In this section of Resonance, we invite readers to pose questions likely to be raised in a classroom situation. We may suggest strategies for dealing with them, or invite responses, or both. “Classroom” is equally a forum for raising broader issues and sharing personal experiences and viewpoints on matters related to teaching and learning science.

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Ecology for Birdwatchers
A Simple Introduction to Optimal Foraging Theory

Foraging ecology is an important branch of behavioural ecology with applications in several disciplines, including conservation biology, wildlife management, human behaviour, and aquaculture. Birds, because of their high visibility and often diurnal habits, are extremely popular study species throughout the world. In India, the study of birds has been popular among professional scientists, teachers, as well as amateurs. Here, an attempt is made to introduce some elementary concepts in foraging ecology by taking up some well-known case studies on aquatic birds and focussing on diet models. Birdwatchers are also increasingly participating in citizen science, in which scientific data are crowd-sourced. This article would be useful to this target group in addition to students to gain an understanding of some important ecological concepts.

Birdwatching is a popular pastime, and many people from diverse backgrounds participate in this outdoor nature study activity, focusing on reporting the presence or absence of different species of birds in specific localities or seasons, or reporting their abundances [1]. One of the most popular birdwatching events organ-

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There are splendid opportunities to disseminate ecological concepts to birdwatchers, who encounter birds in their natural environment and watch them perform various activities. Also, given the enormous diversity of wetland birds in India, the AWC and similar programs offer ecology teachers a unique opportunity to familiarize students and participants with the foraging adaptations of birds and their foraging behaviors (see Box 1 for an outline). Here, an attempt is made to acquaint this specific target group with some basic concepts of optimal foraging theory (OFT), an important branch of modern ecology. Foraging ecology is a broad area, with studies done on a variety of organisms and not just birds. Here, only one type of OFT models, known as the diet models, illustrated with examples of bird studies, are taken up. Simple field studies on the foraging ecology of birds, many of them textbook examples, are included here as case studies, along with some very elementary exercises that can be conducted in the field.

**Basic Concepts of Foraging Ecology**

The ability of living organisms to obtain nutrients is absolutely critical for their survival. While plants obtain nutrients from their substrate or surrounding medium by absorbing them through their tissues (mostly roots), in the case of animals, an individual has to first obtain its food, either by capturing, grazing or siphoning it, before it can be digested and the nutrients released for bodily metabolic processes. ‘Foraging’ is a very broad term, used to refer to a variety of methods that animals use to obtain their food (see Suggested Reading). Foraging includes diverse trophic interactions, which may be as simple as a cow grazing in a meadow, a bird like a shoveller or flamingo straining the waters for invertebrates (filter-feeding), or a hummingbird drawing nectar from a flower with a beak shaped like a needle, or extremely complex and elaborate predatory events.
Box 1. Foraging Adaptations in Wetland Birds

Birds possess unique adaptations of the bill and feet, depending upon their mode of foraging and location of food resources [3]. Adaptations of legs include those for swimming, wading at different depths of water in the littoral zone, walking on aquatic vegetation, etc. Studies have shown that the length of legs dictates the depth up to which shorebirds can wade into the water. The feet of raptors in aquatic habitats are adapted for grasping prey such as fish. Cormorants are said to be ‘self-propelled pursuit divers’, and their feet and wettable plumage play an important role in their foraging activity.

The bills of aquatic birds are adapted to the mode of foraging, viz., visual or tactile. One of the most interesting adaptations is that of the skimmers, which scoop out the prey while skimming over the water surface. Adaptations in the eye have evolved for a variety of different reasons and none is more interesting than the presence of red oil droplets, with colored carotenoid pigments, in the cone of retinas, especially in the case of birds like gulls, terns, and herons, which have to locate their prey through an air-water interface.

Given the tremendous variation in foraging behaviors, several terms such as ‘sit and wait predators’ (herons, kingfishers), ‘pursuit predators’ (raptors, cormorants), ‘search predators’ (skimmers, terns), etc., are in use. Most of these terms are self-explanatory and require no further elaboration. Overall, the shape of the bill has been the subject of considerable interest, and ornithologists have puzzled over questions such as, what is the function of the decurved bill of the curlew (Numenius) [4], what is the function of the gap between the mandibles of the Asian openbill (Anastomus), what is the function of the upturned bill of the avocet (Recurvirostra), etc. At a behavioral level, several interesting patterns have been recorded among waterbirds. While many species tend to be solitary foragers, some (notably pelicans) use social foraging methods.

