

The Influence of Temperature on the Functional Response of the Dragonfly *Celithemis fasciata* (Odonata: Libellulidae)

Susan E. Gresens*, Marian L. Cothran, and James H. Thorp
 Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29801, USA

Summary. 1) Functional response curves were constructed for *Celithemis fasciata* larvae feeding on 6 different densities of midge larvae at 10, 15, 20, and 25° C. Values for attack rate and handling time were estimated with Rogers's random predator equation. 2) Polynomial regression revealed that the functional response curves were linear although a tendency toward decreasing consumption rates at higher densities was shown. 3) The mean number of prey eaten increased with temperature; however, temperature did not alter the fundamental shape of the functional response curve. 4) The attack rate and handling time were linearly related to temperature in general, but changed relatively little between 15 and 20° C.

Introduction

The functional response (Solomon 1949) relates changes in the attack rate of a predator to changes in prey density. Holling (1959) suggested 3 kinds of response: type I, where there is a constant increase in the number of prey eaten to a maximum as prey density increases; type II, where predation rate decelerates towards an asymptote; and the sigmoidal type III, which shows an accelerating consumption rate to a threshold prey density, followed by deceleration to an asymptote. If field densities of prey fall below this threshold, predatory regulation of prey may be significant. Since in a type II response the predator eats proportionately less of the prey population as it increases, a type II response cannot stabilize predator-prey interactions. When stability exists in such situations, it must result from other factors affecting predator or prey (Murdoch and Oaten 1975). Because of this differing impact on population stability, it is important to determine the nature of the functional response of potentially important predators.

Invertebrate predators are generally considered to show a type II response. Several factors, notably, the developmental state of predator and prey (Thompson 1975; McArdle and Lawton 1979), the predator's mode of search (Akre and Johnson 1979) and the availability of prey refuges (Hildrew and Townsend 1977) are known to influence the functional response of invertebrate predators. Temperature is an important physical characteristic having profound effects on the growth and development, distribution, and emergence of dragonflies (e.g., Corbet 1963)

and their prey (e.g., Wieser 1973). Only a few investigators have examined the relationship between temperature and functional response (Messenger 1968; Thompson 1978). Since temporal synchronization is necessary if predators are to exert an effect on their prey, seasonal differences, especially in temperature, can alter the magnitude of predation (Thompson 1978).

Our objective in this study was two-fold. First, we were interested in determining the form of the functional response of larvae of the dragonfly *Celithemis fasciata* Kirby feeding on the midge *Chironomus tentans* Fabricius. Chironomids are an important component of the odonate diet (Pritchard 1964). In previous determinations of odonate functional responses, free-swimming Cladocera, often at unnaturally high densities, have been utilized as prey; the type II functional response was usually observed. Second, we wished to determine if the functional response is altered at different temperatures. *Celithemis* larvae experience a range of temperatures during larval development, and it seemed likely that at certain temperatures regulation of prey might be possible, while at other temperatures the proportion of prey eaten would remain constant or decline with density.

Materials and Methods

Feeding trials were conducted in the laboratory using predators collected from the field and laboratory-cultured prey. The dragonfly *Celithemis fasciata*, the numerically dominant species at our collection sites, were selected as predators. *Celithemis* were collected during June, 1980, from Par Pond, a reservoir in South Carolina. To reduce possible variability in consumption rates, only ultimate instar larvae (head width > 4.5 mm) which were not close to emergence were used. Morphological changes associated with emergence hinder activity and feeding in odonate larvae (Savan 1979).

Celithemis were maintained prior to the experiments in a 10 ± 1° C environmental chamber and fed weekly on midge larvae. The predators were randomly assigned to the treatments and were used only once. Prey consisted of third instar larvae of *Chironomus tentans*. Cultures were raised on a paper pulp substrate in aerated gallon jars and fed a suspension of powdered shrimp pellets and fish flakes. The mean length of experimental midges was 9.85 mm. The experimental containers were 600-ml beakers filled with 500 ml of filtered pond water. A plastic plant provided a hunting site for the dragonfly, and 1 cm of fine sand provided a substrate in which the midges could burrow. The substrate area was approximately 61 cm².

