

ground-truth validated models, and any other means we can find. We need energetic data from more taxa, especially from lizard species that are part of model ecological systems, to hone in on general principles through comparison. An important parallel effort could develop a multiscale neuromechanical modeling framework for legged locomotion that captures essential features across size and morphology. Combining more diverse experimental data with estimates that can only be derived from modeling and the ability to add counter-factual thought-experiments from the model would go a long way towards eliminating some of the confounding factors in our current general models of energetic cost. A critical part of these models would be features at the ‘meso scale’ that link more reductionist, laboratory measures of tissues with the high level, whole animal work done in the field.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Primer

Optimal foraging

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Before visiting your local supermarket, do you write your food shopping list in the order you expect to encounter the items as you walk around, aisle by aisle? This way, you minimise your travel distance, saving time and effort. Many other animals do the same. Baboons (*Papio ursinus*) plan their foraging journeys to out-of-sight resources, moving in an efficient, goal-directed way, and nectar-collecting bumble bees (*Bombus impatiens*) use efficient travel routes when foraging on familiar resources.

Behavioural ecologists studying baboons and bumble bees assume these ‘least-effort routes’ between resources are selected for by natural selection. More precisely, it is assumed that for individuals to maximise fitness, they should adopt a foraging strategy that provides the most benefit (energy) for the lowest cost (time, effort) maximising the net energy gained. This assumption — that natural selection has resulted in foraging behaviour that maximises fitness — is the basic tenet of optimal foraging theory, first formulated in 1966 by Robert MacArthur and Eric Pianka.

Optimal foraging makes predictions about how an animal should forage. The theory can be applied to any given predator and prey feeding system: cheetahs preying upon impala, impala grazing on grass or ticks eating their impala host’s blood. Whilst grazing impala or parasitic ticks are not ‘true’ predators, throughout this primer we normally use ‘predator’ to refer to the forager and ‘prey’ to refer to the food. Applying optimal foraging theory requires researchers to consider how a predator chooses, searches, handles and consumes their prey.

Choosing prey

Predators should ignore low profitability prey items when more profitable items are present and abundant. This is a prediction of the ‘optimal diet model’. Like all optimal foraging models, the optimal diet model has a mathematical description: E is the amount of energy

a prey item provides; h is the time it takes for a predator to consume the prey, the search and handling time. The profitability of a prey item is therefore defined as E/h . This is why you find chopped, peeled and prepared fruit and vegetables in your supermarket — same E , but lower h .

Search and handling time

Search time is intuitive — the time a predator takes to locate a prey item in their environment. Handling time then covers the time it takes the predator from locating the prey item to fully consuming it. This includes catching the prey, preparing it to be eaten and then actually ingesting it. The amount of searching and handling required can vary widely depending on how conspicuous the prey are (Figure 1A), whether they are mobile (Figure 1B), if they have evolved any anti-predator defences (Figure 1C,D) and their size and shape (Figure 1E).

Two experiments on bluegill sunfish (*Lepomis macrochirus*) conducted nearly 40 years apart demonstrate the importance of search time and handling time for predators and prey. In the first, researchers manipulated search time for the fish by varying the absolute abundance of their prey, water fleas (*Daphnia magna*). At low absolute abundance, fleas of different sizes were eaten by the fish as they were encountered. But when water flea abundance was increased, the fish began to leave the small fleas in favour of larger fleas. In the second, researchers used computer-generated water fleas and projected these images onto the side of a bluegill sunfish’s tank as ‘prey’. Because the bluegill sunfish displays a characteristic ‘hovering’ behaviour when foraging, the researchers could estimate the time it took for the sunfish to choose which prey to attack. The sunfish took longer to make this decision when there were more computer-generated fleas to choose from. That is, if the ‘prey’ were in larger groups, the fish’s handling time went up.

