

PREDATION OF *APOCHTHONIUS MINIMUS*
(PSEUDOSCORPIONIDA: CHTHONIIDAE) ON *FOLSOMIA*
CANDIDA (COLLEMBOLA: ISOTOMIDAE)
I. PREDATION RATE AND SIZE-SELECTION

Dan L. JOHNSON and W. G. WELLINGTON

Institute of Animal Resource Ecology, University of
British Columbia, Vancouver, B. C., Canada

INTRODUCTION

Apochthonius minimus (SCHUSTER, 1966) is a small (adult length 1.9-2.4 mm) heterosphyronid pseudoscorpion common in leaf litter, bark and bryophytes of a variety of forests of western British Columbia, Washington and Oregon (BENEDICT, 1978). Pseudoscorpions of this type are known to prefer Collembola (springtails) as food (WEYGOLDT, 1969). This is certainly the case for *A. minimus*: of nearly 150 individuals collected from our study site at the University of British Columbia Research Forest, Maple Ridge, B.C., Canada, nearly all fed on isotomid and entomobryid Collembola while none accepted food of any other kind.

A. minimus is found in relatively high densities at our study site: up to several hundred per m² is not uncommon. It is by far the most common of three pseudoscorpion species found in the site leaf litter. They, along with mesostigmatid mites, are the major predators of springtails in the area. WEYGOLDT (1969) states that "pseudoscorpions probably regulate the densities of small edaphic animals, especially Collembola". EDWARDS *et al.* (1967) found that collembolan densities significantly increased under DDT treatment, apparently, they suggest, because their predators, in this case mites were reduced. Similar concomitant increases in collembolan densities and decreases in predator densities were investigated by OLIVIER and RYKE (1969). As part of a study of factors limiting the densities of springtails, the following questions were of interest to us: how many springtails might the pseudoscorpions eat, what factors influence the predation rates and what are the effects of this predation on the growth of prey populations under controlled field conditions? The last of these questions and its associated hypotheses are examined in another paper (JOHNSON and WELLINGTON, 1980b).

Biology of the predator and prey

Little is known about the lives of pseudoscorpions because, as MUCHMORE (1973) points out, their retiring habits and inoffensiveness to man make them "invisible". Springtails, however, have caught the interest of a relatively large number of researchers, in part because of their high natural densities and presence in a wide

range of habitats. In our study site, *Folsomia nivalis*, *Folsomia candida*, *Folsomia quadrioculata* and other similar isotomids occur at densities as high as 30,000, and commonly 5,000 to 10,000, per m².

Folsomia candida

The springtail used in this study is a small (length 0.2-2.0 mm) cryptic apterygote that inhabits moist spaces between litter and soil particles in a variety of ecosystems. *F. candida* is found throughout Europe and North America in forests and grasslands, wherever the high relative humidity and fungal food it requires occur. The species is parthenogenetic, and has an ametabolous-monophasic developmental sequence in which periodic moults throughout life produce up to 30 instars. It is soft-bodied, blind, and for locomotion is equipped with six clawed legs and a short spring (furcula) arising from the ventrum of the fourth abdominal segment. Detailed observations on the life history and biology of *F. candida* have been made by MILNE (1960), MARSHALL and KEVAN (1962), GREEN (1964a, b), SNIDER (1971), SNIDER and BUTCHER (1973), GREGOIRE-WIBO and SNIDER (1977), HUTSON (1978b) and JOHNSON and WELLINGTON (1980a). Ecological experiments with this species have been conducted by CHRISTIANSEN (1970), USHER *et al.* (1971), TÖRNE (1974), USHER and HIDER (1975) and USHER and STONEMAN (1977).

Regarding the behavior of the prey, we noted that when contacted by the sensory setae of a pseudoscorpion palpal hand, *F. candida* usually runs 1 to 20 mm, seemingly at random, before continuing feeding or resting. This response is very brief; the apparent effects of such contact last only a few seconds, and follow the same sequence that occurs when one collembolan jostles another while searching for food or a moister resting place. Our observations show that "springing" away from predators in arenas, culture pots or intact litter and soil samples is rare. This method of emergency locomotion (accomplished by locking the furcula with the tenaculum, tensing manubrial and abdominal muscles and then releasing the furcula) seems to be employed more as a means of changing position in relation to physical conditions than in escaping from predators.

Apochthonius minimus

A. minimus adults are active in our study site from late March to October. They are found primarily in the litter layer and also are common in larger pieces of detritus, twigs and moss on the forest floor or on fallen logs. It is doubtful that the pseudoscorpions perform daily vertical migrations within the top 5-15 cm of soil, as some springtails are believed to do. Reproduction probably is not restricted to one period, since nymphs are present throughout the summer. A similar pattern in occurrence of *Chthonius ischnocheles* has been reported by JONES (1970).

