



Optimal diet theory: when does it work, and when and why does it fail?

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(Received 19 September 1999; initial acceptance 7 March 2000;
final acceptance 30 June 2000; MS. number: A8652)

Over the last three decades, many studies have attempted to explain forager diets by using optimal diet theory (ODT). Despite some obvious successes, the utility of this theory remains controversial. We reviewed the results of 134 studies of optimal diet theory to test hypotheses on factors that can explain variation in the ability of ODT to predict diets and diet shifts in response to changes in prey availability. Our major conclusion is that while ODT has generally worked well for foragers that feed on immobile prey, the theory often failed to predict the diets of foragers that attack mobile prey. We found only mixed support for the hypothesis that the theory works better when the study scenario more closely fits the assumptions of the model. Contrary to our a priori predictions, forager types (invertebrate versus ectothermic vertebrate versus endothermic vertebrate) did not differ in their likelihood of corroborating ODT. Two explanations for why optimal diet theory does not work well with mobile prey are that studies on mobile prey often lack information on key parameters that are required to rigorously test ODT, and that with mobile prey, variations among prey in vulnerability (encounter rate and capture success) are often more important than variation in predator active choice in determining predator diets.

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An organism's diet is a fundamental aspect of its ecological niche. Quantifying diets has long been and continues to be one of the first steps in studying a species' basic ecology. For the community ecologist, forager diets potentially play a central role in determining the dynamics of competition between species (Pianka 1981; Mittelbach & Osenberg 1994), predator-prey interactions (Sih et al. 1985), and indirect community interactions (Wilbur & Fauth 1990; Wootton 1992). An understanding of diets, and ideally, an ability to predict diet shifts in response to changes in prey value or prey availability, is thus a major issue in modern biology.

One major paradigm for explaining or even predicting forager diets is optimal diet theory (ODT; Emlen 1966; MacArthur & Pianka 1966; Schoener 1971; Werner & Hall 1974; Charnov 1976). Some predictions of these early optimal diet papers have since been found to depend on specific, unrealistic assumptions. For example, while early ODT predicted that foragers should not show partial preferences, later work clarified that partial preferences can arise in an optimal diet via several mechanisms (Lucas 1983; Stephens & Krebs 1986; Sih & Petranka 1988). Other ODT predictions appear more robust; that is,

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less sensitive to alternative assumptions about the foraging process (Stephens & Krebs 1986). Most empirical tests of ODT have examined three relatively robust, fundamental predictions of the theory: (1) foragers should prefer prey that yield more energy per unit handling time; (2) as the abundance of higher value prey increases, lower value prey should be dropped from the diet; and (3) foragers should obey a quantitative threshold rule for when specific prey types should be included or excluded from an optimal diet (Pulliam 1974; Werner & Hall 1974; Charnov 1976).

Despite some obvious successes, considerable controversy exists on the utility of ODT. Paraphrasing from Stephens & Krebs (1986), the alternative views are that: (1) the basic models explain much of observed diet choice, and lay the groundwork for understanding unexplained aspects of diet choice (Stephens & Krebs 1986); (2) ODT works well in the laboratory, but is too simple to work in the field (Zach & Smith 1981); and (3) foraging theory is largely at odds with published data (Gray 1986). Views (1) and (3) represent a classic case of a glass that is either half-empty or half-full, or in this case, 30% empty versus 70% full. As of 1985, 70% of the studies found results that provided a quantitative or at least a qualitative fit to ODT (Stephens & Krebs 1986, Table 9.1). Only 18% of the studies clearly contradicted the basic theory's

predictions (the other 12% were difficult to evaluate). An expanded data set including studies from 1986 to 1995 continues to show that many studies fit ODT, but some do not (see below).

Given mixed results, the interesting question is: what explains variation in the ability of ODT to explain observed diets? More specifically, does the fit of observed diets to optimal diet predictions depend on: (1) whether the study was done in the field or laboratory; (2) whether the study involved experimental manipulations or not; (3) the type of forager: invertebrate versus ectothermic vertebrate versus endothermic vertebrate; (4) the type of prey: in particular, prey mobility; or (5) whether the study system fit the assumptions of the basic, simple models.

Here, we addressed these issues using an expanded review of ODT studies, along with statistical analyses testing hypotheses on factors that might explain variation in the fit of observed diets to ODT. We discuss key reasons why ODT sometimes fails, and present recommendations for future study.

WHEN DOES OPTIMAL DIET THEORY WORK? A REVIEW

To evaluate factors that might explain variation in the ability of ODT to explain forager diets, we analysed the results of 134 studies that included data required to test optimal diet theory. This included all 60 studies from Stephens & Krebs' Table 9.1 that listed a score for 'results' (i.e. for quality of fit to predictions). To these 60 we added 74 studies found in eight journals (*American Naturalist*, *Animal Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *Ecology*, *Journal of Animal Ecology*, *Oecologia*, *Oikos*) from 1986 to 1995 (Table 1).

For analyses, we identified two types of studies: (1) quantitative tests of ODT: these tested quantitative predictions on the threshold abundances of higher value prey required to drop lower value prey from the diet; and (2) qualitative tests: these only tested the qualitative predictions that foragers should show higher preference for higher value prey, or that an increase in the availability of higher value prey should result in an increase in forager selectivity (in particular, the exclusion of lower value prey from the diet).