Consumption rates

How search and handling time combine to determine the prey consumption rate — and so their overall profitability — is described by three





Figure 1. Prey in many guises, with different costs.

(A) Conspicuous prey: fiery-neck nightjar (*Caprimulgus pectoralis*) in leaves. (Photo: Jolyon Troscianko.) (B) Mobile prey: cheetah chasing young antelope. (Photo: Viktoria Altman, CC BY 2.0.) (C) Anti-predator behaviours: a murmuration of starlings. (Photo: ISC-CNR, Starflag Project.) (D) Prey with defences: stinging rose caterpillar moth larvae with detachable spines that contain toxins. (Image courtesy of Megan McCarty, Wikimedia.) (E) Snake (*Leptophis ahaetulla*) eating a frog (*Craugastor gollmeri*) that is a very different size and shape to itself. (Photo: Brian Gratwicke, CC BY 2.0.)

types of functional response (Figure 2A). In a type 1 functional response the handling time is negligible or overlaps completely with search time, so that consumption rate increases linearly with prey density until the point where the predator cannot physically consume prey any faster. But most prey requires at least some handling, setting an upper limit on the rate they can be consumed, resulting in a type 2 response, where consumption rate increases with prey density in a decelerating curve until it reaches this upper limit and plateaus. A type 3 response considers that search and handling times may be longer at low prey densities. Prey may be able to hide in refuges more easily or predators may be less efficient at finding and handling prey. However, as prey density increases, refuges may run out, making prey easier to find, and predators may learn how to find and handle them more efficiently. Therefore,

type 3 responses show an accelerating increase in prey capture at lower prey densities, until handling time limits kick in again (as with type 2), resulting in a deceleration of the curve until it reaches a plateau. Whilst type 2 and 3 functional responses are more realistic than type 1, all three responses have been described in the natural world, for example as consumption rates in a foraging chacma baboon (*Papio ursinus*; Figure 2B).

The next meal

Once a predator has located a prey item, it must then decide when to move on to the next prey item. This is a particularly important decision when prey is found in ‘patches’ in the environment. For example, seeds, leaves and fruits are all concentrated in space (and time) and prey animals are similarly ‘patchy’ in the environment, especially when they live in groups. A

predator’s decision about when to leave one food patch and travel to another is described by the ‘marginal value theorem’ (MVT), formulated by Eric Charnov in 1976.

The MVT describes how predators weigh up the benefits of staying in a patch — the energy per unit time they are gaining from it — against the costs of moving to another patch — the time and energy this travel will use up. This balance between costs and benefits is constantly shifting, as the predator is depleting the patch they are in, reducing its prey density and the energy per unit time they are gaining from it (Figure 2A). This leads to a point where the benefits of staying no longer outweigh the costs of moving to a new patch, and MVT predicts this to be the optimal time for a predator to leave a patch to maximise its overall energy intake from the environment (Figure 2C).