GILBERT (1951) has described the feeding behavior of several pseudoscorpions, including the Chthonioidea. His description of the act of feeding in *Chthonius ischnocheles* is nearly identical to what we have observed for *A. minimus*. *A. minimus*

actively hunts for prey (mainly by touch; it is doubtful that its four ocelli are image-forming) but retains its characteristically timid, cautious approach even when prey is encountered. The predators often run backward in a typical escape attempt when they first contact prey or another predator. When capture is achieved the prey is quickly pinched with the pedipalps and transferred to the powerful chelicerae. The captor then moves to a quiet spot where, with the chelicerae alone, it kills and chews the prey. During feeding, the chelicerae jointly hold the prey, but often grasp and chew independently, since each chelicera has its own serrated, movable section. After the food is macerated, the liquid portion, including the pseudoscorpion's digestive juices, is apparently ingested, and the remaining cuticle is discarded by scraping and wiping the mouthparts on the substrate. A quick defecation and cleaning of the mouthparts, and a lengthy rest period follow. The predator may spend several hours slowly exploring before making another capture. During this period, it is common for the predator to approach a vulnerable prey individual, touch it, and then move on without attacking.

Surprisingly, there have been no studies of predation by chthoniid pseudoscorpions. The larger pseudoscorpion, *Neobisium muscorum* (LEACH), has attracted some attention as a predator of springtails (SIMON, 1966, 1969). ERNSTING and JOOSE (1974) experimented with *N. muscorum* and other predators of larger springtails, and suggested on the basis of indirect observations that this pseudoscorpion might account for a significant portion of the mortality of these collembolans.

METHODS

I. Predation rates

Objectives: to quantify the functional response (as described by HOLLING, 1959) of *A. minimus* to *F. candida* prey and to test the hypothesis that this relationship does not change with prey size or with ambient temperature.

Adult *A. minimus* (body length 1.9-2.4 mm from chelicerae to anus; palpal hand (pincer) 0.7-0.8 mm long) were aspirated from large bags of litter [roughly half feather moss (primarily *Hylocomium splendens* (HEDW.) BSG.) and half needles from Douglas fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) and western hemlock (*Tsuga heterophylla* (RAF.) SARG.)] collected from the study site at the University of British Columbia Research Forest. The sex and exact age of the predators were not determined. Individual pseudoscorpions were transferred to separate arenas and allowed 24 hours to evacuate their guts to reduce variability in hunger before the experiment. The arenas were 150 ml plastic specimen vials (pots) with screw-top lids. Each had a floor 1.0-1.5 cm deep (area 18 cm²) of technical plaster of paris mixed with charcoal (40 to 1). The charcoal in turn was a mixture of 2 parts powdered activated charcoal to 3 parts powdered animal charcoal, which provides a dark substrate with a pH of 5.5-6.0 (HUTSON, 1978a). The floor was kept saturated, but not visibly wet, with

distilled water. About 10 washed Douglas fir needles were added to each pot to provide a more natural environmental texture.

Prey density, temperature, prey size and time were manipulated to characterize the functional response. Prey densities were 2, 4, 8, 12 and 20 individuals per 18 cm² area. Prey were classified as "small" (0.5-0.7 mm long) and "large" (1.0-1.2 mm long) with lengths measured from the mouth to the posterior of the anal segment. These length classes were used instead of stadia because of *F. candida*'s ametabolous growth: moults occur frequently (every 4-10 days) throughout life, although the general body plan does not change markedly from the first instar to the last (JOHNSON and WELLINGTON, 1980a).

All *F. candida* for the experiments described here were obtained from stock laboratory cultures. The pots were divided equally between two identical incubators, one at a constant 8°C and the other at a constant 16°C, and the experiment was carried out in continuous dim light. Since the predators and prey were enclosed in tightly covered pots, there was no need to consider "incubators effects" other than temperature. To avoid a treatment sequence effect and to account for variability among predators, no individual pseudoscorpion was subjected to more than one density-size-temperature combination during the course of the experiment. There were four pseudoscorpions per treatment combination.

In all, 80 pseudoscorpions were used in 80 pots, 40 per incubator. The measured variable was the number of offered prey that were eaten by individual pseudoscorpions; this number was recorded every 12 hours, when the prey that had been eaten were replaced. The experiment was terminated after 48 hours. The pseudoscorpions were observed for 3 days following the experiment to ensure that none suffered any obvious ill effects or dramatic changes in behavior.

II. Predator size-selection

Objectives: to estimate the probability of capture of the different size classes of prey and to test the hypothesis that these probabilities are equal.

