CellPress
Current Biology
Magazine

Primer

The economy of terrestrial locomotion

Andrew J. Spence[1,*],
Simon D. Wilshin[2], and Greg Byrnes[3]

All else being equal, evolution is going to drive animals to require the least food to move a unit distance. What is the best way to do that? Some efficiencies can be 'hard-wired' into the body — the relatively unchanging morphology of the animal. But flexibility is also needed — given the task at hand, state of the body, or state of the external environment, it may be best to dynamically choose an appropriate mode of locomotion. For example, slow walking may be great for searching and foraging, but it won't catch fast moving prey. Similarly, maximum speed gallops may be great for escaping danger, but they preclude eating along the way. This primer summarizes what we know about the determinants of locomotor costs and the strategies animals use to minimize cost. It summarizes key findings across levels of organization, from individual muscles to interactions with other organisms and the environment. At the mid-level of organization we highlight gaits, a particularly interesting topic of inquiry with a rich history. We are in an exciting time for the science of movement because we have more, better tools than ever before for observing and manipulating systems, from the molecular level to herds of animals on the Savannah. Even more importantly, there are so many open, exciting questions to ask.

Force is developed and mechanical work is done by muscle to move the animal. While clever mechanisms can go a long way to minimizing the amount of work that muscles must do, ultimately it is they that make us move. As Sherrington put it in 1924: *"To move things is all that mankind can do … for such the sole executant is muscle, whether in whispering a syllable or felling a forest."* The fundamental question of the economy of locomotion is to determine how the rate of mechanical work (power) done by muscle is linked to metabolic power, or rate of fuel consumed. In the following sections we briefly introduce some key findings, core techniques, and emerging approaches at four length scales. Integration across scales is yielding important insight; here we use distinct scales to clarify presentation.

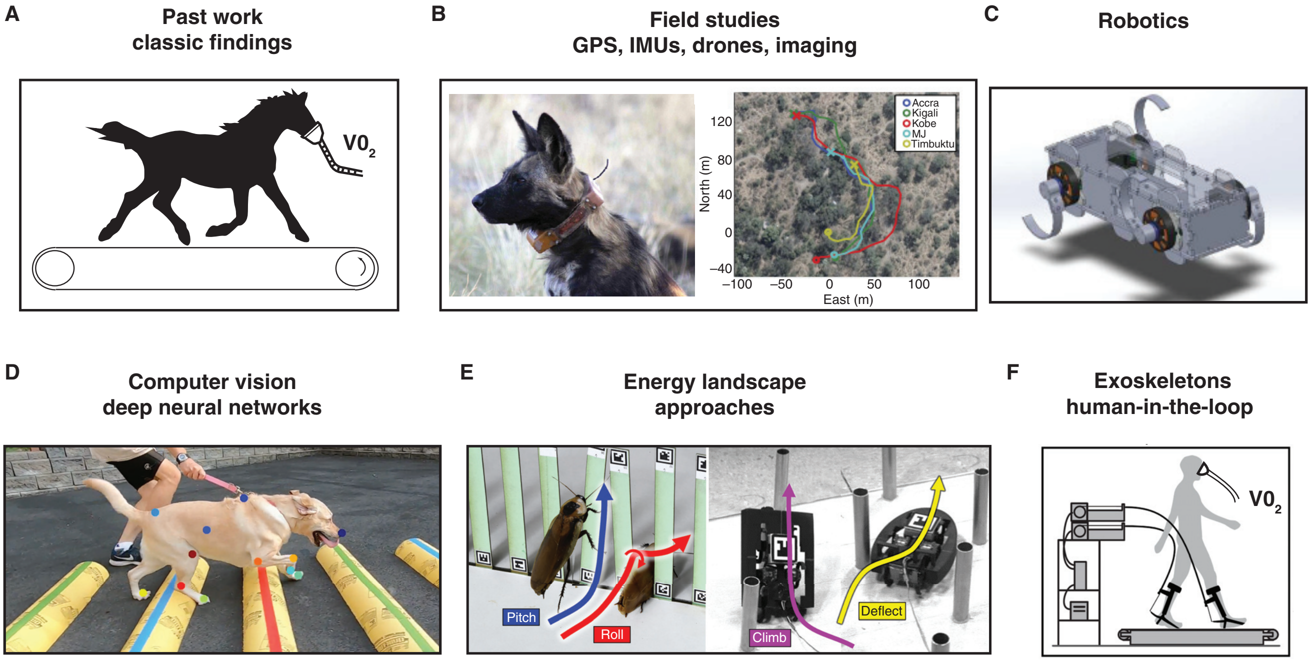
Individual muscles or muscle–tendon units

