Animal foraging: past, present and future

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Studies of foraging behaviour have proliferated over the past 30 years. Two schools of thought have emerged, one focusing on theoretical aspects (so-called 'optimal foraging theory'), the other on empirical studies. We summarize both, showing how they have evolved and begun to coalesce during the past decade. The emerging new framework is more complex than previous models, combining theory with observation. Modern phylogenetic methods promise new insights into how animal foraging has evolved.

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S erious investigation of animal foraging behaviours began three decades ago with publication in 1966 of three important papers (Refs 1–3). The theoretical papers by MacArthur and Pianka[1] and Emlen[2] examined the logic of animal feeding behaviours by identifying the benefits and costs associated with various activities, and introduced optimal foraging theory (OFT). Pianka[3] adopted a more descriptive empirical approach, and on the basis of his observations of desert lizards identified two distinct modes of foraging: 'sit-and-wait' (ambush predators) and 'widely-foraging'

(more active predators). In this article we summarize current knowledge of animal foraging, review what has been learned, and suggest directions that remain to be explored.

Optimal foraging theory

Behavioural ecologists embraced OFT because it conferred apparent rigour and generated testable predictions in what can be a subjective field. During the 1970s and early 1980s, theoreticians suggested many ways of applying the theory (Fig. 1). Several authors have reviewed foraging

theory[4–7]. Schoener[4] introduced two measures of foraging success that remain in standard use – maximization of energy intake rate and minimization of time necessary to obtain nourishment – arguing that foraging success is 'assumed commensurate with fitness'. The history of OFT was reviewed by Schoener[5]. Pyke and colleagues[6] surveyed 97 published papers as well as several unpublished manuscripts and concluded: 'We are optimistic about the value both now and in the future of optimal foraging theory'. Stephens and Krebs[7] reviewed 400 publications and described in great detail the logic and methodology of OFT. Finally, they asked 'can the models explain existing observations?' They listed 112 conclusive tests of OFT; of these, only 6.5% showed 'qualitative agreement with model', whereas 71 (63.4%) were 'inconsistent with model' or only 'partially or qualitatively consistent with model'[7]. Using a college-style grading system and scoring full agreement in Stephens and Krebs' data as a '4' and a complete inconsistency as a '1', OFT's overall mean grade in 1986 was a 2.1 – nothing to crow about, but no indication of profound failure.

Vehement arguments about OFT abound (Box 1), but personal interpretation depends on one's starting point and biases. Stephens and Krebs[7], strong proponents of OFT, concluded (p. 198) that 'foraging theory can qualitatively account for foraging decisions'. Similar results led Gray[17], a strong opponent, to state that 'the more OFT sticks its head out, the more its head is chopped off'.

Studies of foraging have proliferated during the past decade. Of the 13 098 papers in the BIOSIS database that list
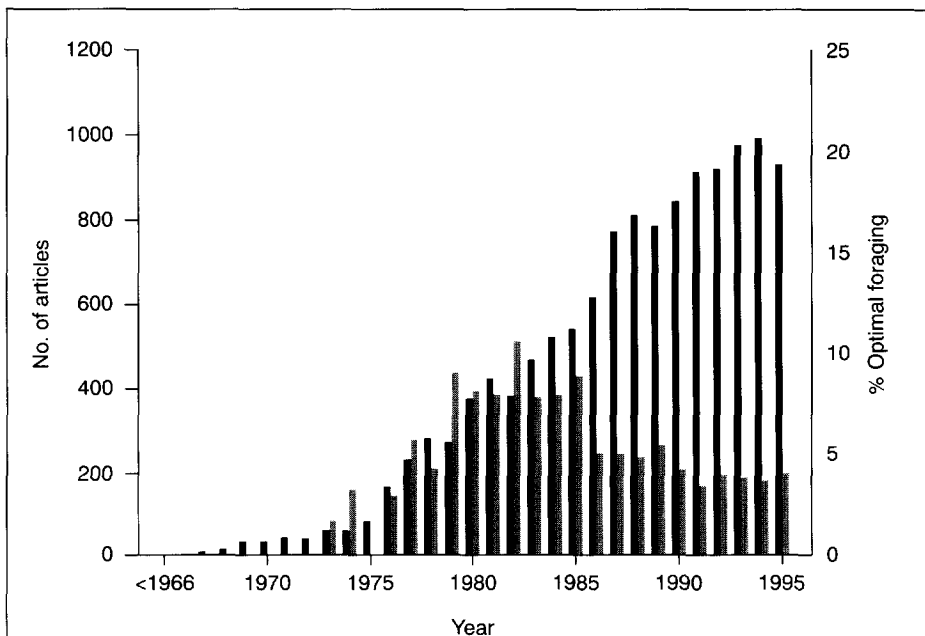
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Fig. 1. Number of articles in the BIOSIS database listing 'foraging' (black bars) or percentage of articles listing 'optimal foraging' (shaded bars) as key words over the interval 1966–1995.