A. minimus adults were collected as described for the experiment on functional response. Three similarly-sized adults were introduced to each of 2 pots of the type described above. After 24 hours, a population consisting of all stages of prey (including eggs) was added to each pot. The predators were allowed 6 hours to become familiar with the prey available. This conditioning period was required because of the possibility that starved pseudoscorpions might feed on prey that they would not normally prefer. This period also allowed the timid pseudoscorpions to adjust to their surroundings. All predatory activity during the following 48 hours was noted and the lengths of captured individuals were also recorded. At the end of 48 hours, the remaining prey were counted, measured, and grouped into size classes with the following mean body lengths: 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0, 1.1, 1.2, 1.3, 1.4 and 1.5 mm.

Prey eaten during the experiment were not replaced.

RESULTS AND DISCUSSION

I. Predation rates

Table 1 shows the results of an analysis of variance of number of prey eaten. Selected main effects and interactions are shown in Table 2, with individual degree of freedom tests of differences in functional response means and shapes.

Table 1. Analysis of variance of the number of prey eaten

| Source | df | Analysis of variance-Numbers eaten | | | |
|------------------|-----|------------------------------------|--------|--------|---------|
| | | SS | MS | F | p |
| Temperature | 1 | 0.050 | 0.050 | 0.058 | 0.8168 |
| Prey size | 1 | 56.113 | 56.113 | 64.901 | <0.0001 |
| Size × Temp | 1 | 0.200 | 0.200 | 0.231 | 0.6323 |
| Density | 4 | 35.519 | 8.880 | 10.270 | <0.0001 |
| Dens × Temp | 4 | 10.294 | 2.573 | 2.977 | 0.0261 |
| Dens × Size | 4 | 12.981 | 3.245 | 3.754 | 0.0086 |
| Dens × Temp × Sz | 4 | 5.956 | 1.489 | 1.722 | 0.1569 |
| Pseudoscorpions | 60 | 51.875 | 0.865 | | |
| Time (hrs) | 3 | 104.463 | 34.821 | 35.790 | <0.0001 |
| Time × Temp | 3 | 2.575 | 0.858 | 0.882 | 0.4515 |
| Time × Dens | 12 | 10.381 | 0.865 | 0.889 | 0.5597 |
| Time × Size | 3 | 25.662 | 8.554 | 8.792 | <0.0001 |
| Time × Tmp × Den | 12 | 10.956 | 0.913 | 0.938 | 0.5104 |
| Time × Tmp × Sz | 3 | 1.725 | 0.575 | 0.591 | 0.6217 |
| Time × Den × Sz | 12 | 18.369 | 1.531 | 1.573 | 0.1024 |
| Tm × D × S × Tmp | 12 | 17.744 | 1.479 | 1.520 | 0.1200 |
| Residual | 180 | 175.126 | 0.973 | | |
| Total | 319 | 539.990 | | | |

Figure 1 shows fits of the observations (pooled over the four periods for illustration) to HOLLING's disc equation (HOLLING, 1961),

$$Na = aTN / (1 + aThN)$$

where

Na = number attacked

a = attack rate

T = total time available

Th = handling time

N = prey density.

Estimating a and Th by fitting the equation

$$Na/N = aT - aThNa$$

with simple linear least squares regression gave unreliable and occasionally unreasonable estimates. More realistic values and lower standard errors of estimate were obtained by non-linear least squares fits. For simplicity, the Michaelis-Menton form,

$$Na = cN / (d + N)$$

Table 2. Orthogonal contrasts (individual degree of freedom tests).*

| Source of variation | df | F | p |
|---------------------------|----|--------|---------|
| a.) Prey density | 4 | 10.270 | <0.0001 |
| Linear component | 1 | 29.115 | <0.0001 |
| Quadratic component | 1 | 11.357 | 0.0013 |
| Cubic component | 1 | 0.400 | 0.5293 |
| Higher order components | 1 | 0.212 | 0.6469 |
| b.) Density × Temperature | 4 | 2.977 | 0.0261 |
| Differences in: | | | |
| Linear components | 1 | 5.392 | 0.0236 |
| Quadratic components | 1 | 2.230 | 0.1406 |
| Cubic components | 1 | 3.636 | 0.0613 |
| Higher order components | 1 | 0.650 | 0.4234 |
| c.) Density × Prey size | 4 | 3.754 | 0.0083 |
| Differences in: | | | |
| Linear components | 1 | 5.049 | 0.0283 |
| Quadratic components | 1 | 6.412 | 0.0140 |
| Cubic components | 1 | 2.565 | 0.1145 |
| Higher order components | 1 | 0.987 | 0.3244 |
| d.) Time | 4 | 35.790 | <0.0001 |
| Linear component | 1 | 84.182 | <0.0001 |
| Quadratic component | 1 | 20.557 | 0.0007 |
| Higher order components | 1 | 2.631 | 0.1065 |
| e.) Time × Prey size | 4 | 8.792 | <0.0001 |
| Differences in: | | | |
| Linear components | 1 | 24.177 | 0.0007 |
| Quadratic components | 1 | 0.463 | 0.4973 |
| Higher order components | 1 | 1.737 | 0.1892 |

* For main effects (parts a and d) p (the probability of an F -value as large or larger) indicates significance of the contribution of a component to the shape of the functional response. For interactions (parts b, c and e), p indicates significance of the change in a component due to the interaction.

where c = the maximum (asymptotic) number eaten = T/Th
 d = the half saturation density = $1/aTh$
 T = total time (2 days in this case),
 N = prey density,

was used for these fits.