Six prey densities were used to determine functional response curves at 4 temperatures. Prey densities of 10, 17, 25, 32, 40,

* Present address: Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA

Offprint requests to: James H. Thorp

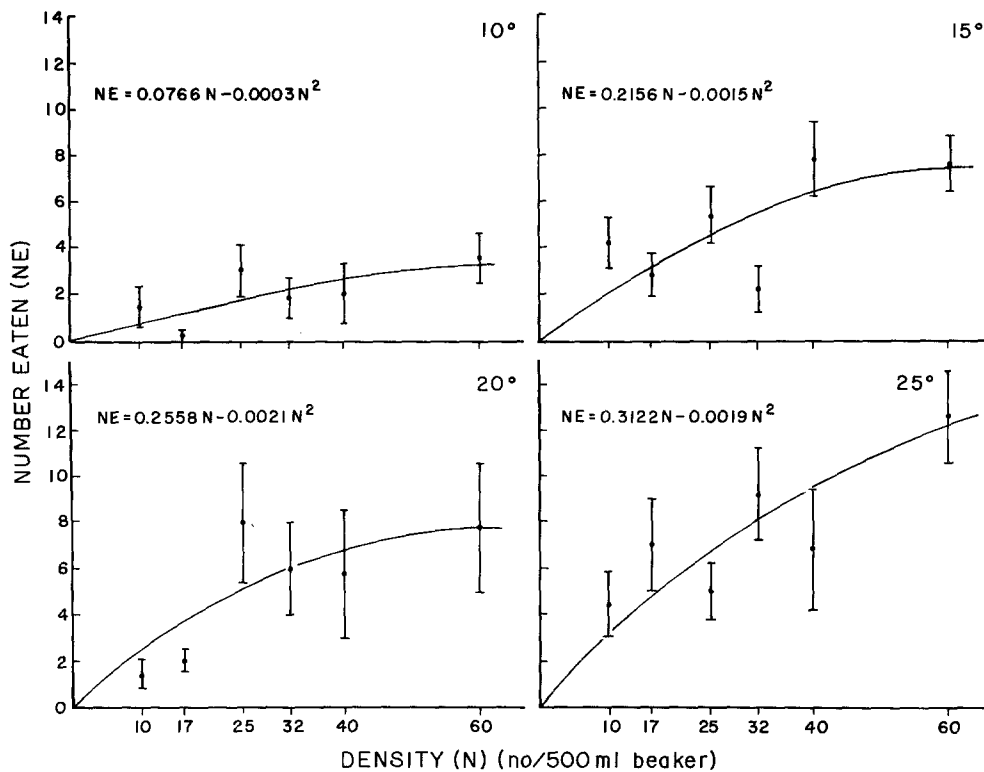


Fig. 1. Quadratic polynomial regressions of *Celithemis fasciata* feeding on *Chironomus tentans* at each experimental temperature. Plotted points are means of 5 individuals (\pm S.E.)

and 60 *Chironomus* per container were run in environmental chambers at 10, 15, 20 and 25° C. Five replicates of each density and temperature treatment were performed. The sequence of treatments was randomized. An abbreviated set of controls were run without predators, to determine non-predatory mortality, and whether wasteful killing (Johnson et al. 1975) was occurring. Two densities, 10 and 32, with 3 replicates each, were run at all 4 temperatures.

Predators were introduced to the treatment temperature two days before the experiment, an adequate acclimation period for feeding trials. They were initially satiated with an excess of chironomid larvae, and a 24 h starvation period immediately preceded the experiment to reduce variability in predator hunger levels. During the predator starvation period, prey were acclimated to treatment conditions in the experimental beakers. Dragonflies were allowed to feed on the midges for 6 h under constant illumination. After the feeding period, the plants were rinsed and the sand was placed in an enamel pan so remaining prey could be counted. The numbers of living and dead prey were recorded. The number consumed was calculated as the initial density minus the prey remaining alive and dead.

Since it was impossible to replace prey as they were eaten, exploitation was a factor in our experiment. Therefore, to calculate values for attack rate and handling time, we used Rogers's (1972) random predator equation:

$$N_a = N(1 - e^{-a(T - T_h N)})$$

where N_a = number of prey eaten, T = total exposure time, T_h = handling time, a = attack coefficient, and N = prey density. Experiments in which exploitation exceeded 80% were not included in the calculations. Statistical analyses were performed on an IBM 360 computer, and the general linear models, correlation, and non-linear procedures of the Statistical Analysis System (SAS) (Helwig and Council 1979) were utilized. The non-linear

procedure was modified to handle Rogers's equation as suggested by B. Sava (personal communication).

Results

We tested for the type of functional response that best accounted for differences in the number of prey eaten at several prey densities by performing a quadratic polynomial regression on the data collected at each temperature. *A priori*, we had the following expectations:

- (1) if no significant deviation from linearity was found, then a constant proportion of prey was being consumed regardless of density (type I);
- (2) if a significant, negative quadratic term was determined, then the proportion of prey eaten was decreasing as prey density increased (type II);
- (3) if a significant, positive second-degree term was found, the proportion of prey consumed was increasing as prey density increased (type III, accelerating phase).

