PREDATION OF *APOCHTHONIUS MINIMUS* (PSEUDOSCORPIONIDA: CHTHONIIDAE) ON *FOLSOMIA CANDIDA* (COLLEMBOLA: ISOTOMIDAE) II. EFFECTS OF PREDATION ON PREY POPULATIONS

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INTRODUCTION

When age or size classes are easy to distinguish within a population, investigators can study the structural as well as the numerical consequences of selective predation for populations or for whole communities. For example, PAINE (1976) described a situation in which larger mussels escaped predation by starfish. GALBRAITH (1967) found that size-selective predation by trout and perch eliminated one large species of *Daphnia* and shifted size distributions of others to the smaller classes. BROOKS (1968) and BROOKS and DODSON (1965) reported a predator preference for larger species of Cladocera, with larger individuals being selected within each species. BROOKS (1968) found that prey survival time was inversely proportional to prey length, so that predation pressure shifted the species composition of the prey towards species with smaller body size. DODSON (1974) demonstrated how zooplankton associations are subject to size-selection at both ends of the size spectrum, and discussed the community consequences. ADDICOTT (1974) showed how the protozoan communities of pitcher plants are altered in relation to the distribution and density of predatory mosquito larvae.

Assessing these structural consequences of predation may be more difficult when age and size classes are superficially indistinguishable, or apparently unrelated. Among the insects and their near relatives, for example, such assessments may be restricted to the predator (BEDDINGTON and FREE, 1976; LeCATO, 1978; EVELEIGH, 1979). In constrast to most insects, however, the Collembola, because of their peculiar form of growth (JOHNSON and WELLINGTON, 1980a, 1980b) provide exceptional opportunities for assessing the structural as well as the numerical population consequences of selective predation. As before (JOHNSON and WELLINGTON, 1980b) we have exploited the preference of the pseudoscorpion, *Apochtonius minimus,* for certain sizes of *Folsomia candida* (Collembola), so that we could assess the population consequences of this selective predation.

METHODS

Objectives: to quantify the effects of predation on growth and age (size) structure

of *F. candida* populations and to test the hypothesis that the presence of predators results in reduced prey numbers.

A simple experiment with a completely randomized design was performed in which the only treatment was the presence or absence of adult *A. minimus*. Litter from the forest floor of the study site at the UBC Research Forest was dried at 60°C for 48 hours to kill and desiccate all microarthropods. Approximately 8 to 10 grams of this litter were added to each of 16 plastic pipe containers (I. D. 5 cm; length 10 cm), moistened, and incubated at 16°C for one day. Ten adults from *F. candida* laboratory stock (ranging from 1.0-1.2 mm in length) were added to each of the containers. (*F. candida* is parthenogenetic.)

The 16 containers were randomly divided into two groups: 8 had no predators and 8 received 3 adult *A. minimus* per container. The pseudoscorpions had been collected the day before at the study site (see JOHNSON and WELLINGTON, 1980b) and stored in incubators that mimicked the field environment.

The containers were covered at both ends with 54-micron plastic mesh held by snap-on rings and sealed with tape. Preliminary field trials and observations under a dissecting microscope showed that not even newly hatched *F. candida* could escape through the mesh. The containers were quickly transported in a humid, insulated cooler to the study site, laid on their sides, and covered with leaf litter until only the uppermost centimeter of their surface was exposed. Their positions were randomly assigned in a 2 m×2 m area shaded by 4 corner trees. Every two weeks the containers were checked for damage and appropriate humidity level. Temperatures at the litter surface were monitored with a 7-day thermograph in a shaded screen on the forest floor. After 46 days (enough time for about 3 generations of the prey) the containers were retrieved and returned to the laboratory in the insulated cooler. There they were extracted with a previously calibrated MACFADYEN (1961) high-gradient extractor which had a measured extraction efficiency of ~96% for *F. candida*. The springtails and pseudoscorpions were extracted over a 6-day period into cold picric acid, counted, and measured. The springtails were grouped into nineteen 0.1-mm size classes over the range, 0.2-2.0 mm (measured from the mouth to the posterior tip of the anal segment). The cylinders were weighed before extraction and again after drying at 70°C in order to estimate moisture content of the litter.