We included studies on foragers of any type (e.g. herbivores, parasitoids, insect seed predators, etc.) as long as the study provided the information required to assess relative prey value. Studies on carnivores (including insectivores, planktivores, etc.) or large herbivores (e.g. mammals) typically included data on energy or nutrient intake per unit processing time for alternative food types, while studies on small herbivores (e.g. insects) often provided data on growth rates or fitness associated with different food types. Some studies correlated herbivore diets with plant traits (e.g. plant chemistry) without including any independent evaluation of food value. While these studies could be seen as providing evidence that herbivores show adaptive food choice, we excluded these studies because they did not include a priori assessments of food value. Following Stephens & Krebs (1986), we did not include studies of central place foraging that

focused on distance effects on diets. Finally, we did not include a study if its stated purpose was to examine effects of other fitness factors (e.g. predation risk) on foraging behaviour. Overall, although we could perhaps have included a few additional studies, given our large sample size ($N=134$), we feel confident that inclusion of a few additional studies would not change our qualitative results.

Following Stephens & Krebs (1986), we recorded the following information about each paper: (1) authors and citation; (2) year of publication; (3) field or laboratory study; (4) experimental or not; (5) type of forager; (6) type of prey; (7) predictions tested; and (8) quality of fit to predictions. Our summaries of the 74 studies from 1986 to 1995 are listed in Table 1. Clarifications of our definitions and categories, and plausible hypotheses on how these factors might affect the quality of fit to ODT are outlined below.

Stephens & Krebs (1986) identified four levels of fit to ODT predictions. In many cases, however, they assigned a split score (e.g. 3–4). We thus recognized six levels of fit to ODT: 6=quantitative agreement, 5=quantitative agreement but with partial preferences, 4=mix of qualitative and quantitative agreement but with partial preferences, 3=qualitative agreement, 2=qualitative agreement but with inconsistencies; 1=inconsistent with model. These correspond to Stephens & Krebs' scores of 1, 2, 2–3, 3, 3–4 and 4, respectively. Because quantitative tests had scores ranging from 1 to 6, while qualitative tests were restricted to scores of 1–3, analyses were done separately for these two types of tests. To emphasize, higher scores indicate a better fit to ODT. Scores of 3–6 are considered to be a good fit to the theory, while a score of 1 or 2 indicates a poor fit to ODT.

As noted earlier, studies vary widely in their fit to ODT. We examined three types of potential explanations for variation in fit to ODT: (1) variation in the study condition's fit to the assumptions of ODT; (2) variation in the types of foragers and prey; and (3) effects of the year of the study. Below, we describe plausible a priori hypotheses for each of these factors.

We examined three factors that might relate to the quality of the fit of the study system to the basic scenario underlying simple ODT: (1) the number of ODT assumptions met; (2) whether the study involved tests of quantitative versus qualitative predictions of ODT; and (3) whether the study was performed in the laboratory or in the field.

Stephens & Krebs (1986) suggested that ODT works best when the assumptions of the theory are met, but that the theory does not work as well when the study system violates the model's assumptions. They suggested that many of the failures of the theory involve attempts to apply the theory inappropriately. The models' assumptions that they considered were that: (1) search and handling are mutually exclusive; (2) encounters with prey are sequential rather than simultaneous; (3) encounters with different prey types are randomly distributed; and (4) prey do not require a recognition time.

Stephens & Krebs (1986, Table 9.1) evaluated the fit of each of 60 studies to the above assumptions of ODT.

Because in many cases, our additional 74 papers did not tell us enough about the predators and prey for us to make an accurate assessment about the above assumptions, we did not expand their data set. However, we reanalysed their 60 studies to address a possible confounding factor in their analysis. All of their studies that provided an excellent fit to ODT (their scores of 1 or 2) were, by definition, tests of quantitative predictions of ODT, while almost all of their studies that yielded a poor fit to ODT (their scores of 3–4 or 4) tested qualitative predictions. By nature, tests of quantitative predictions usually require detailed data on relevant parameters of the models. In contrast, qualitative tests often lacked data on one or more relevant parameters. If more detailed tests are generally better tests of theory, then quantitative tests should be more likely than qualitative tests to corroborate ODT. We distinguished the effects of the type of predictions tested from effects of the number of assumptions met by first comparing the fit to ODT for quantitative versus qualitative tests per se (using our expanded data set), followed by analyses 'within' each type of test for effects of the number of assumptions met on the quality of fit to ODT.

Another comparison that addresses the general notion that ODT works best when it is tested under appropriate conditions involves a comparison of laboratory and field studies. Laboratory studies might be more likely than field studies to fit ODT because laboratory situations are simpler and more likely to fit the assumptions of basic optimal diet theory (Zach & Smith 1981). The Stephens & Krebs (1986) review suggested that this hypothesis does not hold (i.e. that ODT theory does equally well in the field and laboratory). We readdressed this issue using all 134 studies. Some studies included laboratory and field components. These often involved field data on diets combined with laboratory measurements of prey value. We called these field studies because the diets themselves were quantified under field conditions. All studies of diets in the laboratory were experimental. Field studies were called experimental if they involved manipulations of prey availability.

Alternatively, the likelihood of finding a fit to ODT might be influenced by the nature of the study organisms themselves (i.e. forager or prey type). We categorized three types of foragers: invertebrates, ectothermic vertebrates (fish, amphibians and reptiles) and endothermic vertebrates (birds, mammals). Two plausible hypotheses are that: (1) vertebrates should, on average, be better foragers than invertebrates because they have more complex neural or sensory systems for assessing prey and for making decisions about diets; and (2) endotherms should, on average, be better foragers than ectotherms because endotherms have higher energy demands and thus experience stronger selection pressure favouring energy maximization.

Foraging studies can also be classified by prey type. We identified four prey types based on prey mobility relative to forager mobility: 1=completely immobile (flowers, leaves, seeds, dead mealworms); 2=essentially immobile (bivalves); 3=slightly mobile (zooplankton versus fish, worms versus birds); and 4=mobile (mobile insect prey

versus insect predators, small versus large fish, voles versus stoats). Sih & Moore (1990) suggested that because ODT is a predator-based approach to explaining diets, ODT might be less likely to succeed when prey behaviour also influences diets. We further divided immobile prey (category 1), into four types: leaves, seeds, flowers (nectar) and immobile animal prey (pupae or dead animals). Because leaves are often chemically complex (vary in nutrients and toxins), we hypothesized that simple ODT might be less likely to predict the diets of leaf-eaters correctly, as compared to foragers on other types of immobile prey.