Box 1. Optimality: pros and cons

In its simplest form, optimality is the expected result of natural selection over evolutionary time for ever more efficient organisms. When optimality is applied to foraging theory, the argument is that competition for resources benefits those organisms best able to procure resources, and this selection pressure eventually leads to evolution of organisms highly adept at acquiring resources. As obtaining energy is essential for survival and reproduction, the intuitive appeal of optimality approaches to the analysis of foraging behaviours is clear. However, use of optimality criteria in biology has been highly controversial[8-10], engendering heated debate almost since its inception.

In their seminal paper, MacArthur and Pianka[1] cautiously stated that 'such "optimum theories" are hypotheses for testing rather than anything certain.' Unfortunately, a much more optimistic view was adopted during the explosion of optimal foraging theory (OFT) in the 1980s, leading proponents to make some grandiose claims. Stephens and Krebs[7], for example, stated that OFT 'raises the study of design from clever "story telling"'[11] to a position in which 'explicit, quantitative and uncompromising' hypotheses allow biologists to 'recognize logical implication or to demand that there be a precise congruence between theory and observation'. Belovsky[12] predicted the diets of 14 herbivore species and found an extremely good fit ($r^2 = 0.99$) to actual diets.

Empiricists, familiar with the messiness of field data, could not accept such claims. Counter-reaction, directed in part at the 'adaptationist programme'[8,11] and in part specifically at OFT, has often been extreme. Argumentative titles such as 'Do bumblebees forage optimally, and does it matter?'[13] and 'Eight reasons why optimal foraging theory is a complete waste of time'[9] accompanied even more vitriolic arguments at scientific meetings[7]. Fiery debates produced much heat and smoke, but very little light. One critic[14] pointed out that incorporation of error values to accommodate variance around mean feeding values resulted in the high correlation claimed by Belovsky[12] being obtained in only 0.01% of Monte-Carlo runs. However, most criticisms were more conceptual. Many involved various assumptions incorporated into models. Perhaps the most basic argument revolved around the perceived untestability of optimality theory. Opponents claimed that there was no way to reject optimality. Proponents responded that building a modified theory on the wreckage of the old was the epitome of the scientific method. Not satisfied, opponents concentrated on the lack of testing of alternative, non-optimal theories.

To a large extent, both sides were correct: it is valid to produce a more elaborate model from an earlier unsuccessful one, but its usefulness is limited if major underlying assumptions that may well be untrue remain untested. Most damning, however, were disclosures by OFT proponents themselves. Belovsky[15], for example, stated that constraint assumptions used 'worked even if we didn't understand why.' Stephens and Krebs[7] reached the rather curious conclusion that 'when quantitative predictions fail ... it is probably reasonable to conclude that the model has captured the essence of the situation.' Most recently, Rough-garden[16] constructed an elaborate OFT model for *Anolis* lizards that predicted size-dependent growth rate remarkably well, yet was based on an estimate of foraging investment that is 'simply [a] guess' and which was chosen precisely because it 'leads to plausible predictions.'

demands on an organism. Relatively seldom is an animal focused on feeding to the exclusion of other factors such as avoiding predators or finding mates. It can be argued that OFT has been most successful when describing simple situations, such as central-place foraging by birds supplying food to offspring at the nest. Over the past decade, interest in complicating factors such as nutrient requirements, predation risk, and sensory limitations has increased markedly, so that today's models of foraging are much more complex (Boxes 2 and 3). Awareness that simple models often do not provide useful predictions has also increased[8-20]. Topics commonly considered are the effects of incomplete information, sensory limitations and predation risk, the last meriting an entire issue of the *American Zoologist* in 1996. Stochastic dynamic modelling and individual-based models promise to have greater relevance to complex, real-life situations.

Empirical studies of animal foraging developed more slowly than theory. Unfortunately, empiricists were generally as unenthusiastic about testing theoretical predictions as theoreticians had been about incorporating realistic conditions into their models. Such stand-offs between theory and data result in stalemates[21,22] that impede progress.