Metabolic power can be modeled as a (relatively complex) function of muscle shortening velocity, scaled by the maximum force that muscle produces, and for temporally precise models, the muscle activation level. These models are a work in progress. History effects and other extrinsic factors make them in need of further data and refinement, but they represent a now classic and important principle. The fundamental technique to study muscle physiology has been the muscle work-loop method, using force levers to drive *in vitro* muscle (and/or muscle tendon units) through force and length changes, with or without electrical stimulation. The work loop can estimate the mechanical work done by the muscle in a set of working conditions, with specified activation. Exciting new methods are replacing simple prescribed force/length curves with dynamically simulated virtual environments — so called unconstrained work loops. In addition, cyber-robotic systems that couple *in vitro* muscle to 3D printed appendages, which then do their work in hard-to-simulate media such as fluids or sand, are being developed. These systems mean that more complex, naturalistic stimuli can be presented to isolated muscle, revealing the ways in which they may be adapted to their habitat, yet still providing systematic control over muscle, appendage, and environment. Exciting research seeks to integrate from the role of structural proteins up to the mechanics and energetics of muscle, and then to relate the complex, nonlinear properties of muscle to function during *in vivo* tasks.

Muscle–tendon unit to leg, to posture

At the next higher level, muscle–tendon units attach to bone as part of skeletons, which act as jointed lever systems. Vertebrates wrap tendons and ligaments around bone while invertebrates have intricate apodemes connecting complicated exoskeletons. Numerous mechanisms have been discovered for energy savings, damping of vibrations, and power amplification for astounding jumps. For example, tendons are used to great effect to save energy by storage and return of kinetic or potential energy as elastic strain energy during bouncy gaits. Hopping kangaroos and wallabies can store and return enough strain energy in their long tendons to increase speed with no additional locomotor cost. Animal posture can also have large effects on costs. Bones act as lever arms, and changes in joint angles change the effective mechanical advantage of muscle–tendon units, trading off length for force, or vice versa. These factors can help explain why large animals move with more columnar, straight legs, as compared to the bent legs of smaller animals. This change in posture appears to be involved in differences in the cost of locomotion: smaller animals with crouched posture not only have a larger cost of locomotion per kg of animal (in J/kg/m), but also a different scaling of cost versus size, than larger animals with straight legs. This suggests an important role for posture, though other factors such as the frequency with which animals take steps, and concomitantly the velocities their muscles must cycle at, are likely at play.

To determine how leg structure or posture alter the cost of locomotion, whole body metabolic costs of movement are measured by respirometry, measuring the rate of oxygen consumption or CO_2 production from expired air during locomotion (Figure 1A,F). Oxygen consumption has become the default currency for economy that is relatively easily measured, and that most things at the larger scales are related to, either directly or indirectly. These metabolic data are combined with both kinematic data, from videography to determine limb positions and joint angles, and ground reaction forces, measured using a force plate to determine joint moments, to link the locomotor costs to both animal size and leg posture. Additionally, sophisticated computational techniques are now