At the foraging ground, different species remain largely segregated, each specialized in procuring specific types of food/prey, though there can be overlaps. In broad terms, the littoral, pelagic, and deeper zones are utilized in separate ways by different birds. For sympatric forms, which may utilize the same patch, even small variations in the dimensions of the trophic apparatus (and body size) lead to a separation in terms of their foraging activity, spatially, as is the case with Indian cormorants which were shown to all coexist at the same wetland without actually competing with one another [5].

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Figure A. Some examples of foraging adaptations in wetland birds. (A) The bill of herons is adapted for catching diverse types of prey including insects which are found in shallow water and vegetation, (B) the bill of Asian openbill has an opening between the mandibles, an adaptation for dealing with mollusks, (C) the spoonbill has a spatula shaped bill for sieving invertebrates from the mud and shallow water, (D) the lower mandible of pelican has a pouch attached to it for storing fish that it catches, (E) the darter or snake bird catches fish by spearing them underwater, and (F) the shoveller also has a spatula shaped bill for sieving plankton and other invertebrates floating at the surface of water. (Image Courtesy: Dr N K Tiwary)

Predation, which is perhaps the most widely studied aspect of foraging behavior, is often glamorized in wildlife films and other popular narratives. The benefits of predation—obtaining large
amounts of energy at one go—are clearly huge and outweigh the costs associated with it, because potentially it is very risky behavior. In many cases, the prey could be capable of running away or may take a fair amount of time to be actually ingested. If the handling time is prolonged due to the large size of the prey, it may prove to be too costly in energetic terms and therefore not profitable. (However, it should also be mentioned that in some cases, prey traits such as the presence of spines, spikes, or other features, and not just prey size alone, may also influence handling time). Finally, an option, which is also available to some animals is not to bother about capturing prey at all but simply steal it from conspecifics or heterospecifics which may be feeding in the same patch. This is known as kleptoparasitism (see Box 2 for an explanation of these terms).

At each stage of the foraging process, there are interesting questions to be asked, and it becomes the job of a behavioral ecologist to search for meaningful patterns, examine the adaptations and see how efficient they really are. Modern ecology often uses models of different kinds, which help us to spell out the details clearly and unambiguously and in a manner that is amenable to making precise predictions about how the foraging behavior of an animal is likely to change in fluctuating environmental circumstances.

An important aspect that foraging ecology examines is the relationship between the prey density and foraging strategies of different animals (The functional response, see Box 3). However, there are several other issues too, some of which are discussed first, in the following examples. Consider a wading bird foraging in the intertidal zone for worms buried in the sand. An important question in this context could be, what is available to the forager? In other words, how much of the food buried in the foraging patch is actually harvestable, i.e., what quantity can be actually captured and ingested? Not all that is available can be harvested because some of it may simply be beyond the reach of the forager.
Handling time and profitability: Handling time (ht) is the time taken by the predator (in seconds or minutes) to handle its prey right from the stage when it is captured to the time when it is ingested. Therefore profitability is calculated as follows:

\[
\text{Profitability} = \frac{\text{Prey size}}{\text{Handling time}}.
\]

Typically profitability for an item of prey increases with prey size—a surrogate for the energy content of the prey—but up to a point, beyond which it does not, because ht increases.

Figure B. Relationship between the length of prey (fish) and profitability (prey dry weight/handling time) taken by painted stork (*Mycteria leucocephala*) foraging at different sites in the Delhi region. It can be seen (above) that if the prey size is very large, profitability levels off. It has been observed that sometimes, painted stork catch very large fish, which they are unable to ingest probably due to their gape size constraint, and keep holding the prey between their mandibles for a long time [7, 8]. Reprinted with permission from Kalam & Urfi, *Journal of Zoology*, 2008 [6].

Kleptoparasitism (literally, parasitism by theft): Kleptoparasitism is a form of feeding in which one animal takes prey or other food that was caught, collected, or otherwise prepared by another animal, including stored food. More often than not, animals that steal prey happen to be dominant in their social hierarchy. Kleptoparasitism may also be shown by members of one species towards those of another.