Finally, we examined effects of 'year of study' on the fit to ODT predictions. If earlier studies were not done as well as later studies (e.g. earlier studies violated more assumptions of ODT), then there should be a positive relationship between year of study and fit to predictions. Conversely, if top journals show a tendency to publish positive results when a theory is fresh and new, but two decades later, show a tendency to favour results that contradict theory, then there might be a negative relationship between year of study and fit to predictions.

For all tests, the dependent variable was the score for the fit to predictions. Because all variables were categorical, rather than continuous and normally distributed, we used nonparametric tests to examine effects of each independent variable on the fit to predictions. Effects of independent variables that had two levels (laboratory versus field or experimental versus not) were tested using Mann–Whitney *U* tests. For variables with multiple levels, we used a rank correlation test, Kendall's τ , to test specific hypotheses regarding the direction of effect. To further examine the relative effects of different factors in explaining variation in fit to ODT, we used stepwise multiple regressions and partial regression analyses. Because the variables are not strictly normally distributed (although in most cases, they did not deviate significantly from normality), the results of these parametric tests should be viewed with some caution. Fortunately, the parametric and nonparametric tests yielded parallel results (see below). We used one-tailed criteria if we had an a priori hypothesis on the expected direction of an effect.

RESULTS

We assayed 35 studies that included quantitative tests of ODT, and 99 studies that involved qualitative tests. Frequency distributions for our independent variables are shown in Table 2.

The tests we surveyed were evenly divided between laboratory and field studies, and most studies (82/134, 61.2%) included manipulative experiments. Exactly 50% of the studies were done on birds or mammals (which represent <1% of all animal species). Quantitative studies, in particular, are typically done on birds or mammals, whereas qualitative studies are often done on invertebrates and ectothermic vertebrates; the two types of studies differed significantly in the distribution of predator taxa studied ($\chi^2_2=10.6$, $P<0.01$). More than half of all studies (59.7%) involved immobile or essentially immobile prey, whereas only about 20% of all studies (and

Table 1. Optimal diet studies from 1986 to 1995 included in the analyses (continued on next page)

Reference	Study type		Forager	Prey	Test	Results
Allan & Flecker 1988	L	E	Stonefly	Invertebrates	B	1
Ball 1994	L	E	Duck	Various types	B	1
Barclay & Brigham 1994	F	E	Bat	Insects	B	1
Beissinger et al. 1994	F	E	Kite	Crabs, snails	B	1
Belovsky 1986	F	O	Herbivores	Plants	A	6
Bence & Murdoch 1986	L	E	Mosquitofish	Zooplankton	B	2
Bonaccorso & Gush 1987	L	E	Bats	Fruits	B	3
Butler & Burns 1991	L	E	Mite	Zooplankton	B	2
Cayford & Goss-Custard 1990	F	O	Oystercatcher	Mussels	A	5
Christensen & Persson 1993	L	E	Perch	Roach	B	2
Coleman & Jones 1988	L	E	Beetles	Willows	B	2
Craig et al. 1989	F	O	Sawfly	Willows	B	3
Crist & MacMahon 1992	F	O/E	Ants	Seeds	B	3
DeMott & Moxter 1991	L	E	Copepod	Cyanobacteria	B	2
Diaz & Carrascal 1993	L/F	E/O	Lizard	Invertebrates	B	1
Dickman 1988	F	O	Mammals	Insects	B	3
Doucet & Fryxell 1993	L	E	Beaver	Vegetation	A	3
Fewell & Harrison 1991	F	E	Ants	Seeds	B	2
Fisher & Dickman 1993	F	O	Marsupials	Insects	B	3
Frank 1988	L	E	Kangaroo rats	Pellets	B	3
Frank 1994	L	E	Squirrels	Pellets	B	3
Galis & de Jong 1988	L	E	Fish	Zooplankton	A	5
Greig-Smith & Crocker 1986	L	E	Bullfinch	Seeds	B	1
Hart & Hamrin 1988	L	E	Pike	Fish	B	3
Hughes & Burrows 1991	F	O	Dogwhelk	Invertebrates	B	2
Hughes & Croy 1993	L	E	Stickleback	Crustaceans	B	2
Jones 1990	F	O	Bat	Insects	B	3
Jones & Norman 1986	F	E	Fish	Algae	B	3
Kaiser et al. 1992	L	E	Stickleback	Zooplankton	B	2
Kaspari & Joern 1993	F	O	Birds	Insects	A	3
Kelrick et al. 1986	F	E	Rodent, bird	Seeds	B	3
Kerley & Erasmus 1991	L	E	Mice	Seeds	B	3
Madij & Clay 1991	L	E	Birds	Seeds	B	3
Marino et al. 1993	F	E	Leaf miner fly	Trees	B	3
May 1992	F	O	Butterflies	Flowers	B	3
Meire & Eruynck 1986	F	O	Oystercatcher	Mussels	A	5
Minkenbergh & Ottenheim 1990	L	E	Fly	Tomato	B	3
Molles & Pietruzka 1987	L	E	Stonefly	Insects	B	1

Study type: L: laboratory; F: field; E: experimental; O: observational; Test: A: quantitative; B: qualitative; Results: 6=quantitative fit; 5=quantitative fit but with partial preferences; 4=mix of qualitative and quantitative fit but with partial preferences; 3=qualitative fit; 2=qualitative fit but with inconsistencies; 1=inconsistent with model.

only 11.4% of the quantitative studies) examined relatively mobile prey.