Current Biology

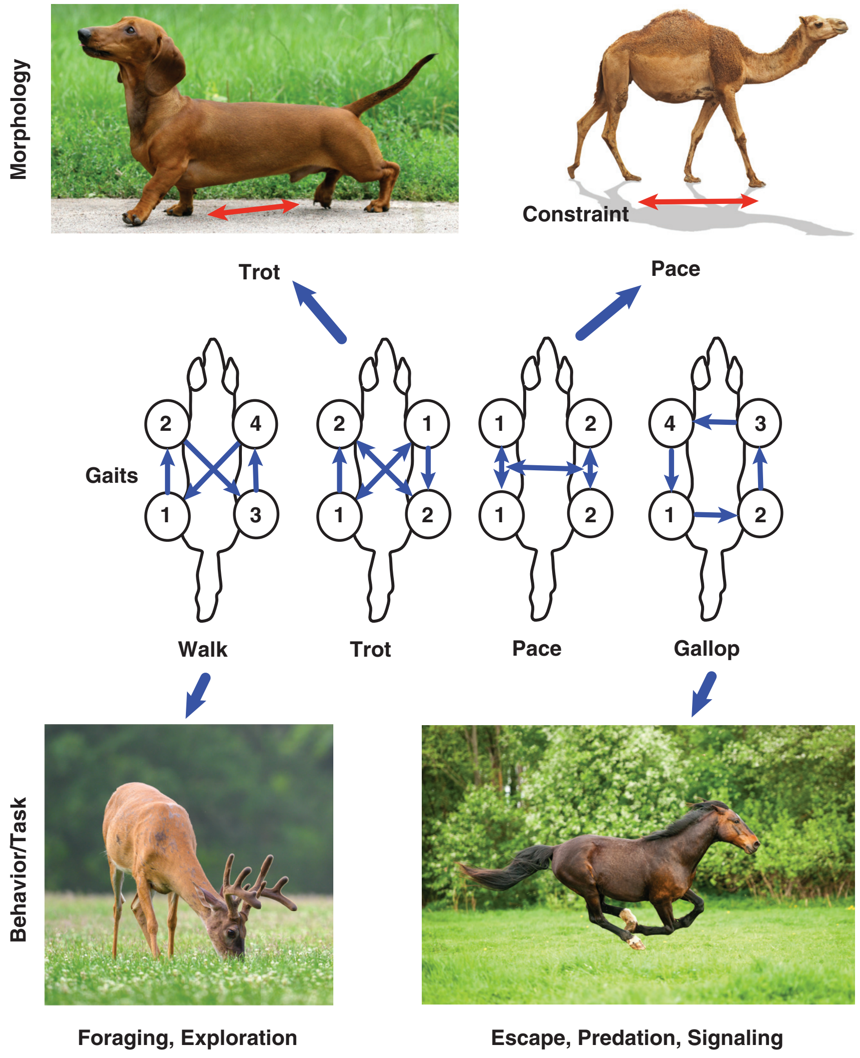
Figure 1. Future directions for research into modes of terrestrial locomotion and their relationship to energetic economy.
(A) Classic findings have relied extensively on laboratory experiments, especially treadmill locomotion. This provides important experimental control and the ability to measure many aspects of locomotion — oxygen consumption, kinematics of motion, forces, and muscle activity, for instance. But motion on treadmills is unnatural and lacks ecological context. New technologies are making some of these measurements more feasible in the field, resulting in several exciting current and future directions, such as the study of collective behavior. Understanding how animals' modes of locomotion are employed in group settings, especially in the field, is an exciting new area of discovery, as sensor technologies improve. (B) Here, African hunting dogs are found to benefit from sharing kills, but not through the expected mechanism of 'coordinated' hunts. Image from Hubel *et al*. (2016). Nat. Commun. *7*, 11034 (CC BY 4.0). IMU, inertial measurement unit. (C) Legged robots can be forced to use a given mode of locomotion (unlike most animals), and their bodies can be systematically modified as a 'physical model' of moving animals. Image from Qian *et al*. (2020). Int. J. Rob. Res. *39*, 1549–1566 (CC BY 4.0). (D) Automated techniques from computer vision are making digitization of movement from video faster and more accessible. (E) Taking a statistical physics approach to insect and multi-legged robot locomotion in complex environments has inspired a new paradigm for approaching destabilizing locomotor modes and transitions between them, and is ripe for linkage to energetic economy. (F) Exoskeletons are allowing investigators to inject perturbations and novel controllers to humans walking on treadmills, allowing them to explore how we optimise our gait under different conditions. With so-called 'human-in-the-loop' experiments, humans continuously optimise their gait to externally applied perturbations, and can be characterized in how they explore the space of possible 'modes' of locomotion and relearn the optimal gait. Image from Song and Collins (2021). IEEE *29*, 786–795 (CC BY 4.0).