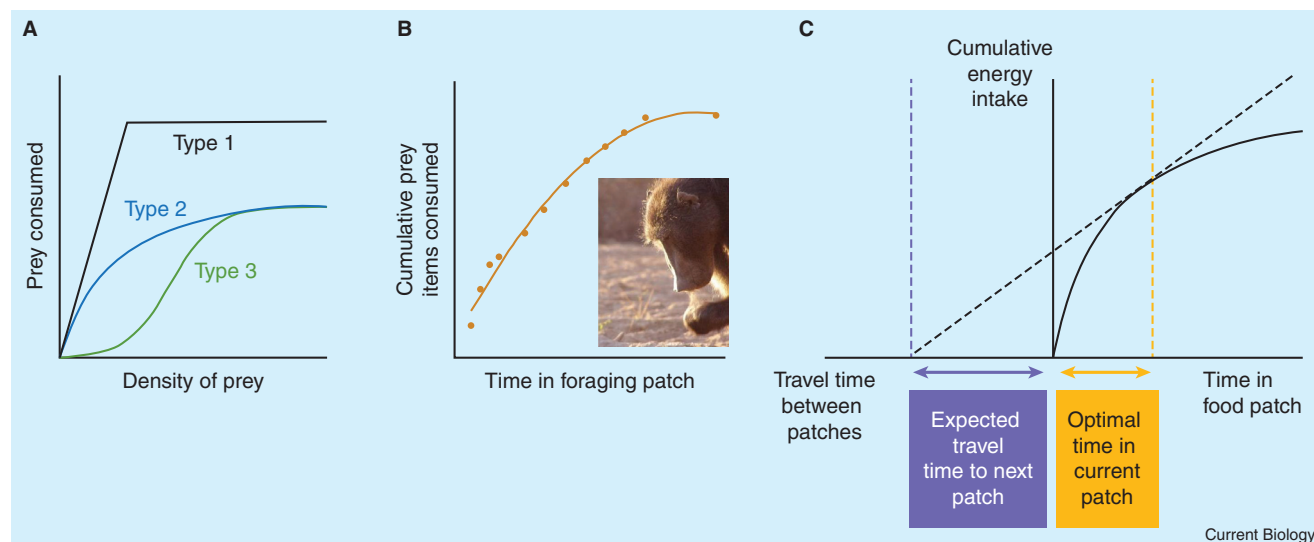


Figure 2. How quickly predators consume prey and when to move on.

(A) The functional response describes how a predator's intake rate changes with prey density. There are three types of functional response: type 1, type 2, and type 3. (B) Male chacma baboon (*Papio ursinus*) foraging in an experimental food patch of dried corn kernels. The rate at which prey items (kernels) are consumed decreases with time in patch as the prey items become more difficult to find (King, unpublished data). (C) The marginal value theorem (MVT). A predator depletes the patch they are in, resulting in diminishing energy returns the longer they stay in it (black curve). Leaving the patch requires an expected amount of time and energy to travel to the next patch (vertical purple dashed line). Plotting a line from this expected travel time on a tangent with the energy intake curve (black dashed line) predicts the optimal time for a predator to stay in a food patch before the returns it receives no longer outweigh the costs of travelling to a new patch and it should leave (vertical orange dashed line).

A key prediction of MVT is that the optimal patch departure time will vary between environments due to differences in patch quality (benefits of staying put) and the distance between patches (costs of moving; Figure 2C). Classic support for this prediction comes from great tits (*Parus major*) foraging in two artificial environments differing in the travel time between patches of mealworms. As MVT predicted, tits spent longer in food patches in the environment with higher travel times between patches. Many different factors have since been shown to influence patch departure decisions. For example, thick-tailed bushbabies (*Otolemur crassicaudatus*) leave food patches in trees earlier when they contain higher concentrations of plant toxins, and even switch to foraging in high-predation risk ground patches containing no toxin when toxin concentrations in tree patches are very high.

The explanatory value of optimal foraging theory

In 1987, a forum article appeared in the journal *Oikos* entitled "Eight reasons why optimal foraging theory is a complete waste of time". The authors argued that any theory based

on optimisation is inappropriate for investigating behaviour, as animals should not be expected to behave optimally, and, anyway, it is not possible to test if they are behaving optimally. If optimal foraging theory is viewed in the narrow sense, this is all true.

However, if you take optimal foraging theory in the wider sense, acknowledging that an animal's behaviour will depend on its state (e.g., energy levels, health, reproductive state), its environment (e.g., predation risk), the foraging behaviour of others in the population (e.g., competing for the same food) and its future behaviour (i.e., actions cannot be considered in isolation), then the notion that behaviour maximises fitness can be used as a tool for generating testable hypotheses and predictions concerning how we expect animals to forage.

