurs between the pride-holder and the nomad, and between the nomad and the female lions, which want to protect their cubs from the infanticidal nomad. In each case the combatants have a resource that is being defended. The pride-holder defends the pride because the females are a reproductive resource and are directly related to his fitness. Without a pride, the male's potential for fitness drops precipitously because not only does he lose his reproductive opportunities, but he also loses his progeny when the nomad kills his cubs.

A single female is no match for a male lion, which is nearly twice as massive. The value of killing the pups for the usurper is clear. The female lions will go into oestrus more rapidly, allowing him to inseminate them with his own sperm. For a lioness, the value of defending her cubs does not outweigh the costs of injury that the female lion might receive from a male that is bent on killing the pups. The male is much larger than the female lion. However, if more than two females defend the crèche, the scales begin to tip in the females' favor.

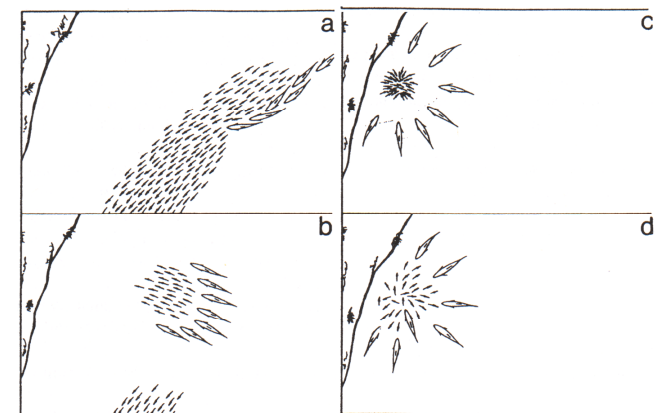
The pride of lions faces another conflict when it must defend its territory from adjacent prides. Without a territory the pride would not be able to reproduce. When conflict arises, the group of lions with the greatest **resource-holding potential or resource-holding power, RHP**, usually wins. RHP is a physical measure of an individual or group to maintain

control over a resource, such as a territory (see Chapter 8). During a territorial contest, each lion group can assess the resource holding potential of the other group by performing a simple head count, assuming of course that lions can count, or in some way perceive the asymmetry between the groups. The RHP of two opposing lion groups is relatively straightforward for an observer to assess. Similarly, the RHP of the multiple females defending the crèche is easy for a male to assess.

Coordinated Hunting versus Beating the Bushes

Many animals use sophisticated hunting tactics and a division of labor is often found between members of the same group. Animals often forage in groups, but true cooperation and mutualism is somewhat difficult to show. Many animals might participate in a feeding frenzy, but the mass action of a group is not the highly integrated actions of cooperative foraging. For example, I have often seen long-billed curlews on the west coast of North America foraging in flocks for grasshoppers. If one curlew flushes out a grasshopper it is highly likely that a neighbor will capture the grasshopper. The neighbor might also do the same. The strategy of "beating the bushes" might be fun and neighborly, but it does not constitute group hunting tactics (Bertram 1978; Mock 1980).

Figure 7.20 Group foraging in the yellowtail, *Seriola lalandei*, when hunting jack mackerel, *Trachurus symmetricus*. a) Yellowtail flank their prey. Some members of the group herd, while others split the prey off from the main school. b) The yellowtail then force the prey towards shore. c) At the shore the prey is effectively cornered. d) Feeding then begins (redrawn from Schmitt and Strand, 1982).



Schmitt and Strand (1982) have two criteria that are useful to apply to coordinated and cooperative group hunting tactics (Dugatkin 1997):

1. individuals adopt different and complementary roles during foraging (e.g., division of labor),
2. individuals exercise temporary restraint by not feeding until prey have been determined to be vulnerable.

Group foraging tactics of lions that are described above clearly fits the list for coordinated group hunting.

Yellowtail, *Seriola lalandei*, a relative of tuna appear to forage in groups that facilitate hunting *per se*. When attacking a large school of fish members of the yellowtail group, take on a variety of roles that serve to herd the prey and split the prey off from the main school. In addition, yellowtail may use different tactics depending on the kind of prey species encountered. Finally, the yellowtails wait until they have successfully split off the prey from the main school before beginning to feed. All criteria for cooperative hunting are fulfilled for yellowtail tuna: there is a division of labor and individuals wait to feed until after the prey is vulnerable.