When cooperation occurs, both theory and empirical understanding benefit. An example is the OFT prediction[1,7] that, in times of food scarcity, individuals cannot be as choosy about what they eat as when food is abundant. As a result, diets are predicted to be broader during 'lean seasons' than during 'rich' periods. Gray[17] reviewed 44 studies examining this hypothesis, and of the 24 conclusive tests most (71%) were supportive. Although additional studies are clearly warranted, this may be OFT's most robust theorem to date. Interestingly, island biogeography theory has generated the related 'compression hypothesis'[1,23,24], which predicts that increasing numbers of competing species should, on an ecological timescale, result in marked contractions in habitat use, but little or no change in diets.

Modes of foraging

The existence of foraging modes[3,25-29] is widely accepted by empiricists. Numerical analyses of foraging behaviour began with the work of Cody[30], who plotted distances moved per unit time among species for various sympatric bird assemblages. Others[25-28] used number of moves per minute and the percentage of time spent moving as indicators of foraging mode; movement rate, which is closely correlated with body size[31], was not used. Huey and Pianka[25] and Toft[29] independently summarized expected correlates of extreme

'foraging' as a topic, 10 024 have appeared since 1985. The annual number of such articles published nearly doubled between 1985 and 1995 (Fig. 1). At the same time, the number of papers published on 'optimal foraging' declined from 47 in 1985 to 37 in 1995, causing their relative contribution to be roughly halved during that period. This was in part a reaction to the overheated arguments of the previous decade (see Box 1), but primarily reflects a growing awareness of just how complex are the

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Box 2. The assumptions of classical optimal foraging theory – a précis

Constraint assumptions
- search and pursuit are mutually exclusive
- sequential encounters – one at a time
- complete information – forager 'knows all' (has access to all information, probabilities of encounter, etc.)
- free choice between patch types or among food types

Currency assumptions
- lifetime reproductive success (fitness)
- time ('time minimizer')
- energy ('energy maximizer' or 'risk of starvation minimizer')
- rate maximization (gain – cost) versus efficiency maximization (gain/cost)

Phenotype set and mode of inheritance assumptions
- population is at equilibrium
- foraging behaviours are heritable
- all kinds of phenotypes or tactics are possible/available
- all traits evolve independently ('phenotypic gambit')
- appropriate genetic variance exists
- genetic correlations do not constrain trait evolution
- phylogeny is unimportant – no historical constraints

Decision variables (choices)
- where to search
- search for palatable prey
- pursue prey item (or not?)
- change patch or not? (marginal value theorem)

Box 3. Factors affecting foraging behaviour

External factors
- prey availability
- risk of predation
- social interactions (e.g. competition)
- habitat structure (e.g. perch availability)
- availability of thermoregulatory opportunities

Internal factors
- hunger
- learned experiences
- age (e.g. ontogenetic dietary shifts)
- sex and reproductive state (e.g. trade-off between feeding and reproduction)
- epigenetic inheritance (e.g. maternal effects)
- dietary preferences, nutrient requirements, toxins, distasteful compounds

Historical (phylogenetic) factors
- sensory limitations
- morphological characteristics (e.g. mouth shape)
- physiological parameters (e.g. sprint speed)
- behavioural set (e.g. conservative foraging mode)

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modes for desert lizards and tropical frogs in similar form (Table 1). Extensive work has also been carried out on spiders[32], aquatic invertebrates[33], and bees[34]. Some correlates have been supported, but not others. For example, differences in the senses used (e.g. olfactory or visual) were supported[35], and the difference in reproductive outputs and morphology derived from the work of Vitt and Congdon[36] were supported by Perry and colleagues[28]. In contrast, the well accepted difference in lizard physiology[37,38] was recently shown to be a phylogenetic artifact: when the appropriate comparison ('sit-and-wait' *Pedioplanis lineo-ocellata* versus its closest 'widely foraging' relative, *P. namaquensis*) is carried out, using the data of Huey *et al.*[38], one finds nearly identical initial and maximal speeds (1.33 versus 1.36 m s^{-1} and 2.64 versus 2.68 m s^{-1}, respectively) – neither

completed the endurance test (G. Perry, unpublished PhD thesis, University of Texas at Austin, 1995). Other predictions remain to be tested.

Pianka's dichotomy[3] is still accepted by many as fundamental. McLaughlin[27] concluded that the foraging modes of birds and lizards are strongly bimodal, although this was disputed by Perry and colleagues[28] for lizards. Cooper[35] and Perry (unpublished PhD thesis) used qualitative and quantitative data, respectively, to demonstrate strong phylogenetic effects on lizard foraging mode. Both studies show that most members of the basal iguanian clade share the ancestral sedentary foraging behaviour, whereas most members of the derived scleroglossan clade forage widely, although reversions have occurred in the Old World lizard family Lacertidae.

