

Wading bird foraging behavior

Animals as a group are what we call "ingestive heterotrophs", to distinguish them from autotrophic organisms like plants, and to distinguish them from fungi, which are "absorptive heterotrophs". Being ingestive heterotrophs simply means that animals eat things to get nutrition. Obviously obtaining food is one of the most important behaviors of all animals, second only to reproduction. How animals obtain food is a topic that has received much attention from behavioral biologists, on both empirical and theoretical grounds.

Theoretical treatments of foraging behavior are in two main camps. The historically older camp, which I call the "population dynamic" approach, attempts to predict how predators affect prey population sizes, and how changes in prey population size affect predator foraging behavior and efficiency. This camp recognizes the "numerical response" and three types of predator "functional response" to changes in prey number. The numerical response is a long-term, ecological response of population size, which means that as prey numbers go up in a habitat, predator numbers eventually follow, because there is more to eat. By the same token, when prey numbers decline, predator numbers must eventually also decline, because they can't find enough to eat. The "functional response" has to do with changes in or limitations on predator foraging function or ability, and not with the Tinbergian functional or adaptive significance of foraging.

The three types of functional response are called, oddly enough, Type I, Type II, and Type III. The Type I functional response describes the prey-catching ability of foragers that are essentially "filter feeders", in that they have a device for straining prey out of a medium (like sponges or baleen whales), and they don't recognize and try to catch individual prey. The rate of prey capture increases linearly with prey availability up to a point at which the straining apparatus is saturated, and then they can't catch any more prey (per unit time) no matter how many are available. This is not a very common situation in the animal kingdom. The Type II functional response describes the foraging behavior of predators that look for individual prey items. In this response, the rate of prey capture increases with prey abundance initially as a linear function, but the proportion of prey available that are actually caught begins to decline as the number of prey increases, until the predator is eating prey items as fast as it can, and other prey items are escaping while the predator handles the one it has. Finally, the Type III functional response also describes the foraging behavior of predators that look for individual prey, but in this case, the predator initially eats fewer of the prey than would be expected on the basis of prey abundance. This is because the predator is feeding on other types of prey, and doesn't initially recognize the prey species in question as suitable prey. In this model, the predator learns that the new prey is available in abundance, and switches its foraging from other prey types to the new one. At this point

the rate of prey capture increases faster than prey abundance increases, up to the point where the proportion of prey captured begins to decline because the predator is feeding as fast as it can and prey escape, as in Type II.

These functional responses are predictions based on expectations about the effect of predator numbers or behavior on prey numbers, and about the effect of prey numbers on predator behavior. A second, more recent camp of foraging behavior theory is the "optimal foraging" approach. In this camp, we begin from the premise that natural selection will act to produce forager populations that are as efficient as possible in their choice among available prey types. How is this efficiency measured? Optimal foraging models assume that efficient foragers should maximize net energy intake per unit foraging time. A particular prey item contains a certain amount of chemical energy (the gross energetic content); from this is deducted any energy tied up in indigestible material like bones, beaks, seeds, exoskeletons, etc. The remainder is the "utilizable energy" from which is deducted energetic costs of foraging (like searching, pursuit, handling, ingestion, and digestion). What remains is the net energy that can be used by the forager for somatic and reproductive growth. "Profitability" is a measure of net energy that can be gained from a type of prey relative to the time it takes to find, catch, handle, and ingest the prey. Thus profitability is a measure of the rate of net energy gain from foraging. We assume that several types of prey are available in the habitat, and different prey types are ranked by the forager in order of decreasing profitability. High ranking items are assumed to be rare in the habitat, and availability is usually assumed to increase with decreasing rank. Foragers are expected to choose among various types of prey items based on the effect of each prey type on the overall profitability of the forager's diet. Obviously foragers have to eat something, so the highest ranking type of prey is always included in the diet. Lower ranking prey types are included in the diet only if inclusion makes the overall profitability of the diet increase. Optimal foraging models predict that prey items that cause the overall profitability of the diet to decrease should never be eaten, regardless of their abundance. This may seem like an odd prediction, but think of it this way: If a forager is trying to feed on fish, some species (like minnows) are so bony and scaly that feeding on them may actually cost more energy (for instance capture, handling, and processing costs) than the forager can get out of them, so the forager should not eat them. Also, if species that are more juicy and tender (like catfish) are relatively common, the forager should concentrate on them and ignore the minnows, even if some minnow species are more meaty and less scaly. Inclusion of a prey type (minnows) in the diet does not depend on that type's abundance, but only on the abundance of higher ranking items (catfish).

