



---

Optimal Diets: Simultaneous Search and Handling of Multiple-Prey Loads by Salamander Larvae

Author(s): A. Sih and J. W. Petranka

Reviewed work(s):

Source: *Behavioral Ecology and Sociobiology*, Vol. 23, No. 5 (1988), pp. 335-339

Published by: [Springer](#)

Stable URL: <http://www.jstor.org/stable/4600224>

Accessed: 23/02/2012 12:52

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer is collaborating with JSTOR to digitize, preserve and extend access to *Behavioral Ecology and Sociobiology*.

<http://www.jstor.org>

## Optimal diets: simultaneous search and handling of multiple-prey loads by salamander larvae

A. Sih and J.W. Petranka

Behavioral and Evolutionary Ecology Research Group, T.H. Morgan School of Biological Sciences, University of Kentucky, Lexington, KY 40506, USA

Received February 24, 1988 / Accepted July 7, 1988

**Summary.** A key assumption of conventional optimal diet theory is that foragers cannot search for prey while already handling one prey item. Some foragers, however, can handle multiple-prey loads; i.e., they can search for, attack and handle further prey when already handling one or more prey. We examined diet selection by small-mouthed salamander larvae, *Ambystoma texanum*, that can search while handling up to two prey at a time. We gave *A. texanum* larvae a choice between two size classes of *Daphnia pulex* at two prey densities. Larval *A. texanum* diet choice did not fit the predictions of conventional optimal diet theory, but fit very well with the predictions of a multiple-prey model. At low prey density, *A. texanum* larvae were nonselective. At high prey density, larvae were non-selective when their mouths were empty, but showed a strong preference for larger, more valuable prey when larvae already had prey in their mouths. In 16 out of 18 instances, foragers either accepted or rejected small prey in keeping with a multiple-prey model's predictions.

### Introduction

A key assumption of conventional optimal diet theory is that search and handling are mutually exclusive activities; i.e., the handling of a prey item precludes opportunities to encounter other items. The "opportunity cost" of an item is defined as the benefit lost due to opportunities missed while handling that item (see Winterhalder 1983). A low value food item should be rejected if the benefit

derived from it is less than its associated "opportunity cost". To emphasize, the handling of a given item only has an energetic opportunity cost if the process of handling that item temporarily precludes search and capture of other items.

Many predators, however, can search for and capture additional prey while handling a given prey. This fact has been accounted for in some recent optimal foraging models. We refer to these models as "multiple-prey models". McNair (1983) and Lucas and Grafen (1985) examined the effects of simultaneous search and handling on optimal allocation of time to patches (including prey items as patches). They predicted that foragers that can search while handling should stay longer in patches than would foragers that cannot search while handling. An unstated corollary is that some patches/prey that would otherwise be rejected, should be accepted by a forager that can search while handling. Stephens and Krebs (1986) followed similar reasoning in suggesting, without an explicit model, that "the ability to encounter items when pursuing others will tend to make rate-maximizing foragers less fussy about the items they pursue." Juliano (1987; personal communication) explicitly modeled the effects of simultaneous search and handling on optimal diets. He assumed that foragers can "fill up" (our term) to a point where handling precludes search, but that it takes more than one prey item to do so. His model predicted that: 1) If high quality prey are abundant, and foragers are unoccupied (not already handling a prey item) then foragers should attack low quality prey; 2) If high quality prey are abundant, and foragers are occupied (already handling an item) then foragers should reject low quality prey; and 3) If high quality prey are scarce, then regardless of whether foragers are occupied or not, they should always attack low quality prey.

Present address and address for offprint requests: J.W. Petranka, Biology Department, University of North Carolina at Asheville, Asheville, NC 28804, USA

Juliano's predictions make intuitive sense if we compare benefits and opportunity costs associated with low quality prey. If high quality prey are scarce, then opportunity costs are low and poor prey should be attacked. If high quality prey are abundant, but the forager is empty, then poor prey can still be attacked with relatively little risk of precluding better prey. If, however, high quality prey are abundant and the forager's capacity is partially filled, then the opportunity cost of attacking a low quality item is relatively large, and low quality prey should be rejected.