RESULTS AND DISCUSSION

Uncontrolled environmental variables

The temperatures of the litter surface ranged from 8.5 to 23.5°C during the experiment. Means and standard errors of the surface temperature at three-hour intervals for the first, middle and last week were 14.1±0.48, 16.1±0.46 and 14.5± 0.27°C. The range of surface temperature was not extreme (between 10 and 20°C), since the study site was well shaded. The temperature at a depth of 5 cm was not

continuously monitored, but was consistently 0.5-1.0°C cooler than the surface temperature whenever checked. Rainfall during the experiment was light, amounting to a total of 15.6 cm. Mean moisture (water loss as a percent of dry weight) of the litter and soil in the containers was 179.6±14.35. Per cent moisture at collection time did not differ between the 8 treatment (183.0±19.5) and the 8 control containers (176.2±22.4). Moisture content of the soil and litter plays an important role in the survival and structure of Collembola populations and communities (VERHOEF, 1977; ERNSTING, 1977). In this experiment, however, the differences in moisture were neither large nor correlated with population size, composition, or mean body length at collection time ($p > 0.3$). Moisture, population size, and mean and median lengths are shown in Table 1.

Table 1. Description of the final populations and contents of the containers at the end of the experiment.

Container number	Per cent moisture	Total no.	F. candida immatures (<.75 mm)	adults (>.75 mm)	mean length (variance)	median length	remaining predators
Control populations:							
1	66.67	136	48	88	.845(.070)	.872	—
2	162.50	202	94	108	.816(.123)	.779	—
3	196.00	86	23	63	.987(.096)	.998	—
4	216.67	91	12	79	.986(.042)	.985	—
5	198.33	132	67	65	.817(.120)	.710	—
6	164.81	438	170	268	.843(.061)	.881	—
7	206.25	6	0	6	1.23(.016)	1.22	—
8	252.94	243	133	110	.743(.100)	.683	—
Populations with predators:							
9	283.54	371	179	192	.780(.058)	.758	3
10	109.14	0	0	0	(Extinct)		1
11	215.63	215	101	114	.821(.081)	.779	2
12	203.77	440	193	247	.827(.078)	.803	3
13	198.55	0	0	0	(Extinct)		0
14	125.61	0	0	0	(Extinct)		0
15	177.05	0	0	0	(Extinct)		1
16	115.63	206	143	63	.664(.065)	.596	3

Interpretation of length-frequency distributions

Several of the length-frequency distributions of the populations that survived the predation treatment (Figure 1) and of the control populations (Figure 2) tended to be bimodal. Normally, size-frequency distributions of Collembola populations could be expected to be nearly continuous, because the insects can lay eggs through most of their lives (from the 6th to the 40th instar according to SNIDER, 1971). The bimodal form of the distributions shown here is a result of the fact that the starting populations were composed entirely of adults. Most of the distributions shown here therefore must include at least three generations: the original adults, their offspring, and the
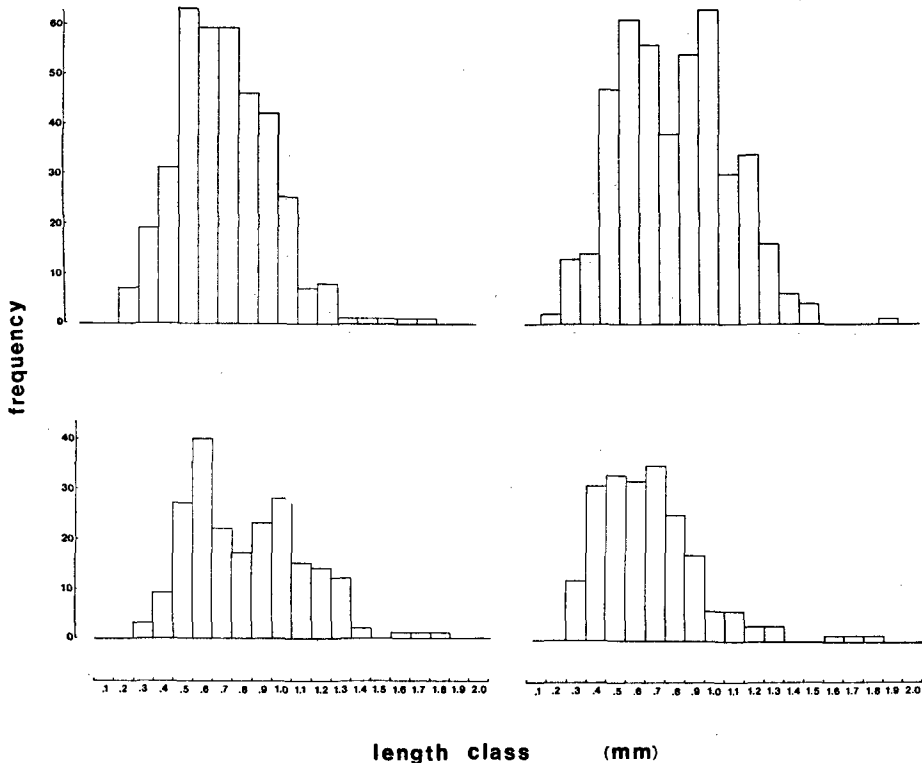
length class (mm)