For each temperature the second-degree terms of deviation from linearity were non-significant; however, in each case a negative coefficient indicated a tendency towards the type II response (Fig. 1). Probabilities associated with the N and N^2 coefficients of the polynomial regression were, respectively: 10°, 0.048 and 0.674; 15°, 0.0003 and 0.176; 20°, 0.003 and 0.207; and 25°, 0.0003 and 0.219. The amount of variation in the number of prey consumed explained by the regression (r^2) was 0.51, 0.75, 0.60 and 0.77 at 10, 15, 20 and 25° C. Flattening of the functional response curves, especially at 25° C, may not be occurring due to the relatively low prey densities used.

We utilized a non-linear least squares technique to estimate attack coefficients and handling times at the experimental temperatures. Attack coefficients (1/h) were 0.005, 0.018, 0.019, 0.028

and handling times (h) were 0.098, 0.081, 0.072, 0.052 at 10, 15, 20, and 25° C, respectively.

When data for densities were combined, the mean number of prey eaten more than tripled (from 2.0 to 7.5) between 10 and 25° C. A Student-Newman-Keuls test of multiple comparisons among means indicated that significant differences existed among all means except the 15° C–20° C comparison.

Using density as a covariable, we tested for homogeneity of slopes among temperatures. No significant interaction was detected between temperature and density; that is, the effect of density on the number of prey eaten was similar at each temperature. Although temperature undoubtedly affected the functional response, a larger sample size would have been necessary to show such an interaction due to the substantial variation in the number of prey eaten.

The number of dead prey remaining at the conclusion of an experiment was quite small, usually zero, but occasionally exceeded 10%. A 3-way analysis of variance involving predator treatment, temperature, and density indicated that neither the presence of a predator nor temperature contributed significantly to the number of midges found dead, but uneaten. However, mortality was significantly greater ($P < 0.05$) at the higher density regardless of predator presence or temperature. This may be the result of a negative midge-midge interaction or may result from an increased probability of including a sick or weak midge in the sample. No wasteful killing was observed.

A significant positive correlation ($r = 0.18$, $P < 0.05$, $N = 120$) existed between the percentage of midges eaten by individual *Celithemis* during satiation and the percentage they consumed during the experiment. No correlation existed between numbers eaten and the head widths of our last instar predators. The range of head widths used was limited enough that any effect of increasing size was not detected.

Discussion

The changes we observed in the functional response curve of *Celithemis* in response to changes in temperature are probably due to the effect of temperature on hunger. Metabolic rates of a damselfly approximately doubled for each 10° C rise in temperature (Lawton et al. 1980), and associated physiological functions such as gut clearance rates also rise (Lawton 1971). Since insect hunger is directly related to emptiness of the gut (Johnson et al. 1975), one would expect greater hunger in *Celithemis* exposed to higher temperatures. Hunger may influence the number of prey attacked by altering the distance at which the predator detects and reacts to prey and by decreasing pursuit time (O'Brien 1979). Temperature may also directly influence the subcomponents of a and T_h , for example, by reducing swimming speed of prey at low temperatures.

Over the temperature range investigated, the attack rate generally rose while T_h decreased in a like manner. The similarity in a and T_h values at 15° C and 20° C may reflect a behavioral insensitivity to temperature change in this range. One would expect that a should increase with higher temperatures to a point and then decline as very high temperatures inhibit feeding. Handling times should behave in a reciprocal manner, decreasing with temperature and then increasing under stressful conditions. Messenger (1968) found this pattern of variation in a parasitic wasp. Thompson (1978) reported that T_h of a damselfly decreased exponentially, levelling off at 16° C, while the attack coefficient increased sigmoidally, levelling off at 27.5° C. The attack coefficients and handling times estimated for *Celithemis*

were smaller than those previously described for Odonata (Thompson 1978; Akre and Johnson 1979; Savan 1979).

The lack of an appreciable plateau in our functional response curves, especially at 25° C (Fig. 1), is probably due to the low prey densities we used. We utilized chironomid densities that were representative of mean densities in Par Pond (Thorp and Bergey 1981), but even these densities probably exceed those actually encountered by *Celithemis* as it climbs on underwater debris. Other researchers, who report unambiguous type II responses for Odonata, have used unrealistically high prey densities. Their maximum prey densities, i.e., 1,200 *Daphnia*/l (Thompson 1978) and 2,000 *Daphnia*/l (Johnson et al. 1975) are an order of magnitude larger than the maximum of ca. 100/l found in some ponds and lakes (e.g., Threlkeld 1979). When lower maximum densities are tested (63/l, Akre and Johnson 1979) evidence of satiation is weak. Our data indicate that as temperature increases higher metabolic demands may make satiation at low, field densities even more improbable.