employed to understand the roles of individual muscles and their interactions within the leg. These neuromechanical and musculoskeletal simulation techniques, with models based on detailed scans and kinematic and kinetic inputs, can ask questions such as how the nervous system may be optimizing muscle activation for a given task (standing, stepping, stability), and how the bone and muscle anatomy may be adapted to intrinsic stability, and more.

Recent advances have begun to increase our understanding of how humans (and potentially animals one day) optimize their energetic consumption by continuously adapting their movement. For example, high speed exoskeletons (Figure 1F) are being employed to inject torques that alter the cost landscape for the walker/runner, allowing a probe of the optimization strategy being used. These 'human-in-loop' experiments could be expanded to amenable animal systems to explore how these optimization strategies may vary with leg number.

Multiple legs to body and gait

Terrestrial animals with legs typically have more than one and must decide how to coordinate them to achieve a fitness-relevant task. They have evolved a spectacular array of modes of locomotion that have fascinated humans for thousands of years (Figure 2). Aristotle pondered the gaits of legged animals in *De Incessu Animalium: "The bendings, then, of the legs take place in this manner and for the reason stated. But the back legs move diagonally in relation to the front legs; for after the right fore leg animals move the left hind leg, then the left fore leg, and after it the right hind leg*." We now know that changing gait influences locomotor costs. In a classic work, respirometry was used to measure energetic consumption versus speed in small horses trained to walk, trot, and gallop on a treadmill (Figure 1A; Figure 2, center). The horses were trained to extend their gaits, however, walking much faster than typically done, and trotting much slower. Each gait yielded a minima of energetic consumption versus speed. By changing gaits as they speed up, animals save energy by linearizing the otherwise steeply increasing cost within each gait. An important open question is whether this is a general



Current Biology

Figure 2. The central role of gaits in understanding many aspects of biology related to locomotion.
Quadrupedal animals have a rich space of possible ways to cycle their legs relative to each other. A choice of leg ordering is referred to as a gait. Perhaps the most ‘classical’ gaits for quadrupeds are walk, trot, pace, and gallop. The illustration at center shows a top down view of a quadruped, with the ordering of the legs for these four gaits shown on each leg. Numbers denote the order of the footfalls during this gait, and arrows illustrate the next leg (or legs) to fall. When pairs of legs move together, they have the same numbering. Gaits are a rich area of study as they link morphology to ultimate evolutionary constraints through behavior. For example, trotting is a bouncy gait that can save energy (evolutionary constraint) by utilizing energy storage and return in springy tendons (morphology). Classic studies of energy consumption show that moving up through these gaits as the animal increases speed reduces the energetic cost of transport. Similarly, sausage-shaped Dachsunds (top left) can trot without the paws on the same side of their body colliding mid-stride (red arrow; injury risk evolutionary constraint). Camels, however, have such long legs relative to body length that they would clip hooves and be injured in a trot; thus, they utilize a pace. Similarly, the walk is an effective gait for foraging and exploration, while maximal performance gaits such as the gallop or pronk are optimised for escape, predation, and possibly signaling.

principle. The hard part is getting more diverse, non-domesticable animals to move at a range of speeds around their preferred speed for the gait.

To overcome this, robot models of legged animals have proven invaluable because their bodies and nervous systems can be controlled, and systematically varied (Figure 1C). Biorobotics has helped to reveal mechanisms of energy savings and stability, as well as to uncover hypothesized control architectures that exist either in the nervous system or are embodied in the mechanics and dynamics of the animal’s physical self and/or movement. Finally, genetic tools that allow for manipulation of brain, spinal, or peripheral sensorimotor neural circuitry promise to give unprecedented insight. For example, recent work has examined the genetics of the unique Tölting gait of Icelandic ponies, which is a kind of super-fast walk with rapid leg recirculation, through comparative work with genetically altered mice, concluding that certain genetic changes are required to ‘unlock’ these non-standard gaits. Here, open questions center on how gait is regulated, and how genetics, spinal cord circuitry, and sensory input are integrated to yield stable movement.