Estimates of handling time and attack rate for the two temperatures and two types of prey are shown in Table 3. Handling time is higher and attack rate lower for the larger prey. Both handling time and attack rate are somewhat higher at the higher temperature. Evidence that the response to prey density is not merely a linear increase is shown in Table 2a. Both the linear and quadratic components of orthogonal contrast tests are highly significant. The curves are all typical Type II functional responses; higher order components account for little or none of the variation (Appendix I contains the contrast coefficients used).

There was no highly significant effect of temperature on functional response. The

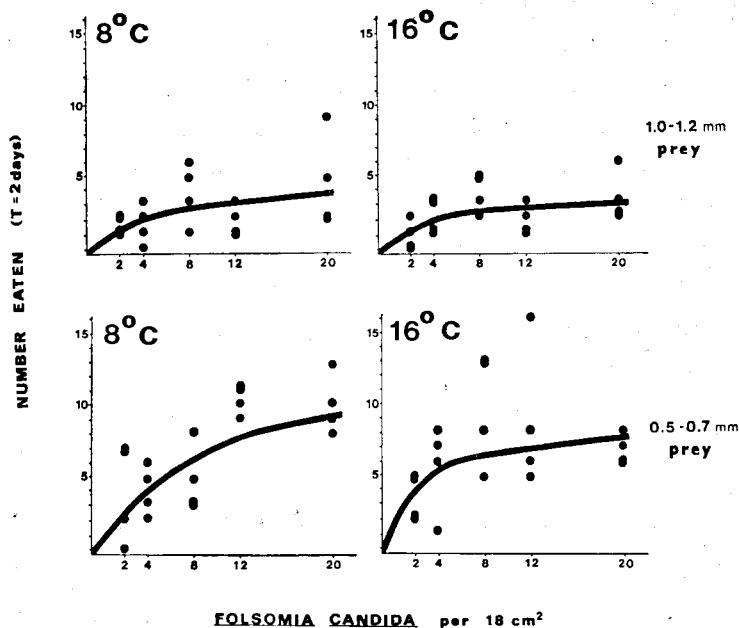


Fig. 1. Type II functional response curves for the two temperatures and two prey sizes. Estimates of the disc equation parameters are shown in Table 3.

Table 3. Estimates of handling time (Th) and attack rate (a) for different prey size and temperature treatments. Each estimate is based on 4 measurements taken on each of 20 pseudoscorpions.

| Prey size | Temperature | |
|-------------|-------------|------------|
| | 8°C | 16°C |
| body length | $Th = .45$ | $Th = .59$ |
| 1.0-1.2 mm | $a = .38$ | $a = .47$ |
| body length | $Th = .14$ | $Th = .24$ |
| 0.5-0.7 mm | $a = .68$ | $a = 1.72$ |

difference in number eaten as a function of density and size was only weakly altered by temperature (Table 1; Table 2b). This result is unlike those of THOMPSON (1978) and EVERSON (1980) who found that functional response parameters seemed to be sensitive to temperature. This difference in results may have arisen merely because 8 and 16°C are well within the range normally encountered by hunting pseudoscorpions. Higher or lower temperatures might alter attack rate and handling time. Preliminary results from an experiment not reported here in fact suggest that both attack rate and handling time are lower at 24°C than at 8 or 16°C.

Of the four main effects studied in the experiment, prey size accounted for most of the variability in gross numbers eaten, suggesting that a well-defined functional response to prey size distribution may exist. This effect was shown in detail by

THOMPSON (1975) for *Ischnura elegans*.

The results of individual degree of freedom tests on prey size relationships are shown in Table 2c. The linear components (overall rises) of the functional response to small prey and the functional response to large prey differ ($p=0.0283$). The quadratic components (shapes) of the curves also differ ($p=0.0140$). These differences are mainly due to the higher saturation level (T/Th) and attack rate (a) for small prey. More small animals are required to satisfy the predators' needs, and they are attacked at a higher rate.