To our knowledge, no previous empirical studies have tested a multiple-prey model. We report here on a quantitative test of optimal diet theory using small-mouthed salamander larvae, *Ambystoma texanum*, that can search while handling zooplankton prey, *Daphnia pulex*. *A. texanum* larvae commonly feed on *Daphnia* in nature (Smith and Petranka 1987). Large *A. texanum* (ca. 0.4 g) can handle up to ten *Daphnia* at a time; small *A. texanum* (ca. 0.06 g) can only handle two *Daphnia* at a time. We used small *A. texanum* in our tests. Using observed encounter patterns, we calculated optimal diet strategies using: 1) a conventional model that does not account for simultaneous search and handling and multiple-prey loads; and 2) a multiple-prey framework that accounts for search while handling. As discussed above, only multiple-prey models make predictions on how patterns of selectivity should change depending on whether the forager's mouth is empty or partially full. Observed diets were then compared to both sets of predictions.

## Methods

Eggs of *A. texanum* were collected from two field sites within 25 miles of Lexington, KY and hatched in the laboratory. Larvae were reared at 21°C in a 16L:8D photoperiod and fed *ad libitum* zooplankton and frozen brine shrimp. They were tested when they were about two weeks old (wet weight,  $\bar{x}$  = 0.061 g, SE = 0.0067). *D. pulex* were collected from a pond about 5 miles from the campus of the University of Kentucky. They were sieved repeatedly to yield two size classes: large (1.0–1.18 mm length) and small (0.6–0.71 mm length). Using Burns (1969) length-mass conversions, the mean masses for large and small prey were 0.0151 and 0.0039 mg respectively.

Experiments were run in 9 cm diameter (63.6 square cm bottom area) plastic petri dishes filled with 60 ml of ionically balanced freshwater. Both prey size classes were offered simultaneously at one of two densities: high (100 large, 100 small) or low (20 large, 20 small). These densities are both very high when calculated as total number/volume (high = 3333/l, low = 667/l). However, because small *A. texanum* are essentially benthic feeders, the total number/area (high = 3.14/cm<sup>2</sup>, low = 0.63/cm<sup>2</sup>) is probably a more useful measure.

Within 5 minutes after prey were counted into a petri dish, a single predator was added. In all cases, experienced predators (see below) began feeding almost immediately. A run lasted for 10 minutes during which time we recorded the time (to the second) of each prey encounter, attack, capture, and the end of handling. We previously determined that most attacks and captures occurred when prey came within 2 mm of the predator's mouth provided that the prey was not at the water's surface. We thus used these criteria for determining when encounters occurred. One of us (JWP) always called out encounters. Although we did not use strictly quantitative methods (e.g., videotapes) for evaluating encounters, we feel confident that other observers would make similar assessments. The end of a handling period was reasonably clearcut. During handling, larvae chewed vigorously with ample movement of gills. The end of handling was marked by swallowing accompanied by particularly vigorous gill movements.

A given predator was tested at the same prey density once per day for four consecutive days. After each run, predators were fed *ad libitum* for eight hours and then starved for 16 hours until the next run. On the first day, several predators appeared unacclimated to experimental conditions; they moved continuously without feeding. By the fourth day, all predators fed voraciously. Thus the first three days were considered training runs. Only data from the fourth day were used in analyses. Eight different predators were run at each prey density.

To measure selectivity we used  $\alpha = p(a_L) / (p(a_L) + p(a_S))$ , where  $p(a_L)$  and  $p(a_S)$  are the probabilities of attack given an encounter with large and small prey respectively.  $\alpha$  varies from zero to one. A value close to one signifies a strong preference for large prey whereas a value close to zero indicates a strong preference for small prey; random foraging is indicated by an  $\alpha$ -value of 0.5.  $\alpha$  need not be transformed to fit the assumptions of parametric tests (Chesson 1983).

The conventional optimal diet model predicts that foragers should attack low value prey if  $\lambda_1 < E_2 / (E_1 H_2 - E_2 H_1)$ , where  $\lambda_1$  is the encounter rate with high value prey; and  $E_1$ ,  $E_2$  and  $H_1$ ,  $H_2$  are expected energy returns and handling times for high and low value prey, respectively (Stephens and Krebs 1986). Mean energy return per attack is the product of prey energy content and probability of capture given an attack. Energy content (in biomass terms) was estimated, as given earlier, from Burns (1969). Mean capture probabilities and handling times were directly observed. Using observed encounter rates, we predicted diet choice for each forager using the conventional equation given above.

To identify optimal diet strategies for predators that can search while handling, we used observed encounter patterns to calculate energy intake rates associated with various possible multiple-prey foraging strategies. Calculations showed that energy maximizers should always attack large prey. Small prey can either be accepted or rejected, and acceptance or rejection can depend on whether the forager's mouth is empty or partially full. For predators that can handle up to two prey at a time, the possible strategies are: (accept, accept), (accept, reject), (reject, accept), and (reject, reject), where for example, (accept, reject) means that a forager accepts small prey when its mouth is empty, and rejects small prey when its mouth is partially full. To calculate reward rates, we simply applied each strategy to observed encounter patterns and measured the energy intake that foragers would have had, if they had used that strategy. The optimal strategy is the one that yields the highest energy intake rate.