Tradeoffs: A tradeoff is a choice that is made (not necessarily consciously, but shaped over evolutionary time) between two options that cannot be simultaneously maximized, such that increasing the gains from one option leads to a decrease in the gains from the other. Thus, while we expect an animal while foraging to optimize energy intake, it may optimize some other currency besides energy (food) instead, say salts, water, or minerals, which are also needed.

Contd.
Box 2. Contd.

Another example is that in a pond, fish may not feed in the best food patch and end up not optimizing energy because in that patch, danger lurks in the form of a fish-eating bird perched on a tree. Therefore, to avoid being eaten, the fish may make a tradeoff and forage in a less energy-rich patch.

Currency: Currency is defined as the unit that is optimized by the animal during its activity. In the context of foraging, ‘maximizing energy intake’ is the currency. In some other cases, the currency could be something else, such as minimizing the risk of starvation, achieving an optimal balance between risks of being predated upon and starvation, etc. In such situations, the animal is likely to make trade-offs. By identifying the currency, one can construct a hypothesis about which benefits and costs are important to the forager in question [7].

Constraints are hypotheses about the limitations that are placed on an animal while foraging. These limitations can be due to features of the environment, or the animal’s physiology or morphological constraints, which could limit its foraging efficiency. For instance, the time that it takes for the forager to travel from the nesting site to the foraging site is one example of a constraint. The maximum number of food items a forager is able to carry back to its nesting site is another example. The more constraints that one is able to identify in a given system, the more predictive power the model will have.

Central Place System: If a forager is forced to return to a particular place every time it makes a foraging trip then such a system is a central place system. For example, a bird may have hungry chicks to feed in its nest so it is forced to return every time to it. This brings into the picture the question of load size, i.e., how large should be the load of food it is carrying. If the load size is very large then the number of trips to make or how large a distance to fly is important from an energetic point of view. [7]
Box 3. The Functional Response

There is an obvious relationship between the density of prey and the encounter rate. If the prey density is high, then correspondingly, the encounter rate will also be high, and the forager will be able to meet its energy requirements quickly. However, if the prey is scarce, then the predator has to spend a lot of time searching for it, and that brings into question the functional response, which basically defines the relationship between the rate of prey capture as a function of food density. Another aspect of foraging relates to the heterogeneity of prey sizes since not all the prey items in a patch are of equal size, and therefore, have different energy values. The larger the prey, the more its calorific content but also significantly, the more its handling time (ht), i.e. the time it takes to manipulate the prey and ingest it. This brings into picture the question of profitability (energy gain/handling time).

The broad contours of the relationships between prey capture rates and food density were elaborated by the Canadian ecologist C S (Buzz) Holling in a series of seminal papers published in the 1950s. Holling identified three general categories of the relationships, which he called types I, II, and III. Type I, the simplest of the three, assumes a linear increase in intake rate with food density up to a point after which the curve abruptly and expectedly flattens. This type of relationship is exemplified by filter feeders, and the underlying assumption is that the time needed by the consumer to process a food item is negligible, or that consuming food does not interfere with searching for food, up to a point. The type II functional response is more common and can be easily modelled by a rectangular hyperbola [8]. The underlying assumption, in this case, is that the predator is limited by its capacity to process food, which is independent of searching for food. In other words, as prey density increases, the predator spends less and less time on search but more time in handling the prey. Insects and parasitoids exemplify the type II response. The type III response, which is very similar to II and usually is sigmoid, is exemplified by most vertebrates.

![Figure C](image.jpg)

Figure C. The relationship between prey density and prey capture rate can take the form of three types of functional response curves Types I, II, and III. Figure reproduced from [7].
Box 4. Simple Field Exercises

Some very simple field exercises for studying the foraging behavior of waders are suggested here. First, some time can be spent in the field just watching, through binoculars (though a telescope mounted on a stand is much more comfortable), the foraging behavior of a bird. Let us say it is a wader probing in the mud and picking up some invertebrate prey items. Some basic aspects of foraging behavior, such as pecking rate (number of pecks or probes made in the mud), success rate (a prey item caught after how many attempts), etc., can be quantified using a wristwatch or a clock on your mobile phone.