The studies above demonstrate the im-

portance of using phylogenetic comparative methods when studying animal foraging; this was previously recognized by various authors, who, in the absence of standardized methods, attempted to correct for phylogeny in various ways[25,37]. Newly developed methods allow data to be interpreted for the first time in a historical, evolutionary perspective, and assumptions about genetic bases of behaviour can be rigorously tested. Most important is that analyses now allow one to remove effects of species relatedness, thus preventing historical pseudoreplication from affecting conclusions. For example, two organisms living in the same habitat and similar in their morphology and ecology may nonetheless differ in their foraging behaviours. If species A resembles in its foraging behaviour its closest relatives, which live in a different habitat, and species B likewise most closely resembles its own relatives living in other habitats, it is unlikely that either behaviour set is optimum in the currently shared habitat; one might conclude that phylogenetic history has 'won' over local behavioural adaptation. Evidence is growing that such is the case much more often than ardent selectionists would have us believe.

Empirical and theoretical approaches to studying foraging behaviour are finally beginning to merge. Many critical behaviours are phylogenetically conservative. Methods used to study modality have sometimes underscored difficulties in achieving optimality. Risk of predation has been studied by theoreticians and by empiricists – and predation risk and rates of movement vary inversely.

The future

Undoubtedly, the use of explicit and numerical phylogenetic methods is an important development that will become increasingly prominent in foraging studies over the next decade. It facilitates the testing of assumptions about phenotype set and mode of inheritance (Box 2) – crucial assumptions over which OFT has often been criticized and that work cited above indicates are not always met. Another significant development is the expanded use of manipulative experiments in both laboratory and nature. Although not new, such studies have recently emerged as a major way to approach questions that are difficult to model or to tackle in complex natural environments[18,20]. We strongly agree with Kareiva[22] that there is a need for combined effort involving experimental, observational and theoretical work. It appears unwise to build more layers of new theory upon a largely untested foundation of older theory – ultimately, only greater cooperation between theoreticians and empiricists will improve our understanding

Table 1. General correlates of foraging modes initially identified

	Sit-and-wait	Widely foraging
Prey type	Active prey	Sedentary and unpredictable (clumped or large) prey
Prey captured per day	Low	High
Metabolic rate	Low	High
Types of predators	Widely foraging	Sit-and-wait or widely foraging
Rate of encounters with predators	Low	High
Morphology	Stocky	Streamlined
Physiology	Limited endurance	High endurance
Sensory mode	Visual	Visual or olfactory
Learning ability	Limited	Enhanced
Clutch mass	High	Low
Niche breadth	Wide	Narrow

of the behavioural, ecological and evolutionary factors that determine foraging behaviour.

Although OFT appears to have lost some of its popularity, it has a vital role to play in future work[39,40]. For example, we need a better definition of optimal foraging. Stephens and Krebs[7] adopted Bellman's circular definition of optimality as 'an optimal policy has the property that, whatever the initial state and initial decision are, remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision.' We define a behaviour as optimal when it maximizes net gain (i.e. long-term difference between profits and costs associated with obtaining those profits). Obviously, time and energy are mere surrogates for fitness[41]. Future workers should define an optimal foraging behaviour as one that maximizes lifetime fitness. This shifts focus from feeding success to fitness, forcing inclusion of additional factors such as predation risk – of which much has been learned in the past decade – and behavioural reproductive trade-offs, which remain largely unstudied.

Another problem that modellers must tackle is to define the goal of OFT. In defending optimization, Maynard Smith[39] asserted that '[t]he role of optimization theories in biology is not to demonstrate that organisms optimize. Rather, they are an attempt to understand the diversity of life.' More precisely, OFT will contribute most by providing two essential functions for empiricists to compare with actual behaviour: (1) a prediction of optimum possible performance, and (2) an indication of potential avenues for future research. Unfortunately, measuring fitness is difficult or impossible in most cases. If there is to be progress, modellers must first acknowledge the difference between optimal foraging and optimal reproductive tactics[41]. Unless the scope of a project is unusually wide, it might be better to define the goal of an OFT model as finding an optimal foraging strategy (i.e. one that maximizes foraging success), rather than an optimal

foraging behaviour (defined above as one that leads to maximal fitness). In this way the scope of endeavours is limited to a more manageable (and more productive) arena, and avoids making the rarely tested assumption that foraging success and fitness are closely correlated.

Whether the complex nature of real environments and the many complicating factors will allow general models to become widely useful in predicting the behaviour of organisms remains to be seen. However, the effort will be not only beneficial, but also fun. As Kacelnik[18] pointed out, most interesting new insights spring from cases where there is a clash between theory and facts – precisely the arena in which theoreticians and empiricists need to cooperate. We look forward to that collaboration and to those insights.

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