The optimal strategy turned out, in all cases, to be either (accept, accept) or (accept, reject). We calculated the "net effect" of accepting small prey in the following way. We define  $E$  to be the energy intake rate associated with a given strategy.

If the optimal strategy was (accept, accept), then the net effect of attacking small prey was:  $\{E(\text{accept, accept}) - E(\text{reject, accept})\}$  when the forager's mouth was empty, and  $\{E(\text{accept, accept}) - E(\text{accept, reject})\}$  when the forager's mouth was partially full. If the optimal strategy was (accept, reject), then the net effect of attacking small prey was:  $\{E(\text{accept, reject}) - E(\text{reject, reject})\}$  when the forager has an empty mouth, and  $\{E(\text{accept, accept}) - E(\text{accept, reject})\}$  when the forager's mouth was partially full. If the net effect of attacking small prey was positive, then they should be attacked and  $\alpha$  should be 0.5; if net effect was negative, then small prey should be rejected and  $\alpha$  should be 1.0.

## Results

For small prey, mean  $p(\text{capture})$  was 0.899 (SE = 0.032,  $n=16$  predators), whereas for large prey it was 0.683 (SE = 0.037,  $n=16$ ). (Calculations weighing all attacks equally, rather than all predators equally yielded almost identical results:  $p(\text{capture})$  of 0.888 and 0.685 respectively). Mean energy return per attack (estimated in terms of biomass) was then 0.0103 and 0.0035 mg respectively for large and small prey. Mean handling times for large and small prey respectively were 14.86 seconds (SE = 0.91,  $n=44$  observed handling periods on single prey) and 12.43 seconds (SE = 0.57,  $n=42$ ). Mean prey value (biomass return/handling time) was then  $6.93 \times 10^{-4}$  mg for large prey and  $2.82 \times 10^{-4}$  mg for small prey. Large prey should thus be preferred.

The conventional model predicted that small prey should be accepted only if the encounter rate with large prey was lower than 0.046 per second; i.e., fewer than 27.6 encounters over a 10 minute run. At low prey density, large prey were encountered, on average, only 9.38 times (SE = 1.40,  $n=8$ ) per 10 minutes; none of the predators had more than 16 encounters/10 min with large prey. Thus the conventional model predicted that at low prey density, all foragers should accept small prey in the optimal diet. The multiple-prey model also predicted that at low prey density, small prey should be accepted, regardless of whether the forager's mouth was empty or partially full. The net effect of attacking small prey was 0.0149 mg (SE = 0.026; paired  $t$ -test vs. zero:  $t=4.19$ ,  $df=7$ ,  $P<0.01$ ) when forager's mouths were empty, and 0.0036 mg (SE = 0.015; paired  $t=2.40$ ,  $df=7$ ,  $P<0.05$ ), when forager's mouths were partially full. Thus both models predicted that at low prey density, foragers should be non-selective;  $\alpha$  should be 0.5.

As predicted, at low prey density, when their mouths were empty, larval *A. texanum* were nonselective ( $\alpha=0.530$ , SE = 0.021,  $n=8$ ;  $t$ -test versus  $\alpha=0.5$ :  $t=1.40$ ,  $P>0.10$ ). At low prey density, all

8 predators combined had only 22 instances where they encountered prey (9 small, 13 large) when their mouths were partially full. Sample sizes were too small to calculate meaningful  $\alpha$ -values. A chi-square test (pooling data for all 8 predators) showed no significant effect of prey size on the probability of attack ( $\chi^2=1.31$ ,  $df=1$ ,  $P>0.20$ ). Overall, both models predicted that foragers should be non-selective, and indeed foragers were non-selective. Because the models did not differ in their predictions and because a prediction of random foraging is not very powerful, these data do not provide a strong test of the multiple-prey model.

At high prey density, all predators encountered large prey at a high enough rate that the conventional optimal diet model predicted rejection of small prey (number of encounters per 10 minutes:  $x=46.13$ , SE = 4.41, range = 34–74); i.e., predicted  $\alpha=1.0$ . In contrast, the multiple-prey model predicted that all foragers should accept small prey when their mouths are empty, and most (6/8) foragers should reject small prey when their mouths are partially full; i.e., predicted  $\alpha=0.5$  when their mouths are empty and, for most foragers,  $\alpha=1.0$  when their mouths are partially full.