Coordinated hunting tactics are characteristic of many marine cetaceans that hunt in pods. Marine mammals that forage under water must return to the surface to breath and thus, are subjected to special constraints on time, depth, and costs of foraging not present in fish (Dolphin 1987; Dolphin 1988). A highly coordinated and integrated hunting behavior is often required to overcome these difficulties. Members of humpback whale (*Megaptera novaeangliae*) pods dive in coordinated groups. Some members of the pod exhale a stream of air (Sharpe and Dill 1997), which is called a **bubble net**. The bubble net has a clear effect on the prey species judging from the behavior of prey when subjected to experimental bubble nets (Sharpe and Dill 1997). Pacific herring, *Clupea harengus pallasi*, were reluctant to swim through the curtain of air formed by the stream of bubbles. Humpbacks appear to exploit a latent fear that herring have to bubbles. Other members of the group rise up through the entrapped fish schools and begin feeding. One idea to explain the paradoxical behavior of the herring is that bubbles may mimic the natural signals that herring use to school. Bright flashes cause many schooling fish to turn, thus, a bubble ring will keep them trapped.

Extreme group coordination is required when killer whales, *Orcinus orca*, attack a whale that is many times larger than they are. Even the large sperm whale is a target for killer whales. Some killer whales clearly develop idiosyncrasies in foraging tactics. These idiosyncrasies are culturally transmitted from mother to progeny (Guinet and Bouvier 1995). For example, many orcas develop a hunting technique in which they intentionally strand themselves on land to capture baby elephant seals. What is remarkable about this behavior, is that the assistance of the mother is required to help return the juvenile that is learning the technique back into the water with the prey. Eventually, juvenile orcas can learn to return to the water. Nevertheless, a lengthy apprenticeship is required to learn this hazardous, but extremely effective skill for scooping unwary but highly profitable elephant seal pups from land.

The division of labor between teaching and hunting among pod members can be quite extraordinary. One individual orca is often primarily responsible for capturing most of the prey for other members of the pod. While this individual is busy delivering food, other individuals specialize in training the younger members of the pod in how to hunt (Hoelzel 1991). Some pods develop the stranding technique while others do not. The different hunting techniques of orca are driven by the availability of prey. Some pods favor seals while other pods favor salmon (Baird et al. 1992). The cultural differences in diet and foraging tactics can become so strong, that it has been suggested to lead to reproductive isolation between pods, which might ultimately lead to the formation of a new species (Hoelzel and Dover 1991).

The Evolution of Mutualisms

The cases described above are considered to be foraging mutualisms. **Mutualisms** are defined to be cooperative interactions between members of a group that lead to a net benefit for both parties. Mutualistic alliances within a species seem quite easy to evolve. Many groups are formed from mixtures of kin and non-kin. In the case of group hunting it seems logical that some members of a group would also be kin. If kin are present in sufficient numbers, then they would be expected to form mutualistic alliances quite readily owing to the power of kin selection (see Chapter 4). The fitness benefit derived from an individual's foraging tactic includes the direct effects on its own fitness and indirect benefits to kin according to Hamilton's Rule (Equation 4.3).

Once a cooperative foraging behavior has been introduced into a foraging group through kin benefit, the behavior might readily spread to non-kin under the following two conditions. First, the interaction between unrelated individuals must lead to a positive benefit to both unrelated parties. Second, the benefits are impossible to realize without two animals cooperating. Under these conditions, the behavior enhances an individual's fitness as well as the group fitness. Genetic (or cultural) tendencies to perform the behavior will spread throughout the group by the power of individual selection (Lima 1989). No individual loses in cooperation, and all gain from enhanced foraging success. Under these conditions, group foraging among non-kin is stable to the invasion of cheaters. A cheater is defined as an individual that reaps the benefits of the hunt (e.g., eats at kill), but does not participate in foraging. A cheater could not invade a group. If one party cheats, both parties lose because of the second condition: the benefits would be otherwise impossible to realize without two animals cooperating. Cheating is not possible.