Using optimal foraging theory, researchers are forced to carefully consider what currency is optimised by the predator (net energy gain per unit time is normally assumed), and the constraints a predator has (e.g., speed, mouth size, learning or memory) when making predictions. Thousands of scientific papers are published on the topic every year. Below, we have picked

three areas of study where researchers have tested and refined some of the (necessary) assumptions of optimal foraging theory to explore different scenarios that predators face in the natural world.

Incomplete information

One of the assumptions of optimal foraging theory is that predators have perfect knowledge of their environment, such as the energy content of each prey item and food patch, how long it will take to travel between patches and how long items will take to find and handle. Clearly this assumption is unrealistic but was necessary to develop the basic tenets of optimal foraging theory.

In reality, predators need to learn about their environment and use this incomplete information to inform their foraging decisions. Models, such as Bayesian updating/learning, and learning rules, such as the linear operator and relative payoff sum, attempt to capture this learning process by describing how predators combine past and present experiences in their decision-making. These models and rules have all received empirical support, and it seems likely that the way in which a predator values and

integrates information depends on the environment's characteristics. For example, chacma baboons' decisions about when to leave a food patch most closely match a Bayesian updating model in a predictable environment, but a marginal value theorem model in a less predictable environment.

Dietary strategies

Individuals from the same species living in similar environments regularly have distinctly different diets. Optimal foraging theory provides a useful framework for understanding these dietary differences by predicting that predators should rank their preferences for different prey based on the net energy gain each will provide. Individuals from the same species vary in aspects such as their morphology, physiological needs, behaviour, experience and learning ability; all of these can influence the net energy a predator gains from prey, and so how each predator ranks each prey type. For example, individual oystercatchers (*Haematopus ostralegus*) that prey on mussels (*Mytilus edulis*) by hammering a hole in their shells have an intake rate 40–50% greater than those that stab their beak between the mussel's valves. The resulting differences in prey preference can lead to individual foraging specialisation, where each individual uses a subset of all the prey used by the population.

Foraging with others

Predators rarely make prey choices in the absence of competition. This is particularly true where animals live together in groups. Within-group competition for prey can influence a predator's diet, as a preferred prey type may already be taken by a more competitive group member forcing them to an alternative prey. For example, lower ranking female chacma baboons will avoid joining higher ranked and larger male baboons at food patches, especially when these food patches are small. These different foraging tactics can be explained by producer–scrounger foraging models: individuals can either search for their food (produce) or join the food discoveries of others (scrounge). In the case of chacma baboons, producing and scrounging tactics change not only depending on an individual's

dominance rank, but also depending on their social affiliations, such that female baboons are more likely to scrounge from their close female friends. Consequently, optimal foraging theory predicts increased competition results in predators using a wider range of prey types. This may lead to less individual specialisation (where all predators rank prey types similarly) or more specialisation (where prey ranking differs between predators). Empirical evidence has started to support the latter. For example, banded mongooses (*Mungos mungo*) living in larger groups have more specialised foraging niches.

The future of optimal foraging theory

Optimal foraging theory has been around for nearly 60 years. Like any theory, it had to start out simple and make some necessary assumptions, in order to formulate some general predictions about how predators should choose and consume a prey item before moving on. Despite criticisms of the theory, these general predictions have proved remarkably useful for biologists trying to explain the patterns of animal and human behaviour they observe. A hallmark of the power of these original predictions is that, in many cases, they do a better job at explaining the behaviour we observe than predictions made by later and more complicated models.

These simple beginnings also provided the foundations for a vast body of work incorporating greater realism into optimal foraging models. The extent of this work means that optimal foraging theory has arguably now graduated from a theory to a much broader theoretical framework within which more recent work sits (such as the examples we have touched on above). Research developing this framework will continue to provide insights into how animal and human behaviour is shaped by the world around them. In turn, this will contribute to our understanding of how this behaviour evolved, how these individual behaviours combine to produce group- and population-level patterns (e.g. collective decisions, migration patterns and population dynamics), and how environmental change will influence these individuals, groups and populations.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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