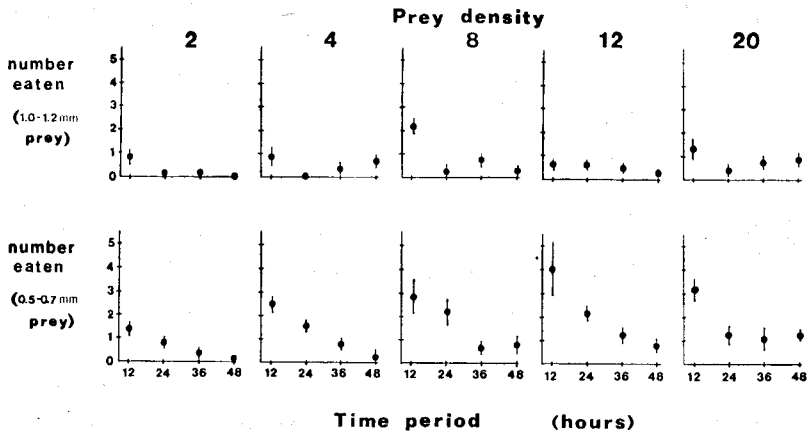


Fig. 2. Changes in the number eaten per 12 hours with changes in prey density, prey size and time. Standard error bars are shown. Each point is the mean of 8 observations (on 8 different predators).

Figure 1 represents the cumulative number of captures over a 48-hour period. There were, however, strong differences in the functional responses of individual predators over time. The changes through 48 hours in the numbers of prey eaten for the 5 prey densities and 2 prey sizes are shown in Figure 2. Recall that each pseudoscorpion was subjected to only one combination of the temperature-density-size treatments but that all were observed over the four time intervals. Figure 2 shows that captures were relatively high during the first 12 hours for most of the treatment combinations. Within the first 24 to 36 hours, the number of captures per 12 hours in most cases levelled off at a minimum. A number of pseudoscorpions were observed for further periods up to 84 hours, but in no case was any dramatic increase or decrease in captures observed in the later intervals (except where two pseudoscorpions were drowned in condensation on the container walls). In general, the change with time had strong linear ($p < 0.0001$) and quadratic ($p = 0.0007$) components with no significant higher degree trends ($p = 0.1065$; Table 2d). We hypothesized that temperature should change this relationship because of expected changes in activity, metabolism and nutritional needs of the predator, but this does not seem to have

happened (Time \times Temperature interaction, Table 1). Prey size, however, did cause a significant ($p=0.0007$) linear change in captures over time, as was expected. The change from the first 12-hour period to the last was greater for small prey, suggesting that the pseudoscorpions "adjust" to eating smaller prey.

II. Size-selection by the predators

The results of the two runs of the size-selection experiment were very similar, so the data were pooled. During the period allowed, the pseudoscorpions ate 26 of the 221 prey available (Figure 3). As in other experiments not reported here, none of the prey eggs were eaten. The data, though few, suggest a strong preference for prey individuals around 1 mm in length. We showed in the functional response experiments that *A. minimus* did not refuse the smaller prey when no choice was available. The equations of MANLY (1973, 1974) for Type Two Selection Experiments (without prey replacement) were used to estimate selectivity statistics. The probability, $\hat{\beta}_i$, that a prey individual from the i th size class would have been selected had there

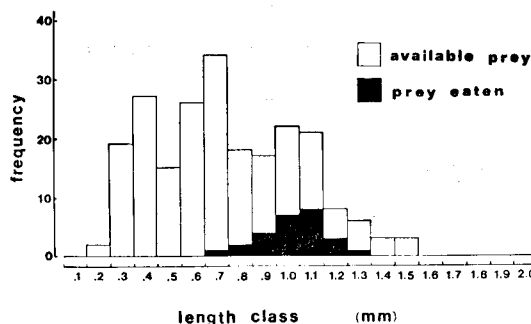


Fig. 3. Size frequency distribution of prey population available to *A. minimus* and the prey eaten.

Table 4. Selectivity statistics for length classes of prey.*

| Class | Pooled length classes | A_i | e_i | r_i | $\hat{\beta}_i$ |
|-------|-----------------------|-------|-------|-------|-----------------|
| 1 | 0.2, 0.3 | 21 | 0 | 21 | 0.0000 |
| 2 | 0.4, 0.5 | 42 | 0 | 42 | 0.0000 |
| 3 | 0.6, 0.7 | 60 | 1 | 59 | 0.0176 |
| 4 | 0.8, 0.9 | 35 | 6 | 29 | 0.1963 |
| 5 | 1.0, 1.1 | 43 | 16 | 27 | 0.4858 |
| 6 | 1.2, 1.3, 1.4, 1.5 | 20 | 5 | 15 | 0.3003 |

* MANLY'S (1973) $\hat{\beta}_i$ is calculated as

$$\hat{\beta}_i = \log(r_i/A_i) / \sum_{s=1}^K \log(r_s/A_s)$$

where A_i =the number of prey of class i initially available

e_i =the number of prey of class i eaten

r_i =the number of prey remaining

K =total number of size classes=6

been an equal number of individuals in each class is shown in Table 4.