The next question is what items of prey constitute the diet of the bird under observation. A literature search will provide clues. In the field, careful observations of what the bird is eating can be supplemented by an examination of the exact spot (the foraging patch) where the bird was present and looking for other clues such as droppings, pellets, etc.

Samples of mud can be collected and taken to the laboratory for further analysis. After sieving the mud and collecting the potential food items, which could be macroinvertebrates (worms, mollusks, etc.), an attempt could be made to identify them using books with descriptions of invertebrate fauna. For freshwater invertebrate fauna (worms, mollusks, aquatic insects, crustaceans, etc.), the book *Fresh Water Animals of India: An Ecological Approach* by Prof. G T Tonapi [24] was found to be extremely useful.

In case a particular species of wader is known to have a preference for a particular species of invertebrate prey (say worms or mollusks), an attempt could be made to quantify the sizes of prey taken by the bird. There are several methods known for estimating the prey size in the field. One innovative method used in a study to estimate sizes of prey (mussels) taken by oystercatchers was to record them as a percentage of bill length [9]. However, it may be possible to record prey sizes as discrete units viz., small, medium, large, etc. Now with image recording devices easily available (even on mobile phones or in electronic cameras), much is possible.

It is always of interest to see if the bird under observation is exercising selection with respect to prey size. To do this, a comparison of prey sizes taken by the bird and the frequency distribution of prey available in the foraging patch is a good starting point [10], and the results are always interesting.

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Figure D. A frequency histogram of the sizes of prey taken by oystercatchers compared with the sizes available in the substrate reveals clear cut differences, indicative of prey size selection. In this figure, redrawn from a study conducted by Goss–Custard et al., (1977) [10] the prey (cockles in this case) taken (below) by oystercatchers are from a different range of prey sizes that are available (top). The values on the x-axis are size class categories ranging from 0 to 40 mm. The number of shells (N or sample size) measured in the upper case are 294 and in the lower case are 68.
Optimality and Diet Models

Quite a lot of modern foraging ecology deals with making predictions about foraging strategies in fluctuating environmental situations and designing experiments by which they can be tested, either by laboratory experiments or by performing ‘natural experiments in the field. In this article, I take up only one set of questions relating to foraging ecology, i.e., given a choice, what prey items to select while foraging.

Let us first discuss the broad framework which helps us to address issues relating to the foraging of animals in general. One can visualize the forager to be making choices for every prey item encountered. Optimality-based modeling or OFT is the basis of much of modern foraging ecology. According to this line of investigation, an ‘optimal’ forager, while attempting to maximize energy intake, needs to make decisions with respect to the type of food to eat, where and how long to search for it, what type of search path to use, etc. Natural selection is likely to favor ‘efficient foragers’ [11] (though this view is also controversial [18–22]).

Originally developed in the 1960s by some mathematically inclined American ecologists, notably MacArthur and Pianka, and independently by Emlen, OFT is not a new concept. Combining empirical work with theory and testing the predictions of simple models, particularly those based on optimality principles, was the hallmark of behavioral ecology research from the 1970s onwards. Since the OFT models made precise, quantitative predictions, it was easy to test them with experimental data collected in the field. However, one of the biggest advantages of this approach was that it helped in framing the ‘why’ questions precisely [11]. The trend for such field-based research using mammals, fishes, invertebrates, and other animals, particularly birds, caught on in the 1970s and 80s, and many classical studies were undertaken then [3].

First, let us try to understand how animals behave optimally while foraging. A textbook example of this is a study on northwest-
Actual observations on the behavior of crows while foraging revealed that 5 m was the height actually chosen by crows for dropping the whelks. At lesser heights, more attempts were required, and at heights greater than 5 m the bird would have to expend unnecessary energy to climb higher, adding to the energetic cost. From this, the investigators concluded that the crows adopted a strategy of dropping the whelks from an optimal height, using minimum time and effort but maximizing the gains.