Quantitative studies are more likely to fit ODT than qualitative studies ($\chi^2_1=10.4$, $P<0.01$). Only four of 35 (11.4%) studies that tested a quantitative prediction of ODT produced results that rejected the theory (results 1 or 2), whereas 41 of 99 (41.4%) of the qualitative tests yielded results that were inconsistent with ODT. Quantitative tests have a broader range of scores (3–6) that indicate a good–excellent fit to ODT than qualitative tests (3 only). However, this represents only a difference in number of gradations of good fits to ODT, and not any inherent bias in the probability of observing a ‘poor’ fit to ODT. In any case, because the two types of tests differ in their range of scores and apparently in the likelihood of a good fit to ODT, we conducted further analyses on factors that explain variation in fit to ODT on the two data sets separately.

Univariate analyses indicated that of the six factors tested, only prey mobility significantly explained variation in the fit of observed diet patterns to ODT (Table 3).

That is, the ability of ODT to explain forager diets was not significantly related to the type of study (experimental or not), where the study was done (laboratory versus field), forager type, the year of the study, or whether the model’s assumptions were met. For qualitative tests of ODT, prey mobility was significantly negatively related to the quality of fit to ODT. Immobile or less mobile prey (prey categories 1–3) corroborated theory in 73.8% (79/107) of the studies, while mobile prey (category 4) fit theory in only 37.0% (10/27) of the studies. The effect of mobility on the fit to ODT remained significant even after a sequential Bonferoni procedure was used to adjust P values for multiple tests. We could not run a parallel analysis for quantitative tests of ODT because of the low number of quantitative tests involving mobile prey.

Multiple regressions using five factors (year of study, laboratory/field, experiment or not, forager type and prey type) further supported the view that increased prey mobility has a negative effect on the average fit to ODT. For both qualitative and quantitative studies, only prey mobility

Table 1. Continued

Reference	Study type		Forager	Prey	Test	Results
Nuutinen & Ranta 1986	L	E	Newt	Zooplankton	B	3
Owen-Smith 1994	F	O	Kudu	Plants	B	3
Papaj et al. 1989	L	E	Fruit fly	Fruits	B	3
Paulissen 1987	F	O	Lizard	Invertebrates	A	3
Peckarsky & Penton 1989	F	E	Stonefly	Mayfly	B	1
Peckarsky et al. 1994	L	E	Stonefly	Mayfly	B	1
Pennings 1990	F	O	Sea hare	Algae	B	3
Perry 1987	L	E	Snail	Barnacles	B	3
Persson & Greenberg 1990	F	O	Perch	Zooplankton	A	5
Persson & Greenberg 1990	F	O	Perch	Invertebrates	A	1
Price 1987	F	O	Finch	Seeds	B	3
Quiring & McNeil 1987	F	E	Leaf miner fly	Alfalfa	B	3
Reavey 1991	L	E	Caterpillar	Leaves	B	1
Richardson & Verbeek 1986	F	O	Crows	Clams	A	3
Ritchie 1990	F	O	Squirrel	Plants	A	5
Roininen & Tahvanainen 1989	L	E	Sawfly	Willows	B	2
Scheel 1993	F	O	Lion	Ungulates	B	3
Sih & Petranka 1988	L	E	Salamander	Zooplankton	A	5
Smith 1990	F	O	Finch	Seeds	B	3
Steenhof & Kochert 1988	F	O	Raptors	Vertebrates	B	3
Sullivan 1987	F	E	Junco	Mealworms	B	3
Takasu & Hirose 1991	L	E	Wasp	Insect eggs	B	2
Tamm & Gass 1986	L	E	Hummingbird	Nectar	A	5
Temple 1987	F	O	Hawk	Mammals	B	1
Thompson & Colgan 1990	F	O	Marten	Mammals	B	2
Thompson et al. 1987	L	E	Junco	Seeds	B	2
Tokeshi 1989	F	O	Sea star	Mussels	B	3
Vivas & Saether 1987	F	E	Moose	Trees	B	3
Vivas et al. 1991	F	O	Moose	Trees	A	5
Vulink & Droost 1991	F	O	Cattle	Vegetation	B	3
Walton et al. 1992	L	E	Bluegill	Zooplankton	A	3
Ward 1991	F	O	Seabirds	Clams	B	2
Ward & Saltz 1994	F	O	Gazelle	Lilies	B	3
Wells & Wells 1986	F	E	Honeybee	Flowers	B	2
Willner 1986	F	O	Bee	Nectar	B	3

Study type: L: laboratory; F: field; E: experimental; O: observational; Test: A: quantitative; B: qualitative; Results: 6=quantitative fit; 5=quantitative fit but with partial preferences; 4=mix of qualitative and quantitative fit but with partial preferences; 3=qualitative fit; 2=qualitative fit but with inconsistencies; 1=inconsistent with model.

was significantly related to the ability of ODT to explain observed diets (qualitative: partial $r = -0.301$, $P = 0.004$; quantitative: partial $r = -0.466$, $P = 0.04$). For quantitative studies, a stepwise regression using $\alpha = 0.10$ as the inclusion threshold included prey mobility as the only significant factor. Interestingly, the stepwise regression for qualitative studies included three factors: prey mobility ($P = 0.004$), year of study (partial $r = -0.176$, $P = 0.07$) and whether or not the study included experiments (partial $r = 0.168$, $P = 0.08$). That is, besides the main effect of prey mobility, there was a borderline significant tendency for earlier studies to yield a better fit to ODT than more recent studies, and a tendency for nonexperimental studies to produce a better fit than experimental ones.