Observed diet choice at high prey density agreed well with the predictions of the multiple-prey model. When their mouths were empty, foragers were nonselective ( $\alpha=0.533$ , SE = 0.026;  $t$ -test versus  $\alpha=0.5$ :  $t=1.27$ ,  $P>0.10$ ), whereas when their mouths were partially full they generally showed a strong preference for large prey ( $\alpha=0.878$ , SE = 0.080;  $t$ -test versus  $\alpha=0.5$ :  $t=4.73$ ,  $P<0.01$ ). A paired  $t$ -test comparing  $\alpha$ -values for a given predator when its mouth is empty versus partially full showed a significant increase in preference for large prey when a forager's mouth was partially full (paired  $t=4.76$ ,  $P<0.01$ ). None of these patterns was predicted by the conventional optimal diet model. Overall, at high prey density, foragers showed a slight preference for large prey ( $\alpha=0.582$ , SE = 0.030;  $t$ -test versus  $\alpha=0.5$ :  $t=2.73$ ,  $P<0.05$ ;  $t$ -test versus  $\alpha=1.0$ ,  $t=13.93$ ,  $P<0.001$ ).

A more precise way of testing the multiple-prey model is to separately examine the predicted and observed diets of individual foragers under the two conditions (mouth empty versus partially full). Figure 1 shows the relationship between the net effect of attacking small prey and the preference for large prey. The bold line is the predicted preference based on the multiple-prey model. 16/18 points fall on or close to the predicted line. This result is not quite as astounding as appears at first glance. In

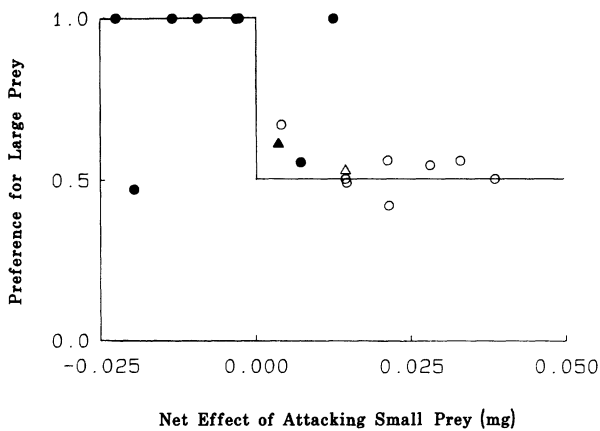


Fig. 1. The relationship between the net effect of attacking small prey and preference for large prey. The line indicates predicted preference based on an energy-maximization multiple-prey framework. Circles=high prey density, triangles=low prey density; open symbols = mouth empty, closed symbols = mouth partially full

14/16 instances, the model predicted that foragers should have accepted small prey when their mouths were empty and rejected small prey when their mouths were partially full. In 13/14 of these cases, foragers obeyed that relatively simple rule. As mentioned above, in two instances, foragers should have accepted small prey even when their mouths were partially full. In 1/2 of these cases, the forager actually was non-selective despite the fact that its mouth was partially full.

## Discussion

Diet selection by *Ambystoma texanum* was well explained by an optimal diet framework that accounts for simultaneous search and handling and the capacity for handling more than one prey at a time. How broadly applicable is this framework likely to be? The capacity for handling more than one prey at a time should often occur when predators are much larger than prey, or when predators capture and quickly incapacitate prey and then consume their food over relatively long periods. One or the other of these criteria would appear to be often satisfied; in fact, they probably apply in many, if not most, situations where vertebrates feed on invertebrates. The simultaneous search and handling criterion might be more restrictive. We suspect that simultaneous search and handling are easier to reconcile if predators search from ambush (e.g., web spiders, some frogs). Although *A. texanum* larvae stalk their prey to some degree, at

high prey density, they are essentially ambush predators. To simultaneously search and handle, actively searching predators must be capable of moving while handling prey (e.g., some planktivorous fish or insectivorous birds). Although we have referred to it as a multiple-prey framework, it should not be applied to foragers that gather and handle multiple-prey during separate time periods. e.g., squirrels that gather nuts, carry them in cheek pouches, and then process them in a hiding place.