The Redshank Study: A Classic Illustration of Diet Model

Field research on shoreline waders (chiefly Charadrii), many of them migratory, has been quite popular in foraging ecology studies. One reason is that most of the relevant parameters, such as prey size, handling time (ht), search time, etc., can be easily quantified in the field with reasonable accuracy. For illustration, we...
can take up the well-known study by Goss-Custard [14, 15] on the foraging behavior of the redshank (*Tringa totanus*), a common wading bird found in most parts of the world (Figure 2). In Scotland, where Goss-Custard’s study was done, the redshank was observed feeding on worms, chiefly *Nereis* and *Nephtys*. Let us think of a redshank walking in the intertidal zone and, using visual cues, poking its bill in the mud and pulling out worms. For simplicity, let us assume that the worms buried in the mud are of two different sizes, large and small. The former has a higher calorific content and also handling time compared to the smaller ones. In a hypothetical scenario, we can ask several questions, such as should a foraging animal be a specialist or generalist? Should it eat only large-sized prey and ignore the smaller ones or eat both types of prey? When should an animal switch to a different strategy, given that the basic assumption is that larger prey takes more time to handle?

Taking the above into consideration the basic equation to examine ‘profitability’ is as follows:

\[
\text{Net energy gained} = \frac{\text{Total calorific value from prey}}{\text{Energy spent in searching and handling for prey}}.
\]

**Figure 1.** Optimal Foraging behavior by north-western crows. The figure shows whelk breaks from experimental drops. The red arrow shows the optimal choice, which is about 5 m. The results of experiments on crows actually dropping whelks of different sizes closely matched the predictions. After Zach, *Behaviour*, 1978, [13].
We can ask the question, in a situation in which the bird encounters a sequence of one large to five small worms, should the bird eat any worm that it encounters or be selective by eating only the large ones and ignoring the small ones? In other words, should the predator be a specialist or generalist? Should it eat large-sized prey which has more energy, ignoring the smaller prey which is not profitable, or eat both types?

In the figure below, the small dots represent small sized prey with a calorific value of only 1 and a ht of 1 sec. The larger dots represent larger sized prey of 20 energy units and a ht of 2 seconds.

There are three ways in which a hungry redshank can behave in this situation. Assuming a total search time of 40 sec, the conse-
quences in terms of intake rate (IR) which is basically \( \frac{\text{Energy obtained}}{\text{Time expended}} \), of a bird reacting in different ways to this food supply are given below with their outcomes:

1. Eat both large and small
   \[ IR = \frac{5 \times 20 + 25 \times 1}{40 + (50 \times 2) + (25 \times 1)} = 1.67 \]

2. Eat only small
   \[ IR = \frac{25 \times 1}{40 + (25 \times 1)} = 0.39 \]

3. Eat only large
   \[ IR = \frac{5 \times 20}{40 + (5 \times 2)} = 0.20 \]

Clearly, the most profitable option in this situation is to ignore the smaller prey with low profitability (0.39) and go for the large ones only (2.0). In other words, the forager should become a specialist, given this type of prey distribution pattern.

Now let us imagine a different scenario of prey distribution (illustrated below). The redshank now encounters a sequence of one large to twenty-five smaller worms. Clearly, the larger prey is not encountered as frequently as in the previous case, though there is an abundance of small prey. Therefore (other parameters being the same as before), the strategy should now be to become a generalist, i.e., take both small and large-sized prey. As the calculations below show, eating whatever is encountered is indeed the most profitable strategy with a gain of 0.67, compared to 0.39 and 0.48 in the other two, i.e., being a specialist.

The consequences of the three possible options are given below for such a prey distribution pattern.
[1] Eat only small
IR = \frac{(25 \times 1)}{40 + (25 \times 1)} = 0.39

[2] Eat only large
IR = \frac{(1 \times 20)}{40 + (1 \times 2)} = 0.48

[3] Eat both large and small
IR = \frac{(1 \times 20) + (25 \times 1)}{40 + (2 \times 1) + (25 \times 1)} = 0.67

Optimality modeling helps in clarifying our assumptions and create a model that will make precise and quantitative predictions; both in a given ecological situation as well as in a fluctuating environment. The redshank example given above provides us the outlines of a model or a mechanism to state the problem clearly and also the assumptions based on our understanding of the real-world situation. The assumption is that animals forage in such a manner to maximize their energy intake rates, i.e., consume food with the most calories while expending the least amount of time and energy. More importantly, the model makes precise predictions, which can be easily tested by field experiments. Although it is not possible to go into the methodological details here, all the relevant parameters viz., ht, prey size, and prey density can be measured through carefully calibrated field methods and observations. The intake rate can be measured in calories using a surrogate such as ‘ash free dry mass’ (AFDM) which can be separately estimated by laboratory experiments.