Because mutualistic cooperation is a win-win situation for both parties, and lose-lose for both, the condition for kin selection being involved at the outset is actually not a necessary condition for the formation of mutualisms. I merely included it because it is quite likely that kin are found in the groups. However, cooperation can also evolve as a **byproduct** of a simple interaction between two or more unrelated individuals that enhances both parties' fitness but entails no costs over and above the costs experienced when an individual hunts alone. Dugatkin (1997) has referred to this kind of mutualism as **byproduct mutualism** or **no-cost mutualism**. Coordinated hunting can easily arise from the "beating the bushes" strategies, particularly if a division of labor characteristic of coordinated hunting tactics develops in the long run. In Chapter 4, we encountered a genetic model for the evolution of cooperation, which may involve an altruistic cost. In chapter 19, we will study another game for the evolution of cooperation and true altruism, which involves a game called the Prisoner's dilemma.

Foraging Mutualisms Within versus Between Species

Forging mutualistic alliances within a species is often facilitated by kin selection; closely related individuals that share an immediate ancestry are expected to cooperate, at least some of the time. Forging mutualistic alliances between individuals in different species presents a major

obstacle to this mode of the evolution of mutualism. No shared ancestry is possible. In spite of these difficulties, there are a few striking examples of foraging mutualism that have apparently evolved between two species. These cases provide compelling evidence for an earlier assertion that I made: true cooperation between individuals does not require kin relationship.

Mutualistic cooperation appears to occur between humans and the greater honey guide, *Indicator indicator*, a bird from Africa whose natural history has become legend. Honey guides routinely lead an aboriginal African people, the Boran, to honeybee colonies that provide a rich reward for both humans and honey guides. The Boran benefit by minimizing the amount of time necessary to search for honeybee colonies, which are dispersed throughout the landscape. The honey guide benefits because the Boran open nests that the birds would not otherwise be able to open. Moreover, the human gatherers leave the bird with pieces of honeycomb from which the honey guide eats both the nutritious larval bees, and the beeswax.

How on earth did such a mutualistic relationship get started? Unfortunately, the answer to the origins of the human-honey guide mutualism may be buried with their prehistoric ancestors. We know from rock paintings in the Saharan region of Zimbabwe and South Africa that humans have collected honey for at least 20,000 years (Isack and Reyer 1989). Even though the origins of the mutualistic association is enigmatic, it is clear that modern Boran appear to communicate with the honey guide during the trek to find the hives.

The Boran also claim to be able to deduce the direction and distance to the nest from the bird's flight pattern, perching height, and calls. All of these claims appear to be true based upon data collected by Isack and Reyer (1989). When a bird disappears periodically during the 'leading behavior', it is probably flying towards the colony to confirm its position. The Boran notice that the honey guide disappears for shorter periods the closer it gets to the nest. The distance the bird makes between stops also drops off as the bird nears the nest. Finally, the perch height used by the birds gets closer to the ground as the bird approaches the nest. The Boran can identify a special locator call given by the honey guide in response to a query from the human followers. The Boran are keen students of animal behavior.