Since *A. minimus* uses its large palpal claws to "pinch" the prey on the abdomen or prothorax, and quickly transfer them to the chelicerae, it is unlikely that the preferred prey size is determined by the maximum size that can be grasped by the foreleg as in the mantid *Hierodula crassa* (HOLLING, 1964; see also HOLLING *et al.*, 1976). We suspect that the size of prey is limited by the ability of the smaller chelicerae to hold and macerate it so that body fluids can be drawn off. But it is also possible, given the morphology of the palpal hand and the manner in which we have observed it being used to "feel" prey, that it is used to estimate prey size at the moment when the decision to attempt capture is made. We believe that a hunting pseudoscorpion first detects prey movement and then, as it reaches for the prey, roughly measures prey size with the pair of long tactile setae on the dorsum of the palpal hand ("pincer"). A decision to attack thus could be based on prey size, predator hunger, and perhaps other information, such as texture or smell. [We have noted that *A. minimus* refuses to eat *Onychiurus armatus* (Collembola) of similar size, shape, activity, and color to *F. candida*. WEYGOLDT (1969) suggested that there may be an olfactory receptor on the tip of the palpal fingers and a taste receptor near the preoral cavity which allow pseudoscorpions to recognize the unpalatable onychiurids.]

The size of prey that is preferred may change over a predator's lifetime. Casual observations of *A. minimus* nymphs suggest to us that these smaller sized predators (length < 1.5 mm) usually prefer smaller, though not necessarily proportionately smaller, *F. candida*.

GODDARD (1976) noted that the feeding response of the pseudoscorpion *Neobisium muscorum* is initiated by movement of the prey. Similarly, the observations of ERNSTING *et al.* (1977) show that movement of collembolan prey is necessary for their detection, pursuit and attack by the carabid beetle *Notiophilus biguttatus* F.. During period of relative inactivity, such as ecdysis, the prey are not detected by the beetle. The relative predation risk of prey species depends on the ratio of active and inactive individuals of a particular species (and other species present) as well as on relative densities (ERNSTING *et al.*, 1977). IWAO and WELLINGTON (1970) found that activity levels of the tent caterpillar, *Malacosoma californicum pluviale* (DYAR), influenced predation by the pentatomid bug, *Podius maculiventris* SAY. The consequences of movement by the more active larvae changed with the prey's instar. The predator was attracted by the movements of small active larvae but was unable to attack the active individuals successfully in later instars because their defensive movements were too vigorous.

We do not believe that size-selective predation by *A. minimus* is a direct function of prey activity. We have not seen any great differences in activity among old and young individuals, although older *F. candida* have a tendency to disperse farther and

faster than the younger instars. Sudden bursts of activity among its prey in some circumstances stimulate *A. minimus* to begin searching but there are many encounters in which the predator makes no attempt to capture moving prey. Sometimes, in fact, movements by the prey lead to flight by the pseudoscorpions. (Pseudoscorpions have their own predators, particularly centipedes; and JONES (1975) also documents spider predation on pseudoscorpions.)

The experiments on functional response demonstrate that *A. minimus* will feed on small *F. candida* if no adult prey is available, but the saturation number of prey eaten and the attack rate are consistently higher for small prey. When *A. minimus* can choose among various sizes of prey, however, it displays a well-defined preference for mid-size to large *F. candida*. Because these size classes represent different age classes with differing reproductive rates (see JOHNSON and WELLINGTON (1980a) for the age-size relationship), we believe that the predator's preference for larger prey has significant effects on the structure and attributes of natural populations. Additional observations suggest that *A. minimus* has the same type of size preference when feeding on *Lepidocyrtus* and *Isotoma* spp., other springtails in our study site. Because of their peculiar post-embryonic growth and developmental pattern, all springtail populations may be particularly vulnerable to the ramifying effects of size-selective predation.

SUMMARY

We investigated the functional response of the predaceous pseudoscorpion, *Apochthonius minimus*, to density of the springtail, *Folsomia candida*, as well as the effects of temperature and prey size on handling time and attack rate. Temperature slightly altered the overall rise in response. Both the rise and shape of the response differed for two prey sizes.

The changes in number of prey eaten over a 48-hour period were also examined, and the attack and feeding behavior of *A. minimus* was described and discussed in relation to the predation experiments. The pseudoscorpion preferred young adult *F. candida*, 0.8-1.2 mm in length, when offered prey in the range, 0.2-1.5 mm.

ACKNOWLEDGMENTS: We are grateful to Dr. G. W. EATON for assistance in calculating the contrast coefficients for the unequally spaced densities. We thank Dr. V. G. MARSHALL for the original stock that formed the basis of our *F. candida* cultures. The staff of the U. B. C. Research Forest were very helpful in providing a study site and relevant information. This research was supported by a Natural Sciences and Engineering Research Council of Canada grant to W. G. W. and a University of British Columbia Graduate Fellowship to D. L. J.