Goss-Custard did a careful study in the field, and his results showed that the redshanks behaved exactly as predicted. In other words, they were observed to be foraging in a manner that maximizes energy intake while minimizing the time spent doing so. Also, the switching over from one foraging strategy to the other (viz., specialist to generalist or vice versa) was complete and instantaneous once the prey distribution pattern changed.

One important conclusion from the calculations shown above regarding the redshank study is that the decision to specialize on the more profitable prey or to be a specialist depends on the abun-
dance of the more profitable prey.

Thus, if the small prey is far more abundant than the larger one, as long as the density of larger prey is sufficiently high, the predator can continue to consume the larger prey alone.

The redshank study also helps us to understand the main components of optimality modeling easily. The first one is the concept of currency, which in this case is ‘maximizing intake rate’ by capturing food most efficiently. In other cases, the currency could be something else, such as minimizing the risk of starvation, achieving an optimal balance between the risks of being predated upon and starvation, etc. In such situations, the animal is likely to make tradeoffs. Something else can be a currency in a different case, say salts, water, or minerals which needs to be optimized (See Box 2).

The second important concept to emerge from the above is that of constraints, which may be a combination of the properties of the environment and those of the forager. While in this case, both handling time and search time are treated as fixed constraints, they may vary considerably. For instance, the handling time of a predator for a given prey type may change from case to case, and here we can take up the example of oystercatchers which can feed on mussels in different ways. One method is pulling off a mussel from the mussel bed by breaking the byssus threads by which it adheres to the substrate, carrying it a short distance away, and drilling a hole either on its ventral side or dorsal side using its chisel-shaped bill and extracting the flesh. This feeding method known as ‘hammering’ may take some time. The other method, known as ‘stabbing’, is to walk on the mussel bed as the tide is receding or approaching and the mussel valves are partly open. This method involves cutting off the adductor muscle by a scissor-like action of the bill and extracting the flesh [16]. Both these methods are quite set within a population, which may have a certain proportion of birds that are exclusively hammerers or stabbers, each with differently shaped bills. In the former case, the bills tend to be long and straight, while in the latter, they are shorter, thicker, and chisel-shaped.
In the case study described in the previous section, while the redshanks appeared to behave optimally as they went about foraging for worms, there could be a host of other factors which could complicate the equation. For example, having predators around increases the risk of death by predation when handling time is high. When food is sparsely distributed, being too picky and the resultant increase in search time might run an animal into the risk of starvation.

The third component of the model is the decision variable, which, in the redshank example, is whether to eat or reject small worms when encountered. Interestingly, the prey may also have an option (decision variable). For instance, in the case of a bird hiding from a predator by sheltering itself in a bush and relying on its protective coloration, the decision variable could be whether to flee or stay. It could fly away and try to outfly the predator or stay put in the bush and rely on its camouflage. In some other context, the decision could be whether to behave like a ‘hawk’ (behave aggressively) or a ‘dove’ (behave submissively), several examples of which are discussed in behavioral ecology textbooks [See suggested reading list]. The animal would be expected to choose the strategy based on the situation.

We come across several examples when animals seem to not be behaving in the manner in which the model predicts. Behavioral ecology literature is full of interesting examples. For instance, a textbook example is that of the study on sticklebacks foraging in a pond.

Another well-known example, often cited in behavioral ecology textbooks, is that of the moose in North America. The animal needs to feed on nutrient-rich plants, but also requires minerals that are available in some energy-poor plants growing in the vicinity of swamps where it feeds. However, grazing on these takes time away from the main task of foraging on energy-rich plants, therefore, the moose has to make a tradeoff and feed sub-optimally, ignoring energy-rich plants for a while. Dozens of other examples are available in the literature.
If field observations are done correctly and reliably, and yet the observations fail to uphold our prediction, it simply means that the animal is not behaving optimally. Having said this, animals need not always forage (behave) optimally. What conclusions could be drawn if the results did not match the predictions in general? It could mean errors in measurement, a shoddy experimental design, incorrect assumptions, or something else. For instance, as already mentioned, the animal may not be optimizing energy but something else and making tradeoffs. This is something that animals are known to do all the time for their survival. A naive question may also be raised about the caloric value of the food. How accurately that can be measured? Other factors may complicate the equation.