Body within the environment

Going even higher on the spatial scale, there is the animal as a whole within its habitat (Figure 1B,E). The classic finding here is that the rate of energy used in movement (per Newton body weight) is inversely proportional to the size of the animal. So, for example, an elephant moves one kilogram of its mass more economically than a cat does. This results from the time of contact of the limb on the ground, with smaller animals exhibiting shorter contact times, and demonstrates the importance of the time course of developing force for predicting cost, mirroring muscle costs’ dependence on velocity. This finding has been expanded in parsimonious ways to more general theories of the cost of terrestrial locomotion, taking into account, for example, resting metabolism.

Understanding the influence of the terrestrial environment on locomotion economy can be non-trivial, however. Many animals move through distinctly different habitats, often with distinct terrain or obstacles to navigate. Few large studies of terrestrial animals freely moving in the wild over varied terrain with detailed data exist at present. But this is an exciting growth area. Miniaturized sensors and global positioning service (GPS) tracking devices are increasingly providing these data (Figure 1B). The data are becoming richer and more able to discern details of the animals' behavior. Recent studies of dogs walking on flat and rough terrain have found that they utilize a more trot-like gait (at the same speed) on rough terrain, likely to improve stability, and potentially also to reduce cost. Furthermore, robot studies on arrays of obstacles have shown that gait choice can steer the robot when it moves over them, inspiring biological work to see whether dogs utilize this strategy (Figure 1C,D). Similarly, Black-backed Jackals in the wild, for example, use a trotting gait roughly equally often on three different habitat types, but only sparingly use a walking gait in the interdune habitat.

Sensor systems are now also being used on groups of animals, including predators and prey, and can be coupled with drones or other aerial observations, satellite photogrammetry and computer vision techniques (Figure 1D) to get at real-world costs of locomotion. Open questions here concern the extent to which individuals may adapt their locomotion for their immediate habitat or current condition (satiated, gravid, etc.), and whether they may employ mixed gait use (switching frequently between standard gaits) that optimizes cost for a given task.

Economy in collective locomotion

It is well established that birds flying in groups can fly more economically. Though lesser known, terrestrial animals can also save energy by moving in groups. There are two major ways that being part of a group can increase locomotor economy: first, by altering the physical environment for the group as a whole, and second, by socio-cognitive forces. For example, in the first case, animals moving through difficult substrates such as sand or deep snow, which are energetically costly to travel across, can improve economy by traveling together. Sea turtle hatchlings that exit the nest in groups do so more economically than those that exit individually. Further, many mammals from deer to coyotes save energy by moving in a group or over snow previously packed by other animals or human activity. Costly locomotor tasks such as active hunting can also be made more efficient by working as part of a group. Some African wild dogs share the work of hunting by using multiple short hunts by different individual members of the group, allowing other members to move more economically to the shared kill (Figure 1B). In addition, hunting hounds move more economically than their chased 'prey', using lower speeds and less steep routes, both of which can make locomotion less costly.

Shared routes, developed through knowledge of the environment, can also make moving to food resources or over challenging terrain more economical. These routes can be learned and shared within a social group, or observed and utilized by conspecifics or even other species through social sampling, thus passing on this form of economy. Examples from primates suggest that shared routes follow least-cost paths to distant resources. Similarly, there is evidence that many human pathways, including traditional hunting or traveling trails, as well as modern recreational trails, often follow least-cost paths through the environment. Although group living can result in increased economy, the benefits are often not shared equally among all members of the group. In order for a group to stay cohesive while traveling, members with different locomotor capacities based on size or age must compromise their preferred speed to maintain a consensus speed across the group. This often means that smaller or more aged members of the group must move faster and thus less economically than they would at their individual preferred speed. In this area, open questions remain of whether terrestrial animals can cooperatively hunt, how they better evade predation as part of a collective, and the extent to which socio-cognitive mechanisms save energy.