Fig. 1. The distribution of length in the four populations that
survived the predation treatment.

last wave of juveniles to occur before the field containers were returned to the
laboratory.

There was great variability in the total number of individuals per container, as
might be expected when the experimental units are confined, growing populations.
This high variance may be due to: (1) the sensitivity of populations to changes in
their structure or quality (as in *Tribolium*, MERTZ, 1969) ; (2) the treatments
themselves [as with the variabilities in size and yield examined by WATT (1955),
USHER et al. (1971), SLOBODKIN and RICHMAN (1956) and HOPPENHEIT (1975)]; or
(3) uncontrolled environmental influences or undetected differences in exploitation rates.

In all but container #7, final population size ranged between 86-440. There was
scarcely any reproduction in container #7. It is possible that undetected adverse
environmental influences or fungal growth affected the fecundity and survival of the
springtails in this container. The following analyses accordingly take this possibility
into account, by including and then excluding #7.

The presence of the pseudoscorpions markedly affected the probability of survival
of the prey populations. Four of these populations became extinct (Table 1). In
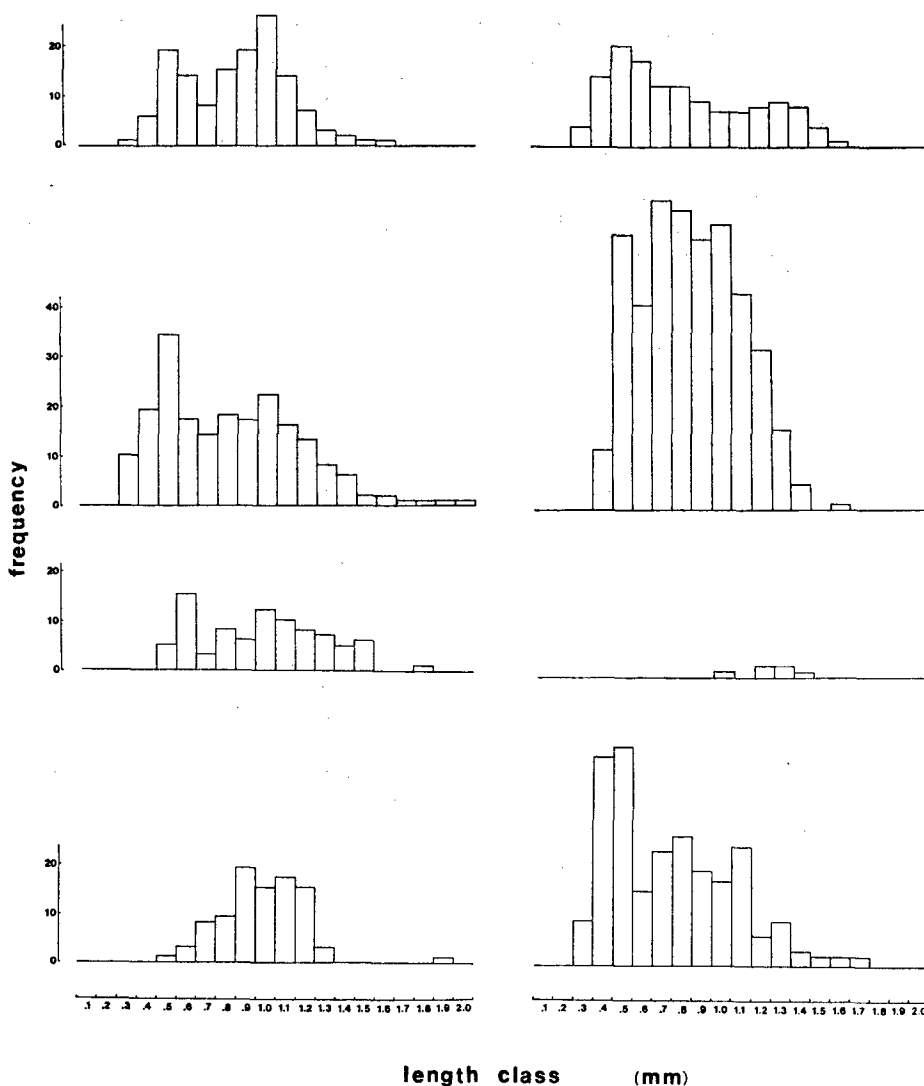these cases, the pseudoscorpions probably managed to find most or all of the original