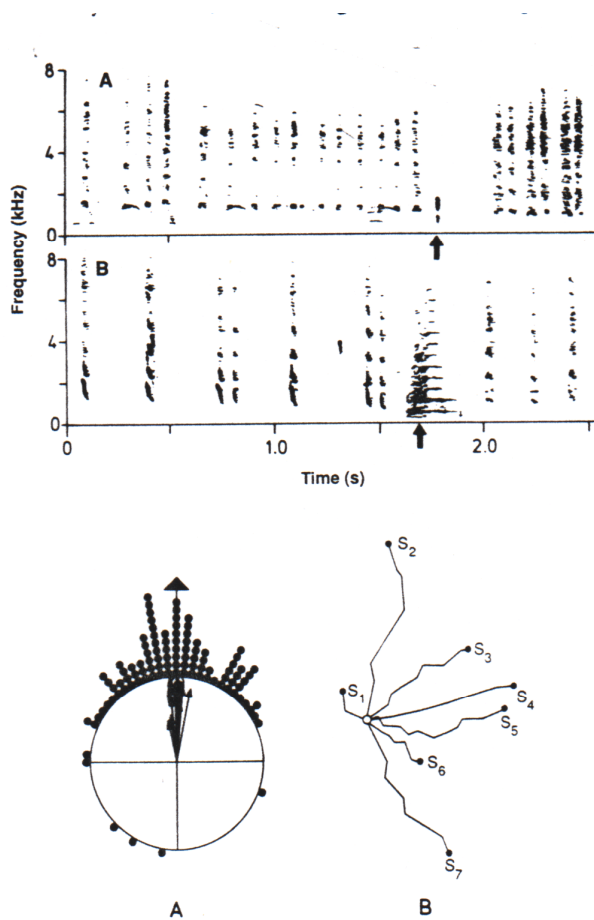


Figure 7.22 (Top Panel) A) Sonograms from a typical 'en route' call produced by the greater honey guide (*Indicator indicator*) during movement toward the honeybee colony. During movement toward the nest, the input of human voice elicits an increase in the rate of *en route* calls by the honey guide. B) The special 'indicator call' is produced by the honey guide when it has arrived at the honeybee colony. The input of human voice at this stage of the trek elicits the special locator call from the honey guide. (Lower panel). A) Orientation of 16 guided routes in relation to the direction of the honeybee nest. The track used by honey guides is highly non-random and the average direction of travel coincides with the straightest direction to the colony. B) Experiments in which humans start at different points (S₁-S₇) result in a route chosen by the honey guide that is straight and directed (from Isack and Reyer, 1989).

The honey guide uses a flight pattern that is so unerringly straight that it seems difficult to suppose that it reflects anything but the behaviors developed to exploit a mutualistic alliance of food gathering. Moreover, experiments in which the same honeybee colony is approached from several directions indicate that the honey guide always takes the shortest distance between the start point and the honeybee colony.

The Information Center and Group Foraging in Osprey

Mutualisms within a species are likely to occur in other situations where sharing information leads to a net benefit. Many birds are colonial nesters and thus central place foragers. The colony is a place where

many individuals can potentially share information with other colony members (Brown 1986; Greene 1987; Brown 1988). Information sharing can be both *active*, with conspicuous signals that communicate information, or *passive*, in which animals observe their colony members. By paying attention to individuals who are returning with rich resources, colony members gain valuable information. A simple rule of thumb to follow would be to head out in the direction from which a successful forager returned. The colony member is likely to run into the same rich resource. Thus, many colonies serve as **information centers** where the foraging rate of all colonists is enhanced by the free (passive or active) exchange of information (Zoltán and Szép 1994).

Osprey are fish-eating hawks that will often form large breeding colonies with as many as 300 pairs of birds (Greene 1987). The members of the colony do not help in rearing young, but appear to help in the acquisition of information regarding the distribution of prey. Fish can be patchily distributed in the ocean surrounding the colony. Transfer of information regarding where fish are distributed would benefit colony members, especially if the fish is a schooling species. Schooling fish are likely to present in large numbers, even when other colony members visit the site at a later time point, using information supplied by foragers.

Male osprey provide most food for young chicks with long foraging flights. The osprey that depart the colony shortly after a male returns exhibit departing foraging flights with a highly non-random direction. They invariably leave in the same direction as the male that successfully returned with fish. Moreover, osprey clearly discriminate the information quality that is provided by a returning male. If males return with a fish that is a schooling species, which are abundant, the osprey of the colony depart in the direction from which the male returned. However, if males return with no fish, or with a non-schooling species, birds in the colony fly off in random directions. Birds that head off in the direction indicated by a successful forager take half as much time to return a fish compared to birds that head off in a random direction. Information transfer has a substantial benefit in foraging efficiency.

Information transfer in the osprey colony does not need to be a mutualistic transfer of information, rather individuals may selfishly observe the return of a male and exploit the information acquired. An example of the active flow of information is when the returning

individual might use a signal to indicate the direction in which food is likely to be found. An example of passive flow is a bird that observes where a returning male came from, and whether he was successful.