Optimality models are fundamentally adaptive theories, and implicit in them is the idea that foraging behaviors in animals have been shaped by natural selection [18–22]. In addition, some of these rules, shaped by natural selection may have a physiological basis. A common fallacy is to think that an optimal forager consciously makes calculations before striking or making decisions (say eat or reject). Of course, they don’t do that, and cartoons depicting them as holding a calculator and doing sums is a caricature. These are behaviors and strategies that have evolved over generations, and we try to explain these behavioral ‘rules’ using our theoretical understanding. If these assumptions are correct, then we see animals behaving accordingly, leading to greater confidence in our understanding of ecological relationships in the natural world.

**Scope and Relevance of Foraging Ecology**

While the optimal diet model is a key concept in foraging ecology, other issues have occupied the center stage too. An important area of inquiry is to ask questions about how long to go on feeding in a patch. If a predator stays in the same patch for too long, then prey depletion is bound to occur, and the decision that the individual has to take is when to leave and find an alternate patch.
Also, the forager may not be just foraging for itself, but it may have to bring food to young ones (say chicks in a nest) located some distance away from the foraging patch. To take another example, a honey bee visiting a flower to collect nectar has to make a two-way trip to the colony (the beehive), which in ecological terminology would be known as a central place system (Box 2). So the question becomes how much nectar to carry, i.e., make several trips carrying small amounts of nectar (if the hive is near) or make a few long trips with a heavy load if the colony is far away. This brings into the picture the question of load size, or how large should the food delivery parcel be? Is there an optimal load size? For addressing such issues, ecologists have developed a theoretical framework, based on marginal value theorem (MVT) known as patch models, which helps us to address them. A full account of these, especially MVT, merits a separate discussion.

From its simple formulations early on, OFT has greatly developed and has been used in a variety of cases, including explaining several facets of human behavior [17]. The human connection demands a full article and separate treatment due to its rich diversity of problems and controversies. It is beyond the scope of a short article to detail all the areas of work as well as review the recent developments in this field or to flag out the several controversies which have dogged the discipline. The purpose here was only to acquaint the reader with the significance of foraging ecology and how to frame questions in order to undertake a meaningful study.

The OFT approach, which became quite a fashionable area of ecological research throughout the world during the 1970s and onwards, always had a strong ornithology component. While studies on the foraging ecology of all manner of birds were published at a rapid rate, papers reporting on studies of wetland birds, particularly waders, which are migratory and use coastal areas (threatened due to sea-level rise) on a global scale were especially popular. A group of researchers (mostly from Europe, the Americas, and Australia) created the Wader Study Group (WSG) to investigate different facets of the ecology of shoreline birds. Many studies on wader foraging ecology have explored the dynamics of invertebrate prey upon migratory shorebirds.

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ynamics of invertebrate prey upon migratory shorebirds. A good example of such a study is on the importance of horseshoe crab eggs to migratory red knots, and the resultant massive declines owing to shoreline reclamation [12].

Recently, while reviewing the literature on food and foraging habits of waterbirds in India, I discovered to my dismay that many field studies (mainly reported in the Journal of Bombay Natural History Society), were devoid of the theory of foraging ecology and, consequently, lacked rigor and substance, ending up as half-hearted attempts to document food and foraging behavior [3]. This suggests that while the natural history tradition of studying birds in the field was strong, we had not kept abreast of ecological theory, particularly in our academic institutions where ecology is taught to students. Happily, the situation is quite different now, with several institutions in India having taken up interesting ecological questions, using a combination of both ecological theory and rigorous field experiments, in the past few decades as some excellent ecological publications have emerged from various institutions. This is a very welcome development because, given the huge popularity that bird study enjoys at a popular level, this offers tremendous opportunities for ecology education using birds as models.

**Conclusion**

Today, while OFT in itself may not be center-stage with respect to ecological problems being tackled by scientists, there are still interesting areas of inquiry and gaps in our understanding which need to be pursued. Even though many relationships with respect to the foraging of waders and other birds have been sorted out, there is still scope for carrying out more studies, with the aim to assist with conservation in the Indian context. Greater emphasis on training in ecology in our colleges and universities will go a long way in this direction.
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