length class (mm)

Fig. 2. The distribution of length in the eight control populations.

springtails before they could reproduce; e. g., in contrast, none of the 8 controls became extinct. But the other four experimental populations that survived along with their predators produced an unexpected result: these four were among the largest of the surviving collembolan populations (Figures 1 and 2). Although the total numbers (ignoring size classes) do not differ significantly between the treatment and control groups $(0.1 < p < 0.2)$, the numbers of surviving immatures do.

The findings of MARSHALL and KEVAN (1962), SNIDER (1971), SNIDER and BUTCHER (1973) and JOHNSON and WELLINGTON (1980a) suggest that *F. candida* begins oviposition in the 6th instar, when individuals usually vary from 0.7-0.8 mm in length and are about 16-21 days old. MARSHALL and KEVAN (1962), HUTSON

(1978), and SNIDER and BUTCHER (1973) have shown that age at first oviposition may vary with temperature, pH and genetics. Table 1 shows totals for length classes 0.2 to 0.7 mm (immatures) and 0.8 to 2.0 mm (adults). The populations surviving predation have more immatures than the controls ($p=0.048$; or $p = 0.03$ if #7 is included). Since the majority of the "immatures" in each container must be members of the most recent generation, this difference, though not large, is worth noting. Relative frequencies of the size classes are shown in Table 2.

Table. 2. Relative frequencies (% of total) of different sizes of
F. candida in the 16 populations.

| Container No.	SIZE CLASS (mm)																		
	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	1.5	1.6	1.7	1.8	1.9	2.0
1	0.0 0.7	4.4	14.0	10.3	5.9	11.0	14.0	19.1	10.3	5.1	2.2	1.5	0.7	0.7	0.0	0.0	0.0	0.0
2	0.0 5.0	9.4	16.8	8.4	6.9	8.9	8.4	10.9	7.9	6.4	4.0	3.0	1.0	1.0	0.5	0.5	0.5	0.5
3	0.0 0.0	0.0	5.8	17.4	3.5	9.3	7.0	14.0	11.6	9.3	8.1	5.8	7.0	0.0	0.0	1.2	0.0	0.0
4	0.0 0.0	0.0	1.1	3.3	8.8	9.9	20.9	16.5	18.7	16.5	3.3	0.0	0.0	0.0	0.0	0.0	1.1	0.0
5	0.0 3.0	10.6	15.2	12.9	9.1	9.1	6.8	5.3	5.3	6.1	6.8	6.1	3.0	0.8	0.0	0.0	0.0	0.0
6	0.0 0.0	2.7	12.6	9.4	14.2	13.7	12.3	13.0	9.8	7.3	3.7	1.1	0.0	0.2	0.0	0.0	0.0	0.0
7	0.0 0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7	0.0	33.3	33.3	16.7	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0 3.7	17.3	18.1	6.2	9.5	10.7	7.8	7.0	9.9	2.5	3.7	1.2	0.8	0.8	0.8	0.0	0.0	0.0
9	0.0 1.9	5.1	8.4	17.0	15.9	15.9	12.4	11.3	6.7	1.9	2.2	0.3	0.3	0.3	0.3	0.3	0.0	0.0
10	(Extinct)																	
11	0.0 1.4	4.2	12.6	18.6	10.2	7.9	10.7	13.0	7.0	6.5	5.6	0.9	0.0	0.5	0.5	0.5	0.0	0.0
12	0.5 3.0	3.2	10.7	13.9	12.7	8.6	12.3	14.3	6.8	7.7	3.6	1.4	0.9	0.2	0.0	0.0	0.2	0.0
13	(Extinct)																	
14	(Extinct)																	
15	(Extinct)																	
16	0.0 5.8	15.0	16.0	15.5	17.0	12.1	8.3	2.9	2.9	1.5	1.5	0.0	0.0	0.5	0.5	0.5	0.0	0.0
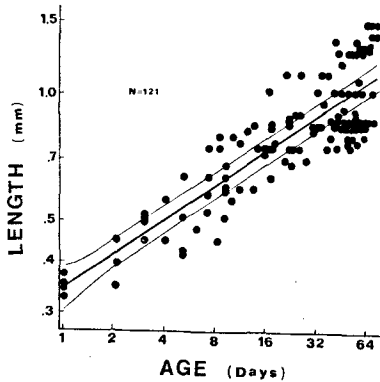
Fig. 3. The relationship between length and age of *Folsomia candida* raised at 16°C. [The regression is ln(length) = 5.853 +0.271 (ln(age)), $r^2=0.749$. The regression line is bounded by 99% confidence intervals for the estimated mean ln(length). (from JOHNSON and WELLINGTON, 1980a.)]