Focusing on studies that used immobile prey, we found that foragers fit ODT most of the time regardless of the type of prey. For studies on herbivores, 78.9% (15/19) yielded at least a qualitative fit to theory, but many of these fit ODT only when we use an extended version of simple ODT. For example, several studies suggested that nutrient and digestive constraints must be included to understand the diets of large herbivores (e.g. Belovsky

1978, 1986; Ritchie 1990). Other studies show that herbivores prefer plant types that produce the highest fitness, even if they do not have the highest energy value (e.g. Craig et al. 1989; Marino et al. 1993). These studies corroborate ODT in the sense that the diet can be explained in terms of food-quality-based optimality theory. Studies on consumers of other immobile prey (seeds, nectar, fruits, dead animals or pupae) fit ODT in 82.1% of the cases (32/39). Herbivores versus other consumers of immobile prey did not differ significantly in their fit to ODT ($\chi^2_1 = 0.08$, NS).

Examples of well-known studies that fit ODT that involve foragers choosing among relatively immobile prey include studies of: (1) birds feeding on dead mealworms or insect pupae (Krebs et al. 1977; Erichsen et al. 1980; Houston et al. 1980); (2) planktivorous fish feeding on *Daphnia* (Werner & Hall 1974; Mittelbach 1981); (3) bees or birds feeding on nectar (Waddington & Holden 1979); and (4) large herbivores feeding on plants (Belovsky 1978). In contrast, examples involving foragers on mobile prey that provided a relatively poor fit to ODT include studies of: (1) mustelids feeding on small

Table 2. The number (percentage) of studies in each category for each variable

	Number of quantitative studies	Number of qualitative studies
Study type		
Laboratory	17 (48.6)	51 (51.5)
Field	18 (51.4)	48 (48.5)
Experimental	18 (51.4)	64 (64.6)
Observational	17 (48.6)	35 (35.4)
Forager		
Invertebrate	3 (8.6)	37 (37.4)
Ectothermic vertebrate	8 (22.8)	19 (19.2)
Endothermic vertebrate	24 (68.6)	43 (43.4)
Prey mobility		
Completely immobile	18 (51.4)	43 (43.4)
Essentially immobile	4 (11.4)	15 (15.2)
Slightly mobile	9 (25.7)	18 (18.2)
Mobile	4 (11.4)	23 (23.2)
Fit to theory		
6=best fit	2 (5.7)	Not applicable
5	13 (37.1)	Not applicable
4	5 (14.3)	Not applicable
3	11 (31.4)	58 (58.6)
2	2 (5.7)	24 (24.2)
1=worst fit	2 (5.7)	17 (17.2)

mammals (Erlinge 1981; Thompson & Colgan 1990); (2) fish feeding on crayfish (Stein 1977); (3) large fish feeding on smaller fish (Gillen et al. 1981; Hart & Connellan

1984; Hoyle & Keast 1987; Hart & Hamrin 1990); and (4) stoneflies feeding on mayflies (Allan & Flecker 1988; Peckarsky & Penton 1989). There are, of course, exceptions to the above 'rule'. In particular, some studies on immobile prey show a poor fit to ODT (e.g. Pulliam 1980; Belovsky 1981; Lewis 1982; Wells & Wells 1983; Reavey 1991). Interestingly, our survey did not turn up any examples of foragers on highly mobile prey showing a good-excellent quantitative fit (scores=4-6) to ODT.

Overall, we draw the following conclusions relative to our a priori expectations.

(1) ODT has generally done an excellent job of explaining patterns of diet choice for foragers feeding on immobile or only slightly mobile prey. This was true regardless of the type of immobile prey (e.g. plant versus animal prey). In contrast, studies using mobile prey often failed to corroborate ODT.

(2) We found mixed evidence regarding the hypothesis that ODT works better when the study scenario better fit the model's scenario. Quantitative tests were more likely than qualitative tests to fit ODT. This might be because quantitative tests are more likely to include detailed data on relevant parameters (i.e. that quantitative tests are, in some sense, better tests of ODT). Within each of these two types of tests, however, contrary to Stephens & Krebs (1986), we found no evidence that ODT worked better when more assumptions of the simple theory were met. This could reflect the possibility that the predictions of ODT (particularly qualitative predictions) might be relatively insensitive to the listed assumptions, or perhaps

Table 3. Effects of factors on fit of data to optimal diet theory

Factor	Quantitative tests of theory		Qualitative tests of theory	
	Scores mean (SE)	Statistical test	Scores mean (SE)	Statistical test
Site of study				
Laboratory	4.00 (0.21)	$U=159$	2.31 (0.11)	$U=1039.5$
Field	3.89 (0.43)	$P=0.84$	2.52 (0.11)	$P=0.14$
Experiment?				
Yes	3.94 (0.21)	$U=151$	2.31 (0.10)	$U=894.5$
No	3.94 (0.45)	$P=0.95$	2.60 (0.12)	$P=0.06$
Forager				
Invertebrate	3.67 (0.33)	$\tau=0.086$	2.38 (0.13)	$\tau=0.060$
Ectothermic vertebrate	3.63 (0.63)	NS	2.37 (0.16)	NS
Endothermic vertebrate	4.08 (0.28)		2.47 (0.12)	
Prey				
Immobile	4.22 (0.33)	$\tau=-0.212$	2.61 (0.10)	$\tau=-0.229$
Essentially immobile	4.25 (0.48)	$P=0.08$	2.40 (0.19)	$P<0.005$
Slightly mobile	4.00 (0.47)		2.44 (0.20)	
Mobile	2.25 (0.48)		2.04 (0.17)	
Year of study		$\tau=-0.038$		$\tau=-0.126$
		NS		$P=0.16$
Number of assumptions met		$\tau=0.188$		$\tau=0.004$
		NS		NS

Univariate statistical tests examining the effects of various factors on the quality of fit to optimal diet theory. For quantitative tests, scores ranged from 1 to 6; for qualitative tests, scores ranged from 1 to 3. Higher scores indicate a better fit to optimal diet theory. For all factors except 'number of assumptions met', $N=35$ for quantitative tests and $N=99$ for qualitative tests. For 'number of assumptions met', $N=20$ for quantitative tests, $N=40$ for qualitative tests.

