

roles of the species in a given area their objects of work (the species) are under severe risk of disappearing. Preserving the fundamental features of life can only be accomplished by ecological studies that provide an assessment of the basic structures and processes of the ecosystems, without which true conservation is not possible.

We won't ever be able to know all the specific components of a community. On the other hand, systematics is becoming less and less practical, as it pays less and less attention to alpha taxonomy, and access to true taxonomic expertise is becoming more and more restricted. Although it is very important to continue systematic and taxonomic investigations, it is equally important to promote a change in the technical approach to assess biodiversity. So, especially for poorly known ecosystems, it is important to identify conservation methods based upon their functional characteristics.

It is well known that ecosystems can be redundant (i.e. possessing species with similar functionalities), so, as far as conservation is concerned, it is very important to know if a certain functional compartment has a number of elements

capable of ensuring, under different situations, its basic functions. Species may be viewed as the result of a long-term process which has taken place within ecosystems, or in other words, within systems of interspecific relations. Evolutionary lines contain thousands and thousands of extinct species and, as far as the evidence suggests, never were these extinctions real tragedies involving an extinction of the ecological systems.

We must know the limits of stability and functionality in order to provide the best proposals for conservation and management. For the maintenance of essential ecological processes and life-support systems we need a good methodology and good techniques. To accomplish this, we must bear in mind that there is not much time left. Furthermore, very often the results of the systematists remain unclear; they need more time along with more money and extra help to describe and revise the descriptions of new species.

It is very important to emphasize that systematic and taxonomic knowledge are essential for conservation's objectives, although according to our understanding, they must be re-organized in order to provide more practical

skills for non-systematists, a task which only can be accomplished by supporting programs in which ecologists and systematists work together to produce resources which consider the practical needs of conservation.

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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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Serious 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 Pianka¹ and Emlen² examined the logic of animal feeding behaviours by identifying the benefits and costs associated with various activities, and introduced optimal foraging theory (OFT). Pianka³ 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 'wily-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

theory¹⁻⁷. Schoener¹ 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 Schoener². Pyke and colleagues³ 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 Krebs⁴ 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'. 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 Krebs⁴, strong proponents of OFT, concluded (p. 198) that 'foraging theory can qualitatively account for foraging decisions'. Similar results led Gray⁵, 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 13 089 papers in the BIOSIS database that list

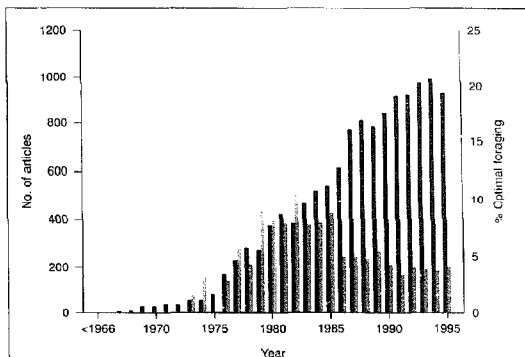


Fig. 1. Number of articles in the BIOSIS database listing 'foraging' (black bars) or percentage of articles listing 'optimal foraging' (shaded bars) as keywords over the interval 1966–1995.

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 secure resources, and this selection pressure eventually leads to evolution of organisms highly adept at securing 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 controversial¹², engendering heated debate almost since its inception.

In their seminal paper, MacArthur and Pianka¹ 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 Krebs², 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 implications or to demand that there be a precise congruence between theory and observation"'. Belovsky¹² predicted the diets of 14 herbivore species and found an extremely good fit ($r^2 = 0.89$) 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'¹³ and in part specifically at OFT, has often been extreme. Argumentative titles such as 'Do bumblebees forage optimally, and does it matter?'¹⁴ and 'Eight reasons why optimal foraging theory is a complete waste of time'⁹ accompanied even more vitriolic arguments at scientific meetings¹⁵. Heavy debates produced much heat and smoke, but very little light. One critic¹⁴ pointed out that incorporation of error values to accommodate variance around mean feeding values resulted in the high correlation claimed by Belovsky¹² 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. Belovsky¹², for example, stated that constraint assumptions used 'worked even if we didn't understand why.' Stephens and Krebs² 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, Roughgarden¹⁶ 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'.

'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 over-heated arguments of the previous decade (see Box 1), but primarily reflects a growing awareness of just how complex are the

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^{16–20}. 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. Gray¹⁷ 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 Cody³⁰, 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 size³¹, was not used. Huey and Pianka³² and Toft²⁶ independently summarized expected correlates of extreme