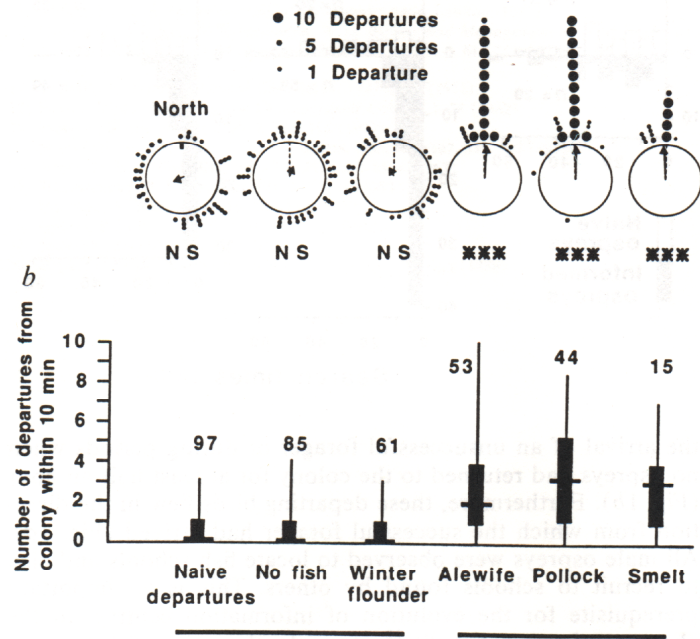


Figure 7.23 Direction of flight by colony members following the return of an unsuccessful male, and the return of a successful male carrying different kinds of fish. The direction of the male's return flight is depicted in the vertical direction on the circular diagrams. Departures of colony members do not show a consistent direction of flight when the returning male had no fish or brought back a species that was not schooling at that time of the year (e.g., the winter flounder, *Pseudopleuronectes americanus*). Colony members departed in the same direction as the male's return flight when the returning male brought back a schooling species (e.g., the pollock, *Pollachius virens*, the alewife, *Clupeus harengus*, and the smelt, *Osmerus mordax*) (Greene 1987).

In osprey, successful foragers occasionally perform an aerial display for the colony to observe suggesting an active flow of information. The informed male will call repeatedly and his flight will undulate in a manner superficially reminiscent of an aggressive display. The display

was only observed when males returned with fish that are schooling species, and usually occurred when no bird in the colony had been successful for an extended period. Colony members headed off on their own foraging flights in the direction indicated by the informed male during his aerial display.

Greene speculates that because the aerial display may have some cost (e.g., flight) this behavior may be a form of kin selection. Male offspring are quite likely to return to the same colony of their birth, referred to as **natal philopatry**. The male may advertise success to his brothers, and at the same time unrelated individuals become privy to the information. Only additional data on relatedness at Osprey colonies can discriminate between competing hypotheses of mutualism versus kin selection, which remain to be collected.

Information parasites

Recent theoretical models have been developed to explain cases in which colony members are not related, but information is still shared. In the case of large crowded colonies, most of the individuals that benefit from the shared information are not related to the individual providing the information. Information is likely to be passively passed from forager to forager. As information spreads, many colony members might head out and exploit the patch. The value of the patch declines, and the original discoverer of the patch is the big loser. Why should the individual divulge information to begin with; why not keep it a secret?

Zoltán and Szép (1994) developed a simulation model as a partial answer to this question. They modeled 3 alternative foraging strategies:

1. **searchers** move over the foraging area by 'random walks',
2. **watchers** move like searchers, but are in fact observing searchers,
3. **followers** stay at the colony, but when a successful searcher returns, they follow the searcher to the food patch.

Searchers are the typical forager encountered in chapter 6, working hard for a living. Watchers really forage for searchers, moving through the world and waiting for the searcher to strike it rich. When this happens, watchers can reap the benefit from the modestly rich patch of food discovered by searchers (Thorpe 1956). Followers are true **information**

parasites (Galef 1991). They lead a somewhat slothful life only moving to swoop in for rewards when someone else strikes it rich. Zoltán and Szép varied the foraging world experienced by their simulated animals in terms of the ratio of patches that contained food, and the duration that each patch was present before the food (prey) moved on to a new patch.

The simulation study indicated that solitary searchers, which forage with no information transfer is the best strategy, when food is distributed widely. However, as food became more clumped the following strategy, which relies on information transfer, could persist at high levels in the population. Moreover, only a few searchers were required to sustain a very high frequency of followers.

Watchers that relied on detecting successful foragers could only exist in the simulated worlds in a narrow range of food patchiness. This is because watchers expend nearly as much energy in “foraging” for information as searches spend in foraging for food. Watchers do well at intermediate levels of food patchiness because they can capitalize on the food resource faster than a follower that must first wait for information provided by the return of a searcher to the colony. By the time a follower makes it to the patch it has been exploited by a watcher, particular in short duration patches. In contrast, the follower strategy is quite cost effective in that they remain at the colony using very little energy, but can reap the benefits of a large resource found by searchers.

Surprisingly, the information center need not require a mutual exchange of information. Both kinds of information parasites, watchers and followers, can exploit the efforts of solitary foragers but still persist in the population at high levels (Zoltán and Szép 1994). The human analogy would be the “data miners” of the information age that search the internet for interesting bits of data without ever having to lift a finger (well I guess they do type). Of course, information parasites cannot be so successful that they eliminate the searchers entirely, or no one would be around to find food or collect information. The population exists indefinitely with a variety of alternative foraging tactics.