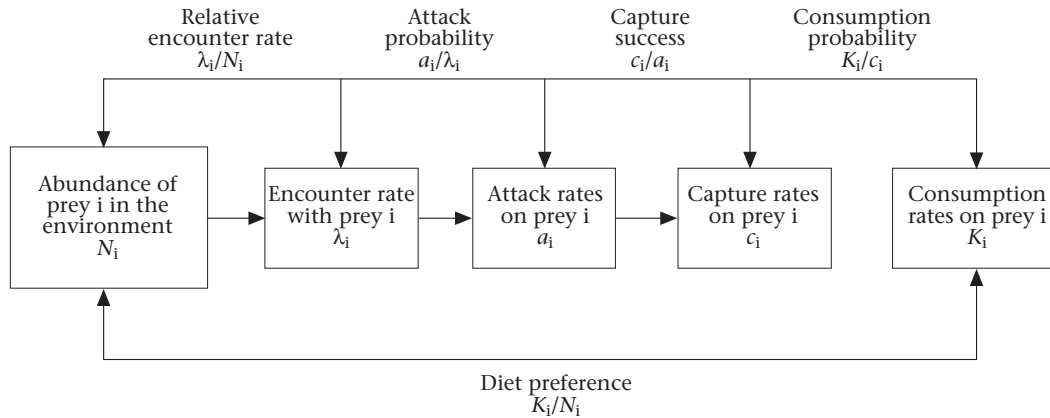


Figure 1. The stages of a predator–prey interaction. Nonrandom diets can arise because of variation among prey in outcomes of each stage. Optimal diet theory makes predictions about forager choices in the attack stage.

that assessments of whether assumptions were met were at least sometimes inaccurate. Finally, we did not find that laboratory studies were more likely than field studies to fit ODT, nor did we find that experimental studies fit better than nonexperimental ones. Indeed, we detected some evidence that nonexperimental studies fit ODT better than experimental studies.

(3) Contrary to our predictions, forager types (invertebrate versus vertebrate ectotherms versus vertebrate endotherms) did not differ significantly in their fit to ODT. Apparently, even organisms with relatively low energy demands or with simple information gathering and processing abilities (e.g. insects, snails or even protozoa) are capable of adaptive foraging.

(4) Interestingly, there was a hint that more recent studies were more likely to produce results inconsistent with ODT. Focusing on qualitative tests, between 1976 and 1990, 47 of 73 tests corroborated ODT (64.4%), whereas from 1991 to 1995, only 11 of 26 studies fit ODT (42.3%). These two distributions differed significantly ($\chi^2_1=3.85$, $P=0.05$). This could reflect a change in the studies themselves, or in the criteria for publishing in top journals.

DISCUSSION

Prey Mobility and Optimal Diets

We suggest two inter-related explanations for why ODT often fails for predators on mobile prey. (1) Diet preferences (nonrandom diets relative to prey abundance) must be distinguished from active predator choice (unequal attack probabilities given encounters with different prey types). ODT addresses active predator choice, while diet studies often measure diet preferences. For immobile prey, these two usually concur. For mobile prey, however, they often differ. (2) For active predator choice, most diet studies quantify only a limited subset of the information required to assess prey value and thus to rigorously apply ODT. For immobile prey, the limited information is usually enough to generate accurate predictions. In contrast, for mobile prey, the missing information often

results in inaccurate predictions. Below, we discuss these two points in more detail.

Diet preferences versus active predator choice: the role of prey behaviour

The key point here is that while the predation act consists of a series of steps (Fig. 1), ODT makes predictions about only one of these steps, the probability of attack given an encounter with prey. The distinction between unequal probabilities of attack on different prey (as predicted perhaps by ODT) and nonrandom predation (that can be caused by predator or prey behaviours in any of the steps in the overall predator–prey interaction) is critical for understanding why ODT often fails with mobile prey.

It is useful in this context to distinguish between two diet-choice-related concepts. By ‘diet preference’ we mean a tendency for predators to consume some prey more frequently than one would expect based on the relative abundances of alternative prey in the environment. By ‘active predator choice’ we mean a tendency for predators to attack some prey more often than others, given an encounter with each prey type.

Diet preferences are ecologically important because nonrandom predation has important effects on the relative impacts of predators on different prey (Paine 1966; Sih et al. 1985). Nonrandom preferences are evaluated by comparing observed diets to patterns of prey abundance in the environment; that is, by comparing K_i/N_i for different prey types, where K_i is the number of prey type i eaten (per unit time), and N_i is the number of type i in the environment. Preference for type i can be quantified as $\alpha_i=(K_i/N_i)/\Sigma(K_i/N_i)$ (Chesson 1983).

Active predator choice is only one of several factors that can produce nonrandom diets. To illustrate, we divide a predator–prey interaction into a sequence of stages (Fig. 1): (1) relative encounter probabilities; (2) attack probabilities (probability of attack given an encounter); (3) capture success (probability of capture given an attack); and (4) probability of consumption given a capture. Overall preference, K/N , is the product of these four

stages, which can be represented as four ratios: λ/N , a/λ , c/a , K/c , where λ , a , c and K are encounter, attack, capture and consumption rates, respectively. One could further divide the sequence into more stages (e.g. probability of detection given an encounter, or probability of recognition as prey given detection); however, for this discussion we will focus on a four-stage view. The key point is that differences among prey types in any of these stages can contribute to nonrandom diet preferences.