We previously recorded lengths of *F. candida* (from the same populations as those used in this experiment) over 75 days at three fluctuating temperatures (with means of 8, 16 and 24°C; JOHNSON and WELLINGTON, 1980a). Figure 3 shows the age-length relationship at a mean temperature of 16°C (12 hours at 14°C, 12 hours at 18°C). Although fecundity and longevity may be overestimated in such laboratory studies, our subsequent confirmatory investigations with another population suggest that the age-length relationship for this species is, in fact, relatively inflexible, so that the relationship shown in Fig. 3 should adequately represent growth rates of individuals under natural conditions.

Some arthropod populations have been shown to adjust mean length and weight in relation to population density (PETERS and BARBOSA (1977)). HOPPENHEIT (1976) has shown that mean weight and length of adult copepods may be inversely related to mean population density, but GREEN (1964b) found no difference between the rate of development of isolated *F. candida* individuals and those in mass cultures. We therefore assume that the springtails in all 16 confined populations grew at the same rate, and that the frequency distributions of their lengths do not include any density-induced changes in length at any age. In fact, the method we used should have prevented such changes, since we started each of our experimental populations with 10 adults, and the final densities of the surviving populations did not vary appreciably at the end of the experiment.

One might also argue that the small number of individuals in the younger classes (0.2-0.4 mm in length) merely implies that all of these populations were either declining or losing a previously dominant age class as the young matured (DAPSON, 1971 ; TANNER, 1978). Alternatively, this small number might be explained by TAKEDA's (1973, 1979) discovery that the efficiency of the MACFADYEN high gradient extractor is low for very small springtails. (Although he could estimate larger size classes of *Folsomia octoculata* reasonably well with this equipment, TAKEDA found that his estimates of classes < 0.5 mm had to be corrected by multiplying by 6.) Thus it might be argued that our young *F. candida* might also have been underestimated during extraction. If this were so, however, all of our populations should have been similarly affected. The differences in the numbers of immatures shown in Tables 1 and 2 and Figures 1 and 2 therefore must reflect a real difference between the treatment and the control groups, so they have not been adjusted.

Preliminary experiments by USHER *et al.* (1971) showed that *F. candida* populations in 15.7 cm² culture vials grew rapidly at first and then stabilized after 10-15 weeks, at 700-1300 individuals, probably because of limited competition for space and food. This finding roughly agrees with our observations of *F. candida* cultures in 18 cm² pots. We suspect that the confined populations used in our experiment were at or near similar limits. There are empirical and theoretical grounds (see WATT (1968) and EMLEN (1977) for discussion) which suggest that populations which are near

environmentally imposed limits may increase their productivity if they are exploited. The magnitude of any such increase in productivity would depend on the rate of exploitation and the age distribution of the survivors. In effect, the degree to which the additional exploitation might reduce competition, together with the number of individuals surviving density-independent mortality, would set the new production rate.