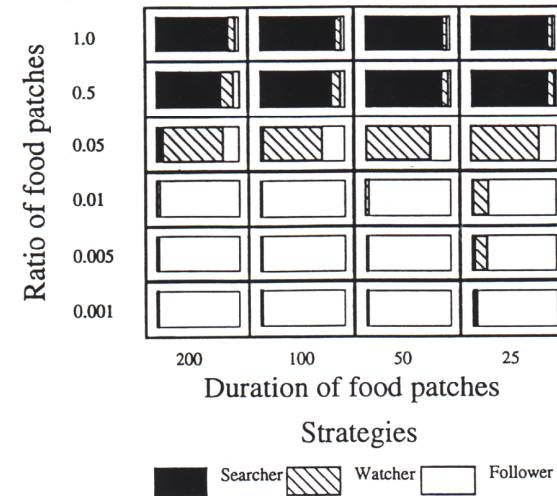


Figure 7.24 Proportion of 3 alternative food-finding tactics at a colony. Foraging took place in a variety of simulated worlds in which the ratio of food in any given patch varied from 0.1% to 100%, and the duration that food (e.g., prey) remained in a patch before moving to a new patch varied over an 8 fold time scale (from Zoltán and Szép, 1995).

Alternative Foraging Strategies

The various foraging modes epitomized by searchers, watchers, and followers can be viewed as strategies in an evolutionary game of life. Many other alternative behavioral modes may require elaborate changes in morphology that allow individuals to behave in different ways. As seen in Chapter 2 and 6, alternative feeding behaviors often require the development of special morphology that allows individuals to handle difficult-to-eat prey. It is not just enough to alter foraging behavior, because the behavior may be particularly ineffective against some prey, even if the prey is very abundant in the environment. The adjustment in behavior is not restricted to the behaviors of individuals over the course of a single bout of foraging. Rather, the behaviors can evolve rapidly in response to the selective pressure that genetically based predators might exert on their prey. Another alternative pathway for changing behavior is a plastic change that is induced by the environment. No genetic

change is required, all individuals have the capacity to develop alternative foraging behaviors within their lifetime. We will explore the genetic versus environmental changes that lead to alternative foraging behaviors. The proximate control of these set of behaviors, a gene cascade triggered by environmental cues, is described in Chapter 2.

The interactions between predator and the prey, or between individuals foraging for the same resources can lead to some extremely interesting behavioral dynamics. A very successful predator is likely to remove so many of its prey from the environment that the prey become depleted. When this happens, it is no longer is profitable to feed on that species of prey and the predator should switch to another species of prey. This leads to a game of sorts, where the decision rule to switch from one resource to another may entail changes in behavior and morphology that allow the predator to effectively handle the prey. We will begin our exploration of behavioral games and the evolution of alternative strategies using an example from spade foot toad larva (Chapter 2, 6) that can develop into either a carnivore morph or an omnivore morph.

Omnivorous versus Carnivorous Tadpoles

Spade foot toad tadpoles assume a carnivorous morphology when they ingest shrimp (see Chapter 2). Shrimp are likely to found in ephemeral ponds that dry up rapidly compared to more long-lived ponds. Long-lived ponds, which have few shrimp, tend to harbor a higher frequency of the omnivorous form of shrimp. Thus, the presence or absence of shrimp provides a reliable cue for the tadpoles to assume the alternative feeding morphology (Pfennig 1990). Once tadpoles begin transforming to carnivores, if they do not continue ingesting shrimp, they will revert back to the omnivorous form (Pfennig 1992; 1992).

The ability of tadpoles to flip-flop between morphs gave David Pfennig (1992) a unique opportunity to test the idea that too many carnivores make less shrimp for all, and that there is an appropriate frequency of tadpoles that should transform into carnivores. Each pond has a carrying capacity for carnivores that is dictated by the number of shrimp/tadpole. Some ponds should be able to sustain a high frequency of carnivorous tadpoles, while other ponds can only sustain a low frequency of carnivorous tadpoles.