Active predator choice (variation among prey types in a/λ) is usually treated as a predator decision; however, because prey behaviour can influence relative prey value that, in turn, affects predator choice, prey behaviour can indirectly influence active predator choice. More importantly, variations in the other stages of the predator-prey interaction are often determined primarily by prey behaviour. Relative encounter rates with different prey depend on: (1) predator/prey habitat and microhabitat overlap, which can be determined by the relative tendencies for predators to use patches with more prey versus for prey to avoid patches with more predators (Sih 1984, 1998; Hugie & Dill 1994); (2) prey refuge use within the habitat (Sih 1987; Lima & Dill 1990); (3) prey versus predator activity and movement speed (Werner & Anholt 1993); and (4) prey versus predator reactive distances. Capture success depends on prey versus predator mobility (e.g. relative speed, acceleration and manoeuvrability), and the probability of consumption following capture can depend on prey postcapture defences (e.g. chemical defences, spines).

Optimal diet theory makes predictions on active predator choice. Thus to test ODT, a study should ideally quantify variation in the probability of attack given an encounter with different prey types (a/λ). In many cases, however, tests of ODT actually quantify nonrandom diets relative to prey abundance in the habitat (i.e. K/N). Diet preferences provide a good indication of active predator choice if variation in diets primarily reflects variation in attack probabilities. This is likely to be true if prey are immobile (i.e. if prey lack antipredator behaviours). For example, if all prey are immobile and exposed to predators (e.g. dead mealworms on a conveyor belt), then encounters per prey (λ/N) are equal for all prey types, and capture (c/a) and consumption (K/c) success are essentially 100% for all prey. Thus, as we found in our survey, diet preferences for immobile prey should often fit ODT, despite the fact that many of these studies do not actually quantify encounters and attacks per se.

In contrast, if prey are mobile, then antipredator behaviours can easily produce diet patterns that do not fit ODT. Imagine, for example, an ambush predator that has two alternative prey types. If one type is much more active than the other, then even if the two prey types are equally abundant, and equally likely to be attacked, captured and consumed given an encounter, the prey type that is more active will be 'preferred' (over-represented in the diet) simply because it is more active (Persson & Greenberg 1990; Sih 1993; Mittelbach & Osenberg 1994). Similarly, if prey vary in the proportion of time that they spend in refuge, then if all else is the same, prey that hide more will be eaten less. The preferred prey will be the prey

types that hide less (Persson & Diehl 1990; Sih 1993; Christensen & Persson 1993).

Alternatively, mobile prey often differ in escape (and thus capture) success (Hart & Hamrin 1990; Sih 1993; Juanes 1994; Christensen 1996). For two reasons, prey that have lower escape ability should tend to be 'preferred' (over-represented in the diet). First, if all else is the same, prey that are easier to capture have higher prey value (higher expected net energy intake/handling time). Thus, if all else is the same, ODT predicts that predators should actively choose (show higher attack probabilities on) prey with low escape ability. However, even if predators show no active choice (i.e. do not obey ODT on attack probabilities), variation in capture success per se generates a 'preference' for (i.e. a nonrandom tendency to consume) more easily captured prey.

If prey hide from predators, then encounter rates with high value prey might be quite low. If prey have effective escape responses, then capture success might be relatively low. Under these conditions, ODT often predicts that foragers should be nonselective (i.e. attack all prey encountered that can be feasibly captured; Juanes 1994). If these foragers are indeed nonselective, then technically speaking, they fit the predictions of ODT. However, in this case, ODT clearly has low explanatory power; that is if attack probabilities do not differ on different prey, variation in diets cannot be explained by understanding attack probabilities. With mobile prey, it might often be that to understand and predict diets, one must study variation in prey behaviour that underlies variation among prey types in encounter rates and capture success.

Missing information in predicting active predator choice

A second major type of explanation for why ODT often fails with mobile prey involves missing information required to generate rigorous predictions on optimal active predator choice.

Schoener (1971) provided an overview of the components of the basic optimal diet model. Prey value is defined by net energy intake per unit handling time (e_i/h_i , where e_i is the net energy intake from prey item i and h_i is the mean time spent handling that prey item). Energy intake for a prey item i is the product of its assimilatable energy content, E_i , and p_i , its probability of capture given an attack. Energy costs can accrue during each stage of the predation act (Fig. 1). The energetic cost of pursuing prey item i (q_i) is only fully expended if the pursuit is successful. If prey escape during pursuit, then only a fraction, f_i , of that cost is expended. Similarly, m_i , the energetic cost of manipulating prey item i only occurs if the prey item is captured and consumed. Mean handling time also must be weighted by the probability of occurrence for the successive stages of the predation act. That is, h_i depends on t_{qi} , the time spent in pursuit of prey item i if the pursuit is successful; f_i , the fraction of pursuit time taken during unsuccessful pursuits, and t_{mi} , the time spent manipulating prey item i if prey are successfully captured. Overall, prey value can be calculated as follows:

$$e_i/h_i = (p_i E_i - ((p_i + (1 - p_i) f_i) q_i + p_i m_i)) / ((p_i + (1 - p_i) f_i) t_{qi} + p_i t_{mi}) \quad (1)$$

In practice, most ODT studies measure assimilatable energy (or just prey mass) per unit manipulation time (E_i/t_{mi}) and not prey value (e_i/h_i). That is, ODT studies frequently estimate prey value without accounting for variations among prey in capture (or escape) success, energy costs or pursuit time. Below, we argue that this missing information might be relatively unimportant for immobile prey, but much more important for mobile prey.

For immobile prey, prey types do not vary appreciably in escape (or capture) success. All prey cannot escape and are typically captured with about 100% success. In contrast, for mobile prey, prey types almost always vary considerably in escape (capture) success (see references above). Highly mobile prey often have high escape success and thus low prey value (Christensen 1996). Furthermore, equation (1) assumes that if prey escape, they do so during the pursuit phase and not after capture; however, in many systems, prey can escape after an initial capture. The effects of variation among prey in escape success and the possibility of escape after initial capture are often ignored in empirical tests of ODT. Both might be common reasons why mobile prey often appear to violate the predictions of simple ODT.