REFERENCES

- BENEDICT, E. M. (1978) A biogeographical study of currently identified Oregon pseudoscorpions with an emphasis on western Oregon forms. PhD. thesis, Portland.
- CHRISTIANSEN, K. (1970) Experimental studies on the aggregation and dispersion of Collembola.

Pedobiologia 10: 180-198.

- CHRISTIANSEN, K. (1971) Factors affecting predation on Collembola by various arthropods. *Annales de Spéléologie* 26: 97-106.
- EDWARDS, C. A., E. B. DENNIS and D. W. EMPSON (1967) Pesticides and the soil fauna: effects of aldrin and DDT in an arable field. *Ann. appl. Biol.* 60: 11-22.
- EVERSON, P. (1980) The relative activity and functional response of *Phytoseiulus persimilis* (Acarina: Phytoseiidae) and *Tetranychus urticae* (Acarina: Tetranychidae): the effect of temperature. *Can. Ent.* 112: 17-24.
- ERNSTING, G. and E. N. G. JOOSE (1974) Predation on two species of surface dwelling Collembola. A study with radio-isotope labelled prey. *Pedobiologia* 14: 222-231.
- ERNSTING, G., J. M. MARGUENIE and C. N. DE VRIES (1977) Aspects of behavior and predation risk of two springtail species. *Rev. Ecol. Biol. Sol.* 14: 27-30.
- GILBERT, O. (1951) Observations on the feeding of some British false scorpions. *Proc. Zool. Soc. Lond.* 121: 547-555.
- GODDARD, S. J. (1976) Feeding in *Neobisium muscorum* (LEACH) (Arachnida: Pseudoscorpiones). *Bull. Erit. arachnol. Soc.* 3: 232-234.
- GREEN, C. D. (1964a) The life history and fecundity of *Folsomia candida* (WILLEM) var *distincta* (BAGNALL) (Collembola: Isotomidae). *Proc. R. Ent. Soc. Lond. (A)*. 39: 125-128.
- GREEN, C. D. (1964b) The effect of crowding upon the fecundity of *Folsomia candida* (WILLEM) var *distincta* (BAGNALL). *Ent. Exp. Appl.* 7: 62-70.
- GREGOIRE-WIBO, C. and R. M. SNIDER (1977) The intrinsic rate of natural increase: its interest to ecology and its application to various species of Collembola. In: *Soil organisms as components of ecosystems*. *Ecol. Bull.* 25: 442-448.
- HOLLING, C. S. (1959) The components of predation as revealed by a study of small mammal predation of the European sawfly. *Can. Ent.* 91: 293-320.
- HOLLING, C. S. (1961) Principles of insect predation. *Ann. Rev. Ent.* 6: 163-182.
- HOLLING, C. S. (1964) The analysis of complex population processes. *Can. Ent.* 96: 335-347.
- HOLLING, C. S., R. L. DUNBRACK and L. M. DILL (1976) Predator size and prey size: presumed relationship in the mantid *Hierodula coarctata* SAUSSURE. *Can. J. Zool.* 54: 1760-1764.
- HUTSON, B. R. (1978a) Effects of variations of the plaster-charcoal method on a collembolan, *Folsomia candida*. *Pedobiologia* 18: 138-144.
- HUTSON, B. R. (1978b) Influence of pH, temperature and salinity on the fecundity and longevity of four species of Collembola. *Pedobiologia* 18: 163-179.
- IWAO, S. and W. G. WELLINGTON (1970) The influence of behavioral differences among tent-caterpillar larvae on predation by a pentatomid bug. *Can. J. Zool.* 48: 896-898.
- JOHNSON, D. L. and W. G. WELLINGTON (1980a) Post-embryonic growth of the collembolans, *Folsomia candida* and *Xenylla grisea*, at three temperatures. *Can. Ent.* 112: 687-695.
- JOHNSON, D. L. and W. G. WELLINGTON (1980b) Predation by *Apochthonius minimus* (Pseudoscorpionida: Chthoniidae) on *Folsomia candida* (Collembola: Isotomidae). II. Effects of predation on growing populations. *Res. Popul. Ecol.* 22: In preparation.
- JONES, P. E. (1970) The occurrence of *Chthonius ischnocheles* (HERMANN) (Chelonethi: Chthoniidae) in two types of hazel coppice leaf litter. *Bull. Erit. arachnol. Soc.* 1: 77-79.
- JONES, P. E. (1975) Notes on the predators and prey of British pseudoscorpions. *Bull. Brit. arachnol. Soc.* 3: 104-105.