Figure 7.27. (left panel) The alternative pathways for development in spade foot tadpoles, *Scaphiopus multiplicatus*. If a tadpole does not ingest shrimp it will invariably develop into an omnivore. However, individuals that ingest shrimp can transform into the carnivore morph with probability (p). Carnivores must continue to consume shrimp or they will revert back to the omnivore morph (right panel) The carnivore has an enlarged orbitohyoideus muscle (OH) and greatly shortened intestine compared to the omnivore morph (from Pfennig 1992).

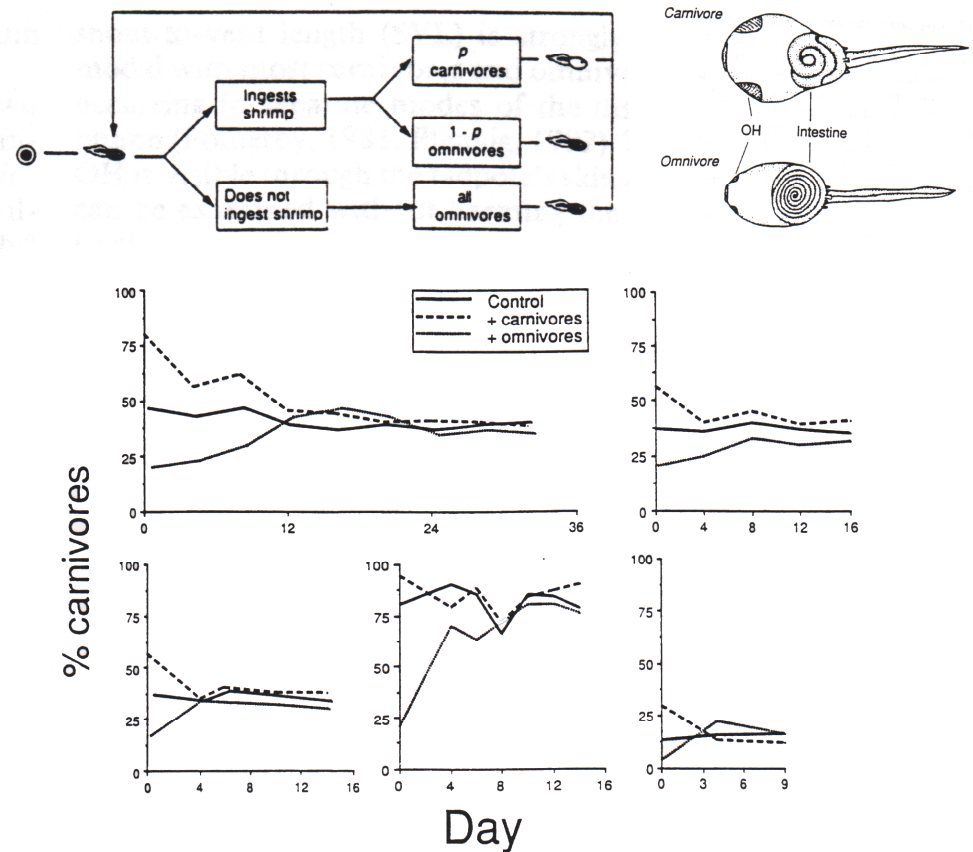


Figure 7.28. Frequency of carnivore tadpoles of *Scaphiopus multiplicatus* in five pond experiments. Each pond was set up into three treatments: added carnivores, control, and reduced carnivores. Within a few days after manipulation of carnivore frequency treatments with altered carnivore, the

frequency (high and low) re-equilibrated back to the carnivore frequency that is characteristic for each pond (Pfennig 1992).

Pfennig designed a large-scale experimental manipulation of the frequency of carnivorous versus omnivorous tadpoles. He split ponds into six sections: two sections received the natural frequency of carnivores that was unique to each pond at the start of the experiment, two sections got a higher frequency of carnivores, and two sections got a lower frequency of carnivores. As Pfennig predicted, the treatments with excess carnivore frequency declined back to control levels, while treatments with reduced carnivore frequency climbed back up to control levels. The carnivores in enhanced-frequency treatments competed for a more limited supply of shrimp and most did not forage on enough shrimp to sustain their morphology. Some of the excess carnivores reverted back to the omnivore morph. In the reduce-frequency treatments, there were fewer carnivores to consume all the shrimp and many omnivores foraged successfully on shrimp and transformed into carnivores. As more omnivores transformed to carnivores, the frequency of carnivores climbed back up to the frequency observed before the manipulation.

