

## EVOLUTION OF HANDLING TIME: THE FUNCTIONAL RESPONSE OF A PREDATOR TO THE DENSITY OF SYMPATRIC AND ALLOPATRIC STRAINS OF PREY

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A large body of theory regarding the evolution of life history parameters in populations has been developed with emphasis on the importance of interspecific interactions and environmental uncertainty (see Stearns, 1976, for a recent review of the ideas, and Gill, 1974). Strangely, although the development of theoretical models of predator and prey relationships has been equally elaborate, predator-related parameters as evolved characteristics of prey life history have yet to be included into the array of hypotheses concerning life history evolution. This omission becomes more glaring when the documentation of the evolutionary importance of predation is noted in comparison with evidence concerning resource competition as a selective agent.

Adaptation to predation may occur in numerous ways (e.g., cryptic coloration, mimicry, unpalatability, evasiveness, indigestibility, defensive tactics, structures or chemicals), and the evolution of a particular tactic will ultimately influence either the rate at which the prey are captured or the time required for ingestion.

This paper describes an experiment designed to assess the evolutionary impact, if any, of a predator on its functional response relationship with its prey. To do this, I present estimates of the functional response parameters for predation on sympatric and allopatric strains of prey, i.e., prey which have evolved with and without the predator.

The most frequently used description of experimental functional response relationships is the disc equation of Holling (1959):

$$\frac{N_a}{P} = \frac{aNT}{1 + aNT_h} \quad (1)$$

This equation predicts that the number of prey killed per predator will rise with prey density ( $N$ ) in a negatively accelerated fashion until a plateau is approached, at which the number of successful attacks ( $N_a$ ) will be limited by the handling time ( $T_h$ ) which incorporates the time spent by the predator after capture has occurred until the predator seeks its next prey. The height of the plateau in experimental con-

ditions is determined by the ratio of the total time of exposure ( $T$ ) to the handling time. The rapidity with which the plateau is reached is determined by the attack rate ( $a$ ), or "rate of successful search."

The valid use of this equation requires the acceptance of a number of assumptions. The attack rate and handling time are assumed to be constants, determined by attributes of the predator which relate to efficient search, capture and ingestion, and prey attributes relating to evasion, disguise, escape, distastefulness or defense. Interactions among predators, such as cannibalism or interference, and among prey are assumed to be unimportant. The descriptive use of the equation for experimental data presents further difficulties, particularly because no allowance is made for a change in prey density due to predation (Royama, 1971; Rogers, 1972). The predator is assumed not to form any type of search image which would modify the attack rate in a density dependent manner. Severe departures from these assumptions produce more complex relationships. Hassell et al. (1976) and Murdoch and Oaten (1975) provide thorough reviews of functional response relationships. The widespread adequacy of the disc equation in the description of experimental data for invertebrate predators indicates that departures from these assumptions are either minor or that they leave the general form of the relationship intact.

The accuracy of the disc equation in the absolute determination of attack rates and handling times has been questioned by Rogers (1972). The objection is justified by the failure of the disc equation to incorporate changes in prey density due to exploitation. Rogers has proposed an alternative equation in which exploitation is considered. Unfortunately, the alternative equation, in its linear form,

$$\ln \left[ 1 - \frac{N_a}{N} \right] = aT_h N_a - aTP, \quad (2)$$

cannot be used in regression analyses for the estimation of the parameters  $a$  and  $T_h$  without violating statistical assumptions (Livdahl and Stiven, unpubl.). Despite its shortcoming, the disc equation provides a useful method for estimating these parameters for comparative purposes. The use of such parameters in the prediction of population dynamics would assume a much larger risk of invalidity.