Does any of this have anything to do with the real world? It does, and there are many data sets that address both functional responses and optimal foraging. We will discuss both the models and the data later in this course, so do not despair if the information above makes little sense. I will explain it again later, and will give you handouts (no surprise there). For the purposes of this lab exercise, we might guess that one of the energetic costs of foraging is locomotion while searching for and in pursuit of prey.

Different species might have different locomotion costs, so there might be differences among species in this aspect of foraging strategy. Some might be active searchers, and others might be "sit and wait" foragers. A first approximation of the differences in foraging costs and strategies might be to compare the locomotion patterns while foraging of different species in the same foraging habitat. We might also predict that there would be differences in number of times foragers of one species attempt to capture prey relative to foragers of another species, if they are feeding on different prey with different costs of capture, handling, and processing. The proportion of capture attempts that are successful might also differ if the prey differ in ability to avoid predators. We could quantify these aspects of foraging behavior by direct observation of foragers of two different species, preferably phylogenetically related species foraging in the same habitat.

Our goal for this lab is to compare the overall foraging strategy of three species of wading, fish-eating birds (including pursuit and prey-catching tactics), and to compare aspects of the preferred foraging microhabitat, social interactions while foraging, and if possible, preferred prey types.

The subjects of this lab are the Great Blue Heron (*Ardea herodias*), the Great Egret (*Casmerodius albus*) and the Snowy Egret (*Egretta thula*). Great Blue Herons are large grayish-blue birds, about 1 m tall, with long legs and a long neck (see the specimen outside my office). The feet have three long toes in front and one in back. The yellow bill is long and straight. These are wading foragers. Great Egrets are also wading foragers. They are nearly as tall as Great Blue Herons, but are all white. They also have long legs, neck, and bill. Snowy Egrets are smaller than these two (about 0.5 m tall), and are also wading foragers. Apart from size they are morphologically similar to the Great Egret. All three of these species feed on fish and other small vertebrates (frogs, tadpoles), and capture them by jabbing the bill into the water. These species have similar foraging microhabitat preferences, and routinely forage in fairly close proximity to each other (and to a number of other "shorebirds").

Our locality for this lab will be Hagerman National Wildlife Refuge, northwest of Sherman on Lake Texoma. The area of Hagerman that we will visit is the "oil jetties" area on the Big Mineral arm of the lake. Big Mineral Creek enters the south side of Lake Texoma, and forms a number of mudflats which are covered with water when the lake is up, and are exposed and dry when the lake is down, as it is now. Many species of birds inhabit Hagerman, and one can usually find several species of fish-eating birds in addition to the Great Blue Heron, Great Egret, and Snowy Egret. Double-crested Cormorants are very common at certain times of the year, as are American White Pelicans, Forster's terns, Ring-billed Gulls, and other gulls. Belted Kingfishers are common along Big Mineral Creek upstream from the lake. In addition to these fish-eaters, we will see a variety of invertebrate-feeding shorebirds, including Greater and Lesser Yellowlegs, Killdeer, Wilson's Phalarope, and White-faced Ibis. Several species of dabbling ducks are also regular inhabitants of Hagerman.

Our goal is to collect quantitative data on water depth, distance from shore, distance from nearest conspecific, rate of locomotion while foraging, number of feeding attempts, and proportion of feeding tries that are successful. We will use focal animal sampling, and will first characterize foraging microhabitat, then simply count number of steps taken by our subjects in a brief observation periods, the number of feeding attempts in the same period, and the number of tries that are successful. We will then be able to compare foraging microhabitat preferences and foraging strategies of the three species.