In such situations, the type of individual which survives to reproduce is as important as the number. MERTZ (1969) has drawn attention to the correspondence between methods which use behavioral and physiological types to determine population quality (WELLINGTON, 1964) and methods which analyze insect populations according to age-groups. Both types of study are concerned with population quality and with the contributions of different types of individuals to the performance of the total population. MERTZ has shown that behavioral differences among *Tribolium castaneum* adults of different ages may be as important as physiological and reproductive differences between instars. For example, there are striking differences in the rates at which different adults eat eggs; beetles 45-135 days old are most effective in preventing outbreaks. Thus if a predator fed preferentially on beetles in this age group the end result might be a higher, rather than a lower, population density. Certainly, productivity would temporaily increase. Our data suggest that the larger springtails in our containers were exerting comparable pressures, direct or indirect, on the immature members of the confined populations, all of which were near their environmental limit. Thus when the pseudoscorpions ate the larger individuals, more immatures were able to survive, and the mean age (length) of the experimental populations decreased in relation to the mean age of the controls.

The actual dynamics of exploited populations differs greatly from calculated values that are obtained by ignoring age- and size-structure. WATT (1955) measured the productivity and standing crop of populations of the flour beetle *Tribolium confusum* at different rates of exploitation of different stadia, and found that the regimen producing the optimum yield was one in which only a small number of adults were left behind. Because of such age-related factors, the maximum sustained yield differed greatly from that predicted by a logistic equation. In fact, the age composition that would ultimately produce the *maximum* number of adults was one from which adults were initially absent. NICHOLSON (1954) observed a similar response after removing 99% of the adult blowflies from his experimental population. And SLOBODKIN and RICHMAN (1956) also found that age structure greatly influenced the response of exploited populations of *Daphnia pulicaria*. In short, before the effects of further exploitation of populations can be gauged, one must know the effects of age structure on productivity, and the probable age distribution after harvest (WATT, 1955). *A. minimus* preys upon *F. candida* in the 0.7-1.3 mm range when these individuals are available (JOHNSON and WELLINGTON, 1980b). The effects of this size-selective predation on the productivity of the surviving age classes thus will depend on the

behavior and reproductive value of this exploited age class as well as on any density-related changes in fecundity.

GREEN (1964a) found that laboratory populations of *Folsomia candida* attained their maximum fecundity when available space per individual neared 1.2 cm². Reduced fecundity at higher densities was due to: (1) the complete inhibition of oviposition by some individuals; (2) a general reduction in the number of eggs laid by others, and (3) a reduction in the duration of oviposition. GREEN suggested that "jostling" and general interference with oviposition among crowded adults were contributing factors. Although the number of *F. candida* with ovaries reduced in size was the same in dense and less dense populations, a greater proportion of individuals were capable of ovipositing in the sparser populations (judging by the appearance of the genital aperture). Cannibalism was equally high in dense and less dense populations in GREEN's experiments. Average losses usually approached 2 eggs per animal per day (usually 11-18% of the total number of eggs).

GREEN was also able to show that crowding during early life, conditioning of the substrate, competition for food, and competion for oviposition sites did not significantly affect fecundity. His data on fecundity versus density show an "Allee" pattern (FUJITA, 1954) in which fecundity is maximal at some low to intermediate density. [It is not clear why a parthenogenetic insect should exhibit this type of pattern instead of a simple monotonic decreasing function of density ("*Drosophila* type") or an effect at high density only ("intermediate type", WATT, 1960). Aggregation has been shown to be important in the ecdysis and subsequent reproduction of sexually reproducing species of Collembola (VERHOEF and NAGELKERKE, 1977). Perhaps aggregation could stimulate oviposition even in parthenogenetic species.]