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## MATERIALS AND METHODS

The large, predaceous tree hole mosquito, *Toxorhynchites rutilus septentrionalis* was selected as the predator in this study. This species occurs sympatrically with other mosquito larvae (*Aedes triseriatus*, *Orthopodomyia signifera* and *Anopheles barberi*) throughout the Southeast, extending north along the East Coast into Pennsylvania (Bradshaw and Holzapfle, 1975) and into the Midwest as far north as the Ohio River Valley (Jenkins and Carpenter, 1945). Two larvae were found by Parker (1977) in Point Pelee National Park, Ontario, although there is no information regarding the establishment of a self-sustaining population that far north. *Aedes triseriatus*, the prey species in this study, extends into Wisconsin, Minnesota and Ontario (Jenkins and Carpenter, 1945).

Collecting sites were selected according to this distribution. Prey which are allopatric to the predator were collected in two forests near St. Charles, Illinois. *Aedes triseriatus* that have evolved in the presence of *Toxorhynchites* were collected in forests surrounding Chapel Hill, N.C. Eggs were obtained from the field by suspending plastic cups, with oak slats inserted, on the trunks of trees. *Aedes triseriatus* females found the oak slats to be suitable oviposition sites. The slats with eggs were then transported to the laboratory for storage in humid conditions. *Toxorhynchites rutilus* were then intensively sought in natural tree holes while the *Aedes* eggs awaited submersion for hatching. When enough *Toxorhynchites* eggs were found at one time, the experiment ensued. *Aedes triseriatus* eggs were collected in the spring of 1977. *Toxorhynchites* eggs were collected in July, 1977.

The *Toxorhynchites* eggs were isolated in deionized water within the cells of plastic ice cube trays to prevent cannibalism after hatching. As soon as hatching among these eggs began, the prey eggs were prepared for hatching by submersion into brewer's yeast suspensions. First instar *Aedes triseriatus* larvae were removed 24 h later, and dispensed into plastic cocktail cups in densities of 3, 6, 12, 18, 24 and 48 larvae per cup. This was followed by the addition of 150 ml deionized water and one predator per cup.

The experimental habitats were then placed in a controlled environment chamber (26 C, 16L:8D photoperiod) for 24 h, after which the predators were removed and the surviving prey were counted. Position in the chamber and the order in which predators were inserted and removed were randomized.

This technique allows a fairly high degree of con-

trol over the size and experience of the prey (24 h since hatching) and the size and degree of hunger of the predator (24–48 h since hatching, none had eaten).

Originally, there were 50 cups for each strain, with each density replicated between seven and ten times. Cases in which the predator had died were excluded from the analysis.

## RESULTS

Functional response parameters were estimated for both strains of prey using the following linear transformation of the disc equation:

$$\frac{P}{N_0} = \frac{1}{aT} \cdot \frac{1}{N} + \frac{T_h}{T} \quad (3)$$

This transformation produces the attack rate as the reciprocal of the slope of the least squares equation divided by the time of exposure, and the handling time as the intercept multiplied by the time of exposure (24 h). Table 1 summarizes the results of the regressions for each strain. The predicted functional response relationships, determined by regression, are presented in Figure 1 against the background of actual data.

A test for the difference between slopes reveals that the slopes do not differ significantly ( $F_{1,28} = 0.221$ , n.s.). Consequently, the attack rates have not been shown to differ. Because the slopes are homogeneous, analysis of covariance can be used to test the significance of the difference between intercepts. In this case,  $t_{82} = 3.575$  ( $P < .001$ ). The handling times differ significantly.

## DISCUSSION

The difference in handling times probably reflects an evolutionary adaptation by *Aedes triseriatus* to the presence of *Toxorhynchites rutilus* in North Carolina. The surprising aspect of this analysis is that the attack rates are not shown to differ. Prior investigations of adaptation to predation have dealt with characteristics in the prey which reduce the likelihood of attack, e.g., cryptic coloration (Kettlewell, 1958), production of toxins (Whittaker and Feeny, 1971), behavioral deception (Robinson, 1969), distastefulness with conspicuous coloration, and mimicry of distasteful species by palatable ones (Brower, 1958a,b,c; Brower and Brower, 1962). These types of adaptation should decrease the attack rate,  $a$ . They are also very easy to explain in evolutionary terms: types of individuals that are attacked with less fre-

TABLE 1. Results of regressions for the estimation of the functional response parameters for allopatric (Illinois) and sympatric (North Carolina) prey. 95% confidence intervals are given.