The ability to transform into a carnivore morph in the presence of enough shrimp, or to revert from carnivore to omnivore is adaptive. Carnivores can metamorphose much more rapidly than omnivores giving them an advantage in short-lived ponds. Omnivores grow more slowly and acquire more fat reserves, so their strategy is likewise adaptive, but this strategy only has an advantage in long-lived ponds. Omnivores have enough time to metamorphose to the adult form if ponds are long-lived. Despite the plasticity in morphology and foraging behavior, a tadpole may not be able to assess how many competitors of each morph it is up against in any particular pond; rather, the number of shrimp that it encounters provides a reliable cue to undertake the transformation.

Summary

Each of the studies presented in this chapter illustrate that optimal foraging 'decisions' are contingent upon other salient ecological interactions that animals may experience in the wild. In the case of a foraging stickleback, perceptual constraints limit it from always feeding

on a dense patch of prey. Shifting its preference to less dense prey allows the stickleback to divide its attention between foraging and predator vigilance. Likewise, squirrels are sensitive to the presence of predators and tend to travel to safe cover and will only eat large seeds, or when cover is close by. The different currencies between predation risk (e.g., survival) and foraging efficiency (e.g., calories) make it difficult in most situations to come up with quantitative predictions between theory and behavior. In a few situations there is a natural link between predation and foraging, such as when both are dependent on body size, and it is possible to reconcile the different currencies. For example, when foraging bluegill sunfish achieve a critical body size, they shift between foraging in low-risk and low-yield areas of a lake to higher-risk but higher-yield areas.

If competitors that forage in patches of different quality are equally matched and free to choose among patches, they will distribute themselves according to the ideal free distribution, in which each animal gets the same amount of the resource. The best patches tend to support more foragers than poor patches. The ideal free distribution assumes perfect knowledge, but perceptual constraints and memory may greatly limit the ability of most animals to conform to ideal free expectations. More importantly, individuals vary in competitive ability or in the order in which they settle in vacant habitat. This allows some animals to develop an ideal despotic distribution where they control the best resources. In the case of oystercatchers territories, there are no apparent differences among individuals, rather, some happen to take control of a territory while waiting in the 'queue' for high quality territories. Likewise, beavers that settle early into pristine habitat get a despotic distribution of territories that provide an optimal return across the winter and summer seasons. Late settling beavers get poor quality territories.

The costs and benefits of territoriality lead to an optimal territory size. However, animals will abandon territoriality when it is too costly to defend a territory, or when the benefits or value of the defended resource becomes too low. The costs of territory defense are not just restricted to the energetics of defense. Animals also pay a price in the vigilance time that interferes with their ability to forage at rates expected under simple models of foraging, such as the marginal value theorem.

One of the most important developments in the evolution of foraging behavior is the mutualistic benefit that arises from group foraging. If animals can forage more efficiently in groups, selection will favor cooperation and a division of labor. The division of labor can culminate in the formation of striking social behavior, which is discussed in greater detail in Chapter 19: Societal Evolution.

The benefits of groups are not restricted to the mechanics of prey capture, but also extend to the dynamics of information acquisition. Colonies are likely to serve as an information center, where animals exchange information about the location of particularly abundant resources. Information exchange can be passive, in which animals watch their neighbors, or it can be active, as when animals share information by the use of a display. However, in the case of a passive exchange of information, the interaction need not be mutually beneficial as information parasites can exist at high frequency at the expense of others that forage by traditional means.

The evolutionary interactions among competing individuals or predator and prey can be likened to a game in which, the ideal strategy or frequency for a behavior and foraging morphology, changes depending on ecological circumstance. A given predatory strategy may be most effective when the prey upon which it specializes occurs at high frequency. Therefore, understanding the role of frequency dependent selection, the subject of the next chapter, is critical to understand the kinds of stable social systems that evolve in animals.

Study Questions for The Ecology of Foraging

1. Describe the problems faced by a predator during foraging and contrast these with the problems faced by a prey during foraging.
2. Explain the basic premises of the ideal free distribution. Are there any animals that exhibit the ideal free distribution? (Why or why not?).
3. What are the costs and benefits of territorial behavior? Describe a simple graphical model of these trade-offs.
4. What are the advantages to group hunting? Why is the observed size (2-4) of lion prides greater than the optimal size (1-2)?
5. What is an information center? What kinds of alternative information parasites can invade an information center and under what ecological conditions is each kind successful?
6. Explain the advantage of being a rare strategy.