The possibility of an Allee effect on fecundity offers an alternative explanation of the extinctions, as well as the relatively large populations, that occurred in our experimental containers. If predation by *A. minimus* on the original *F. candida* adults in these containers held the prey numbers below 0.5 individuals per cm² (cf. GREEN's data) during the initial stages of population growth, fecundity would drop below the recovery level, and such populations would, perforce, become extinct. On the other hand, slightly higher densities (equivalent to 0.5-2 individuals per cm²) would allow much higher fecundity in the surviving treated populations than the greater crowding in the unchecked control populations would permit. If such an effect did occur in our experimental populations, the mean length of their individuals would be reduced by the second or third generation because of the larger number of juveniles those populations would then contain. (In fact, as long as there were fewer adults in the experimental containers than in the controls during the first two generations, this result could still be obtained, even if the numbers of adults were nearly equal by the end of the three generations.) Since this scenario could have led to our results, its underlying hypothesis should not be rejected until it can be tested further. The mean

length of the springtails in the four populations that survived predation was only 0.784 mm (n=1232, SD=0.300), whereas the individuals in the eight control populations had a mean length of 0.839 mm (n=1334, SD=.271; see also Table 1). The difference is highly significant ($p < 0.001$) whether or not container #7 is included (if excluded, the mean length of the controls is 0.837).

USHER et al. (1971) performed a series of removal experiments to test the hypotheses that productivity of F. candida populations would increase with increasing exploitation, that selective exploitation would result in higher productivity than non-selective exploitation, and that the availability of food would change the relationship of productivity to exploitation. They found that, in general, exploitation increased production because reproduction increased, although differences among standing crops at different rates of exploitation were not significant. Increasing the proportion of adults removed from one- to two-thirds every two weeks increased both the numerical and biomass production by 150%. (If the same increase in exploitation rate was applied non-selectively to the total population, numerical production increased by 50% and biomass production increased only 10.5%).

Relatively high rates of exploitation also resulted in shorter mean body length, because the competitive barriers to reproduction were relaxed when more of the older individuals were removed. As noted earlier, this latter response might explain the relatively high numbers of animals and the reduced mean lengths recorded in our experimental populations. Selective exploitation of the adults by the pseudoscorpions would be followed by increased fecundity (or egg and juvenile survival) among the remaining springtails. Although such populations might not change much numerically, at the end of 46 days they would have the large number of juveniles and the short mean lengths that were described above.

SUMMARY

This study utilized the preference the pseudoscorpion, A. minimus, displays for certain sizes of the springtail, F. candida, in order to assess the population consequences of this selective predation. Although predation drove half of the treated collembolan populations to extinction, the populations which survived were not reduced in size and were in fact larger than most of the control populations (Figs. 1 and 2). During the first two weeks of the experiment, the predators apparently fed mainly on the original adults and the larger individuals of the second generation, thus increasing available space and improving the prey's chances for successful reproduction. The resulting demographic shift accounts for the significant decrease in mean length that occurred in the experimental populations without any accompanying significant change in their total numbers. Some effects of density, food, and age-structure on the fecundity of F. candida, acting in concert with the effects of size-selective predation, may lead to a variety of population consequences. In some circumstances, predation may cause

increased production with decreased mean size, and no drastic change in standing crop. In different circumstances, a local population may become extinct. These results should further our understanding of the sporadic record of establishment and growth displayed by springtail populations in the small, moist litter patches where they tend to aggregate.

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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 II. 餌種個体群に対する捕食の影響

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ある範囲のサイズの *F. candida* を選択的に *A. minimus* が捕食するが，このことを用いて，選択的な捕食が餌種個体群におよぼす影響を調べた。捕食の結果半数の個体群は絶滅したが，生き残った個体群では個体群サイズの減少はなく，捕食者を除いた大部分のコントロールの個体群よりもむしろ大きくなった。実験を始めてから最初の2週間では，最初に与えた成虫と第2世代の大きい個体を主に捕食した。このため餌種の利用空間は増加して，増殖のチャンスが増えた。したがって，平均体長が減少した。*F. candida* の産卵におよぼす温度，食物，令組成の影響は，捕食のさいの餌サイズの選択による影響とともに，個体群の結末の多様化をもたらすと思われる。ある場合には，平均体長の減少で，現存量を変えずに生産を増やすかもしれない。また他の場合には，局所的な個体群の全滅が起るかもしれない。これらの結果から，湿り気の多い落葉枝に小パッチ状に集まる *F. candida* の個体群において，散在的に見られる本種の生息や成長を説明できるはずである。