Strain	Slope	Attack rate	Handling time	r <sup>2</sup>
Illinois	0.96 ± 0.13	0.038 ≤ a ≤ 0.050	1.23 ± 0.48	0.85
North Carolina	0.89 ± 0.25	0.037 ≤ a ≤ 0.065	2.56 ± 0.84	0.58

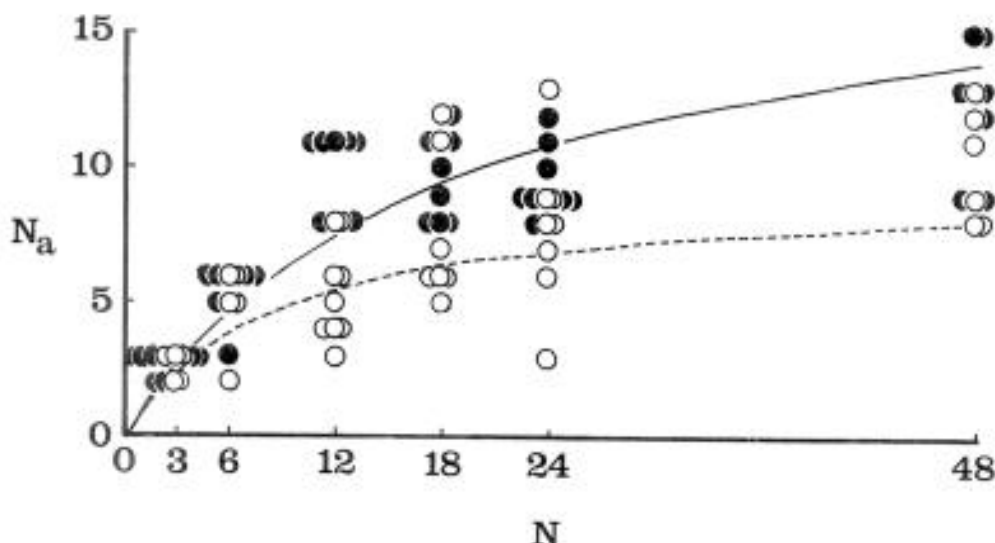


FIG. 1. The predicted functional response relationship between prey density ( $N$ ) and number of prey eaten ( $N_a$ ) for sympatric prey from North Carolina (dashed line, open circles) and allopatric prey from Illinois (solid line, closed circles).

quency will be the most successful in the perpetuation of their genes. The evolution of characteristics that require a higher handling time on the part of the predator is more complex. The characteristics that contribute to the handling time do not manifest themselves until capture has already occurred.

Selection for increased handling time could occur if there is a chance for escape without undue injury after the initial capture. This could lead to the differential survival of individuals with attributes (e.g., toughness, spines, or the tendency to struggle profusely) that contribute to the overall handling time of the predator. In some cases, if the prey take long enough for the predator to subdue and eat, their chances for escape may be improved. Another possibility could occur if many of the prey within a habitat tend to be closely related. In this case, an individual with attributes that increase the time spent in its demise will help to perpetuate the genes of its siblings merely by occupying the predator for a longer period of time, increasing the probability of their survival. Which of these or other explanations applies to this case is uncertain because the mechanism for the increased handling time and the degree of relatedness among the prey within a tree bole are not known.

The evolutionary adjustment of functional response parameters by the prey will not likely occur without the investment of some proportion of resources. The result should be a decline or loss of characteristics which produce the combination of the intrinsic rate of increase, competitive ability and performance under conditions of food or space limitation. Which of these other life history characteristics will be most affected will depend on the degree of environmental uncertainty, the presence or absence

of interspecific competition, the nature of such interactions (exploitative or interference), and the nature of the population dynamics of the predator-prey interaction.

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