The fact that at high prey density, most *A. texanum* larvae employed a relatively sophisticated feeding strategy that fit predictions based on an energy-maximization premise raises an interesting issue concerning selection pressures and the evolution of optimal foraging strategies. It has been suggested that natural selection should only result in optimal responses to environmental conditions if: 1) selection pressure favoring such responses is strong (Wiens 1977; Sih 1982); and 2) the population has had a history of selection under similar conditions. Selection pressure for maximizing the rate of net energy intake ought to be strong if predators are food-limited, and relatively weak if predators have superabundant food. *A. texanum* larvae are often food-limited (Petranka 1984; Petranka and Sih 1986). Reduced food intake decreases larval growth and developmental rates (unpublished data) and thus decreases survivorship relative to habitat drying (Petranka and Sih 1986, 1987). *A. texanum* larvae thus typically experience strong selection pressure favoring efficient foraging.

The specific conditions of our experiment, however, are probably rarely seen by *A. texanum* in nature, and are conditions where there was probably little cost to sub-optimal foraging. Although zooplankton can be found in dense patches, to our knowledge, *A. texanum* larvae relatively rarely experience prey densities as high as those found in our high density treatment. Furthermore, at high prey density, even sub-optimal foragers can probably achieve near maximum feeding rates, and the cost (in fitness terms) of a small reduction in feeding rate is generally low when overall feeding rate is very high (Sih 1982). Calculations based on observed encounter rates in our experiment showed that if *A. texanum* larvae had chosen either of two simple but sub-optimal strategies (always reject or always accept small prey), at high prey density, the mean cost of these suboptimal strategies would have been only a 2–5% reduction in energy intake.

Although we have no direct evidence on evolution in the sense of a historical pathway of change,

the above points suggest that for *A. texanum*, selection favoring high energy intake rates under food-limited conditions has resulted in the evolution of proximate mechanisms that produce efficient foraging, even under conditions that are rarely seen in nature and where the cost of sub-optimal foraging is low.

Our results also have potentially important ecological implications. The effect that predators have on prey communities is often heavily dependent on patterns of predator selectivity (Paine 1966; Connell 1978; Zaret 1980; Sih et al. 1985). Predators that can search and handle prey simultaneously are likely to have a generalized diet even at very high prey densities. In general, these foragers should be non-selective when their mouths are empty and should only specialize when prey density is high and their mouths are partially full. For *A. texanum* larvae, even at extremely high prey density (higher than is usually seen in nature), most encounters with prey still took place when predators' mouths were empty. Thus although these larvae specialized on large prey when their mouths were partially full, over the entire run, they showed only a slight tendency to prefer large prey. Our experiments were done using predators that handle only two prey at a time. Predators that can handle more than two prey simultaneously should show an even greater tendency to be non-selective.

*Acknowledgements.* This work was supported by a grant from the National Science Foundation BSR 85-00329. Rex McHutton and the Raven Run Nature Preserve of the city of Lexington kindly gave us the right to use animals collected from their lands. Becky Elkin, Marie-Sylvie Baltus-Sih and Loric Sih provided various types of aid and stimulation.

## References

- Burns CW (1969) Relation between filtering rate, temperature and body size in four species of *Daphnia*. *Limnol Oceanogr* 14:693-700
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297-1304
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310
- Juliano SA (1987) Simple queueing models for predation: consequences for foraging theory. *Bull Ecol Soc Am* 68:334
- Lucas JR and Grafen A (1985) Partial prey consumption by ambush predators. *J Theor Biol* 113:455-473
- McNair JN (1983) A class of patch use strategies. *Am Zool* 23:303-313
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65-75
- Petranka JW (1984) Sources of interpopulational variation in growth responses of larval salamanders. *Ecology* 65:1857-1865
- Petranka JW, Sih A (1986) Environmental instability, competition and density-dependent growth and survivorship of a stream-dwelling salamander. *Ecology* 67:729-736
- Petranka JW, Sih A (1987) Habitat duration, length of the larval period and the evolution of a complex life cycle of an amphibian. *Evolution* 41:1347-1356
- Sih A (1982) Optimal patch use: variations in selection pressure for efficient foraging. *Am Nat* 120:666-685
- Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K (1985) Predation, competition and prey communities: a review of field experiments. *Ann Rev Ecol Syst* 16:269-311
- Smith CK, Petranka JW (1987) Prey size-distributions and size-specific foraging success of *Ambystoma* larvae. *Oecologia* 71:239-244
- Stephens DW and Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton
- Wiens JA (1977) On competition and variable environments. *Am Sci* 65:590-597
- Winterhalder B (1983) Opportunity cost foraging models for stationary and mobile predators. *Am Nat* 122:73-84
- Zaret TM (1980) *Predation and freshwater communities*. Yale University Press, New Haven