Individual larvae were quite consistent in the amount of food they consumed. A larva which refused to eat during the satiation period, for instance, rarely consumed prey during the experimental period. T. Folsom (personal communication) observed a similar phenomenon in *Anax junius*, but Savan (1979) did not find such consistency in *Pyrrhosoma nymphula* or *Coenagrion puella*. In related experiments run at 15° C (Cothran and Thorp, unpublished data), individual ultimate instar larvae chose reasonably uniform rations of 2 prey types consistently over 1 month's time.

Evidence from our laboratory experiments suggests that dragonfly nymphs cannot stabilize prey population fluctuations in the field. Alternative modes of population stabilization by predators include: (1) switching between alternative prey species as relative availability changes, and (2) transfer between patches when prey density reaches a critical lower threshold. The respite from predation gained by prey species in both these cases could allow time for population recovery. Concurrent laboratory experiments on switching between two prey species (Cothran and Thorp, unpublished data) suggest, however, that transfer between patches may be the only viable mode of population stabilization by dragonflies.

Acknowledgements. We are grateful to the following persons for aid in data analysis and/or manuscript preparation: Jean Coleman, Gus Cothran, Todd Folsom, Dan Johnson, Debbie Perks, and John Pinder.

Research support came from contract DE-AC09-76SR00819 between the University of Georgia and the United States Department of Energy, and through an interagency agreement (EPA 79-D-X0533) between the United States Environmental Protection Agency and the Department of Energy.

References

- Akre BG, Johnson DM (1979) Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. *J Anim Ecol* 48:703–720
- Corbet PS (1963) A biology of dragonflies. Quadrangle Books, Chicago
- Helwig JT, Council KA (1979) Statistical analysis system user's guide. Statistical Analysis System Institute, Raleigh NC
- Hildrew AG, Townsend CR (1977) The influence of substrate on the functional response of *Plectrocnemia conspersa* (Curtis) larvae (Trichoptera: Polycentropodidae). *Oecologia* 31:21–26
- Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can Ent* 91:293–320
- Johnson DM, Akre BG, Crowley PH (1975) Modelling arthropod

- predation: wasteful killing by damselfly naiads. *Ecology* 56:1081-1093
- Lawton JH (1971) Ecological energetics studies on larvae of the damselfly *Pyrhosoma nymphula* (Sulzer) (Odonata:Zygoptera). *J Anim Ecol* 40:385-423
- Lawton JH, Thompson BA, Thompson DJ (1980) The effects of prey density on survival and growth of damselfly larvae. *Ecol Entomol* 5:39-51
- McArdle BH, Lawton JH (1979) Effects of prey - size and predator - instar on the predation of *Daphnia* by *Notonecta*. *Ecol Entomol* 4:267-275
- Messenger PS (1968) Bioclimatic studies of the aphid parasite *Praon exsoletum*. *Can Entomol* 100:728-741
- Murdoch WW, Oaten A (1975) Predation and population stability. *Adv Ecol Res* 9:1-125
- O'Brien WJ (1979) The predator-prey interactions of planktivorous fish and zooplankton. *Am Scientist* 67:572-581
- Pritchard G (1964) The prey of dragonfly larvae (Odonata:Anisoptera) in ponds in northern Alberta. *Can J Zool* 42:785-800
- Rogers D (1972) Random search and insect population models. *J Anim Ecol* 41:369-383
- Savan B (1979) Studies on the foraging behavior of damselfly larvae (Odonata:Zygoptera). Ph D Diss, University of London
- Solomon ME (1949) The natural control of animal populations. *J Anim Ecol* 18:1-35
- Thompson DJ (1975) Towards a predator-prey model incorporating age structure: The effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *J Anim Ecol* 44:907-916
- Thompson DJ (1978) Towards a realistic predator-prey model: The effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *J Anim Ecol* 47:757-767
- Thorp JH, Bergey EA (1981) Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. *Ecology* 62:365-375
- Threlkeld ST (1979) The mid-summer dynamics of two *Daphnia* species in Wintergreen Lake, Michigan. *Ecology* 60:165-179
- Wieser W (1973) Temperature relations of ectotherms: A speculative review. In: Wieser W (ed) *Effects of temperature on ectothermic organisms*. Springer-Verlag, New York, pp 1-24

Received February 1, 1982