- MANLY, B.F.J. (1973) A linear model for frequency-dependent selection by predators. *Res. Popul. Ecol.* 14: 137-150.
- MANLY, B.F.J. (1974) A model for certain types of selection experiments. *Biometrics* 30: 281-294.
- MARSHALL, V.G. and D.K. McE. KEVAN (1962) Preliminary observations of the biology of *Folsomia candida* WILLEM, 1902 (Collembola: Isotomidae). *Can. Ent.* 94: 575-586.
- MILNE, S. (1960) Studies on the life histories of various species of arthropod Collembola. *Proc. R. Ent. Soc. Lond. (A)* 35: 133-140.
- MUCHMORE, W.B. (1973) Ecology of pseudoscorpions: a review. In: *Proc. 1st soil microcomm. conf.*, Syracuse, N.Y., pp.121-127.
- OLIVIER, P.G. and P.A. J. RYKE (1969) The influence of citricultural practices on the composition of soil Acari and Collembola populations. *Pedobiologia* 9: 277-281.
- SIMON, H.R. (1966) Der Pseudoskorpionide *Neobisium muscorum* (LEACH) als Collembolenfeind. *Inst. Fur Natursch.* 8(3).
- SIMON, H.R. (1969) Der Mosskorpion *Neobisium muscorum* (LEACH) und seine Stellung im Okosystem. *Mitt. Pollichia* 3: 149-159.
- SNIDER, R. (1971) Laboratory observations on the biology of *Folsomia candida* (WILLEM) (Collembola: Isotomidae). *Rev. Ecol. Biol. Sol.* 10: 103-124.
- SNIDER, R.M. and J.W. BUTCHER (1973) The life history of *Folsomia candida* (WILLEM) (Collembola: Isotomidae) relative to temperature. *Great Lakes Ent.* 6: 97-106.
- THOMPSON, D.J. (1975) Towards a more realistic predator-prey model incorporating age-structure: the effects of predator size and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *J. Anim. Ecol.* 44: 907-916.
- THOMPSON, D.J. (1978) Towards a 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.
- USHER, M.B., B.C. LONGSTAFF and D.R. SOUTHALL (1971) Studies on populations of *Folsomia candida* (Insecta: Collembola). The productivity of populations in relation to food and exploitation. *Oecologia* 7: 68-79.
- USHER, M.B. and M. HIDER (1975) Studies on populations of *Folsomia candida* (Insecta: Collembola): causes of aggregation. *Pedobiologia* 15: 276-283.
- USHER, M.B. and C.F. STONEMAN (1977) *Folsomia candida*—an ideal organism for population studies in the laboratory. *J. Biol. Educ.* 11: 83-90.
- WEYGOLDT, P. (1969) *The biology of pseudoscorpions*. Harvard University Press, Cambridge, Mass.

APPENDIX I

When treatments are equally spaced, standard orthogonal contrast coefficients listed in most biometrics textbooks can be used. However, because of the need for realistic predator-prey ratios and for enough measurements to achieve acceptable precision and better allocation of effort in the ranges where parameters are changing rapidly, equally-spaced density treatments are not often employed in functional response experiments.

Coefficients for the density treatments used in our functional response experiment are shown below. Standard coefficients were used for the equally-spaced periods.

| Source of variation | X1 | X2 | X3 | X4 | Means | | | | | |
|---------------------|------|------|------|-------|-------|-------|------|------|------|------|
| | | | | | X5 | X6 | X7 | X8 | X9 | X10 |
| Coefficients: | | | | | | | | | | |
| Prey density | | | | | | | | | | |
| Linear | -18 | -13 | -3 | 7 | 27 | | | | | |
| Quadratic | 1059 | 155 | -981 | -1221 | 988 | | | | | |
| Cubic | -505 | 511 | 531 | -682 | 145 | | | | | |
| The rest | 64 | -135 | 120 | -54 | 5 | | | | | |
| Density × Size | | | | | | | | | | |
| Linear | -18 | -13 | -3 | 7 | 27 | 18 | 13 | 3 | -7 | -27 |
| Quadratic | 1059 | 155 | -981 | -1221 | 988 | -1059 | -155 | 981 | 1221 | -988 |
| Cubic | -505 | 511 | 531 | -682 | 145 | 505 | -511 | -531 | 682 | -145 |
| The rest | 64 | -135 | 120 | -54 | 5 | -64 | 135 | -120 | 54 | -5 |

フシトビムシの1種 *Folsomia candida* に対するカニムシの1種
Apochthonius minimus の捕食 I. 捕食率と餌の大きさの選択

D. L. JOHNSON • W. G. WELLINGTON

F. candida (被捕食者) の密度に対する捕食者 *A. minimus* の機能の反応を調べた。また餌処理時間と攻撃係数に対する温度と餌サイズの影響も調べた。温度はわずかではあるが、全体的に機能の反応が増すような効果を示した。機能の反応の増加と形は餌サイズによって違っていた。

48時間に捕食された餌の数の変化も調べた。*A. minimus* の攻撃と捕食行動について、捕食実験と関連して記述、議論した。体長0.2~1.5 mm の *F. candida* を与えたところ、*A. minimus* は若い成虫(体長0.8~1.2 mm) を選択的に捕食した。