Energy landscapes on large and small scales

Looking across an environment, it's easy to imagine that some regions will be less costly to traverse than others. For example, moving some distance through a river valley will likely take less energy than moving a similar distance through a mountain range. Recently there has been an effort to quantify potential 'energy landscapes' that relate position in the landscape to the cost of locomotion at that position. Energy landscapes are best understood for flying animals, especially those that use thermal or orographic updrafts to soar over long distances. If the bird has some knowledge of the location of these updrafts, or they occur in predictable relation to observable landscape features, birds can increase economy by soaring from one updraft to the next. Though less is currently known about how terrestrial animals interact with their energy landscape to increase locomotor economy, there is growing evidence that they do so. Much like in aerial environments, energy landscapes are generally defined by the potential energy of locations in the environment and terrestrial animals can use this potential energy to move more efficiently (Figure 1E). For example, to climb from a region of altitude with low potential energy to a region of higher altitude and increased potential energy will be costly for the animal. In contrast, moving downhill or on the same level will be less costly.

Other features of the landscape can also affect cost. Moving over substrates that are compliant and absorb energy such as sand or narrow tree branches or over regions with deep snow cover will be more costly than stiffer substrates such as hard ground. At smaller scales, obstacles roughly the size of the organism or smaller can also be overcome efficiently. Center of mass oscillations resulting from the dynamics of legged locomotion allow animals to transition across small variations in the potential energy landscape. Increased leg length or larger center of mass oscillations reduce cost of transport over rough terrain in some lizards, keeping the center of mass from becoming stuck in low potential energy basins as animals cross the landscape. In the larger picture, opportunities here could extend these energy landscapes to be a proxy for fitness landscapes, informing ecology; they could also be used in robot design, allowing the robot to 'funnel' itself towards achieving a task or locomotor goal.

Broad future directions

For energetics in terrestrial animals, we are in need of more, better ways to measure the cost of locomotion in the wild, through better sensors, 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.

FURTHER READING

Andersson, L.S., Larhammar, M., Memic, F., Wootz, H., Schwochow, D., Rubin, C.J., Patra, K., Arnason, T., Wellbring, L., Hjälm, G., and Imsland, F. (2012). Mutations in DMRT3 affect locomotion in horses and spinal circuit function in mice. Nature *488*, 642–646.

Biewener, A., and Patek, S. (2018). Animal Locomotion (Oxford: Oxford University Press).

Hubel, T.Y., Myatt, J.P., Jordan, N.R., Dewhirst, O.P., McNutt, J.W., and Wilson, A.M. (2016). Additive opportunistic capture explains group hunting benefits in African wild dogs. Nat. Commun. *7*, 11033.

Ijspeert, A.J. (2014). Biorobotics: Using robots to emulate and investigate agile locomotion. Science *346*, 196–203.

Othayoth, R., Thoms, G., and Li, C. (2020). An energy landscape approach to locomotor transitions in complex 3D terrain. Proc. Natl. Acad. Sci. USA *117*, 14987–14995.

Shepard, E.L., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A., and Vosper, S.B. (2013). Energy landscapes shape animal movement ecology. Am Nat. *182*, 298–312.

Wilshin, S., Reeve, M.A., Haynes, G.C., Revzen, S., Koditschek, D.E., and Spence, A.J. (2017). Longitudinal quasi-static stability predicts changes in dog gait on rough terrain. J. Exp. Biol. *220*, 1864–1874.

[1]Department of Bioengineering, Temple University, Philadelphia, PA 19122, USA.
[2]Structure and Motion Laboratory, Royal Veterinary College, Hawkshead Lane, Hatfield, Hertfordshire AL9 7TA, UK.
[3]Department of Biology, Siena College, Loudonville, NY 12211, USA.
*E-mail: aspence@temple.edu

Primer

Optimal foraging

Andrew J. King[1] and Harry H. Marshall[2]

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