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' (that 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)

modes for desert lizards and tropical frogs in similar form (Table 1). Extensive work has also been carried out on spiders³², aquatic invertebrates³³, and bees³⁴. Some correlates have been supported, but not others. For example, differences in the senses used (e.g. olfactory or visual) were supported³⁵, and the difference in reproductive outputs and morphology derived from the work of Vitt and Congdon³⁶ were supported by Perry and colleagues²⁸. 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.*³⁹, 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 dichotomy⁴ is still accepted by many as fundamental. McLaughlin²⁷ concluded that the foraging modes of birds and lizards are strongly bimodal, although this was disputed by Perry and colleagues²⁸ for lizards. Cooper²⁵ 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 Kareiva²² 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 the 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 unproductive (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^{29,30}. For example, we need a better definition of optimal foraging. Stephens and Krebs' 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 fitness³¹. 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 Smith³² 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 tactics³³. 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 (or -ing) 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 Kacelnik¹⁸ 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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Symbiosis, fisheries and economic development on coral reefs

Charles Birkeland

Life-history traits of commercially important species, physiological attributes of the framework species, and characteristics of ecosystem processes make coral reefs especially vulnerable to export of biomass. Organisms in ecosystems driven by upwelling and terrestrial nutrient input are more amenable to biomass yield. Nonexportive approaches to resource management, exemplified by Palau, are compatible with the attributes of coral-reef ecosystems; they satisfy to a greater degree the economic demands and pressures of growing human populations, and they provide motivation to manage.

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Coral reefs have been touted as having the greatest gross primary productivity and highest standing stock biomass of marine ecosystems. It has been calculated that the coral reefs of the world can produce a sustainable fisheries yield of 20-35 million metric tonnes per year^{1,2}.

But high yields have not been sustained when the fisheries are exploited commercially. Although average annual fisheries yields have been documented to be as high as 26.6 metric tonnes per km² yr⁻¹ for some coral reefs, the yields on these same coral reefs eventually demonstrate a decrease of up to 70% catch per unit effort, a decrease of 75% in number of fish per hectare, and a major shift in relative abundances among species, with a drastic decrease in the species preferred by fishermen³. There are a number of examples of coral-reef fisheries being found to be more vulnerable to commercial overexploitation than predicted by the initial standing stock or potential yield calculated for the system⁴. This special vulnerability is largely from the life-history characteristics of the important species (Table 1) and the characteristics of the ecosystem (Fig. 1).

Although pelagic fishes can also be overharvested⁵, they can support a greater

biomass yield per unit gross primary productivity of the ecosystem than can coral-reef fishes (Fig. 1). Tropical pelagic fishes search widely for dense concentrations of food, feeding intensely in 'foamers' or 'boils' when they find concentrations, consuming as much as 25% of their own body weight in one day. They can grow to 5 kg (skipjack, *Katsuwonus pelamis*), 9 kg (mahimahi, *Coryphaena hippurus*) or 14 kg (yellowfin, *Thunnus albacares*) within their first two years⁷, although they do tend to have short lifespans (skipjack and mahimahi live for a maximum of four or five years). When finding a dense patch of food, feeding activity by tunas is sometimes so intense that the body temperature can rise above that of the surrounding seawater and cause 'burns' in the muscle tissue that lower the market value of the catch. Thus the tropical pelagic fishes that search out and feed on patchy concentrations of abundant resources are characterized by fast growth, early reproduction and rapid population turnover, traits that are relatively favorable for the adjustment of their populations to exploitation.

Although some coral-reef fishes can grow to a great size (the grouper *Epinephelus itajara* can grow to 300 kg and the

wrasse *Cheilodius undulatus* to 87 kg), coral-reef fishes generally grow at a rate less than one kg per year in the diverse and highly competitive coral-reef ecosystem. The intensity of predation on coral reefs is indicated by the disproportionate prevalence and diversity of predators in the community structure⁸, and the ratio of juveniles to adults in populations on coral reefs is much less than in neighboring mangroves or seagrass beds. Although even smaller coral-reef fishes can live for decades once they reach adulthood, the survivorship of juvenile fishes in their first year is as low as 0.007 (*Acanthurus lineatus* in American Samoa, central Pacific)⁹ or 0.008 (*Haemulon flavolineatum* at St Croix, Caribbean)¹⁰. The uncertainty of survival in a tightly competitive system with high rates of predation probably contributes to selection for large size, longevity and multiple reproduction. These traits of coral-reef species reflect the low rates of population turnover and vulnerability to overharvest¹¹ in groupers, giant clams, spiny lobsters and sea turtles. These life-history traits of coral-reef animals have recently contributed to the conclusion that marine protected areas are the most practical and effective method for management of coral-reef fisheries¹¹⁻¹³.

Ecosystem processes

There are also fundamental differences at the level of ecosystem processes between coral reefs and regions subjected to pulses of concentrated nutrient input. Oceanographic processes such as upwelling are the major driving forces in large-scale current ecosystems (Humboldt, Benguela, Oyashio, Kuroshio), while species interactions (e.g. predation) are a major controlling factor in coral-reef ecosystems¹⁴⁻¹⁶. The complexity of these interactions has contributed to the conclusion that a holistic approach to fisheries management such as marine protected areas is the most practical and effective method for management of coral-reef fisheries¹¹⁻¹³.

Overfishing by humans does not influence the process of upwelling. On coral reefs, in contrast, overfishing can have large-scale, long-term, ecosystem-level effects¹⁴⁻¹⁶. In recent recognition of the