With regard to energy costs, costs of pursuit are often essentially nonexistent for all immobile prey, so it is usually a reasonable approximation to cancel q_i out of the parameter estimation. Prey mobility, however, often generates variation in q_i . If pursuit time, t_{qi} , is prey-item specific, then prey will vary in q_i even if prey types do not differ in energy expenditure per unit pursuit time. In fact, q_i/t_{qi} probably often differs between prey types. For example, when foragers are gape limited (Zaret 1980), they often achieve the highest energy return per unit manipulation time, e_i/t_{mi} with the largest ingestible prey class (e.g. Harper & Blake 1988; Juanes 1994); thus, ignoring pursuit costs, large prey should be preferred. However, the largest ingestible prey class can also require by far the highest t_{qi} and also the highest energy expenditure per time unit spent in pursuit. This can lead to no correlation or even negative correlations between prey value (e_i/h_i) and the ratio that is often used to estimate prey value, E_i/t_{mi} (Christensen 1996).

Similar problems arise with assessing handling times for mobile prey. Estimates of handling time typically focus on manipulation time after prey are captured, and often ignore precapture pursuit times. With immobile prey this is often a reasonable approximation ($t_{qi} \approx 0$ for all prey types). Mobile prey, however, often require extended pursuits to be captured (e.g. prey fish for piscivores: Christensen 1996; squirrels for martens: Thompson & Colgan 1990). For mobile prey, pursuit times can be much larger than manipulation times, and can thus be of major importance in determining h_i for a specific prey item, i . Variation in pursuit times can then play a major role in governing variation in prey value.

Finally, to test the quantitative predictions of ODT one must have estimates of encounter rates, λ_i , with different prey classes. λ_i is often estimated as a linear function of the relative densities of different prey classes. With immobile, noncryptic prey (e.g. mussels, nuts or meal-

worms on conveyor belts), encounter rates are probably well approximated by a linear function of relative densities. However, as noted above, if prey vary in activity, crypticity or microhabitat use, then such differences can easily be more important determinants of realized encounter rates than relative densities per se (Osenberg & Mittelbach 1989; Persson & Diehl 1990; Mittelbach & Osenberg 1994; Christensen 1996). Encounter rates with more mobile prey will, all other factors being equal, be higher than those with less mobile prey (Werner & Anholt 1993). Thus, with mobile prey, a calculation of the optimal diet based on relative densities can deviate significantly from calculations of optimal diets based on actual encounter rates (Werner & Hall 1974; Mittelbach 1981; Osenberg & Mittelbach 1989, Persson & Diehl 1990; Persson & Greenberg 1990; Mittelbach & Osenberg 1994).

Conclusions and Suggestions for Future Study

Our main conclusion is that while optimal diet theory usually does a good job of explaining the diets (both preferences and changes in preferences with changing prey abundances) of foragers that consume immobile (e.g. leaves, seeds, nectar, mealworms) or essentially immobile (e.g. zooplankton relative to fish) prey, the theory often fails to predict the diets of predators on mobile prey (e.g. small mammals, fish, zooplankton relative to insect predators). One might argue that ODT was never meant to be applied to foragers on mobile prey. Even if this is true, it has not prevented ecologists from doing so. We urge caution when applying ODT to foragers on mobile prey, and suggest a need to modify ODT to account for mobile prey, or to develop a new framework to study diets of foragers on mobile prey.

Predators that feed on mobile prey sometimes show little or no active choice (Sih 1993; Juanes 1994; Christensen 1996). This might fit ODT in the sense that if prey generally have effective antipredator traits, then the result is very low realized prey availability (i.e. according to ODT, under these conditions, predators should be nonselective). In other cases, foragers on mobile prey display active choice (i.e. variation in attack probabilities on different prey). To use ODT to explain these choices, one must not take shortcuts; one must gather data on the full optimal diet model (Schoener 1971; equation (1), plus actual determinations of λ_i).

Furthermore, with mobile prey that can hide or escape from predators, it is important to study variations among prey in all stages of the predator-prey interaction (i.e. not just in the probability of attack given an encounter). Nonrandom diets are often caused by variations among prey in either encounter rates (relative to abundance in the environment) or escape success from the focal predator. A full understanding of these events requires information on interactions between the traits of both predators and prey (e.g. microhabitat use, activity, sensory abilities, mobility).

At one level, it should be useful to simply quantify variations among prey in the key traits (e.g. in refuge use or escape ability) and to use this information to explain

predator diets. At a deeper level, one can use optimality theory to explain why prey differ in their key anti-predator traits. For example, theory exists on optimal prey refuge use or activity given the conflicting demands of avoiding predators and gathering food (Gilliam & Fraser 1987; Sih 1987, 1998; Werner & Anholt 1993; Hugie & Dill 1994). A future direction could be to use this theory to explain differences among prey in antipredator behaviour, and to thus predict predator diets based on variations in the conflicting demands faced by different prey (e.g. Matsuda et al. 1996). Alternatively, antipredator behaviour might not fit optimality theory. Evolutionary constraints (e.g. genetic constraints, phylogenetic inertia) might be invoked to explain why some prey show ineffective antipredator traits (Sih 1992; Sih & Gleeson 1995). An explicit integration of theory and experiments on the evolution of prey traits and their effects on optimal diets for predators on mobile prey should prove valuable.

Acknowledgments

We thank J. Lucas, G. Mittelbach, T. Schoener and an anonymous referee for useful comments on the manuscript, and L. Sih and M-S. Baltus-Sih for hospitality for B.C. and for stimulating discussions of adaptive foraging. This work was supported in part by grants from the National Science Foundation (A. Sih), the Kempe Foundation and the SJFR (B. Christensen).

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