CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

PAIRWISE COMBINATIONS OF SEVEN SPECIES OF COLLEMBOLA IN CULTURE

A thesis submitted in partial satisfaction of the requirements
for the degree of Master of Science in Biology

by

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ABSTRACT

PAIRWISE COMBINATIONS OF SEVEN

SPECIES OF COLLEMBOLA IN CULTURE

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Seven species of Collembola extracted from litter samples from Ventura County and Los Angeles County, California were cultured in the laboratory, and were used for studies of increase in numbers in monoculture and pairwise combinations. Species studied were identified as: *Lepidocyrtus* sp. J, *Lepidocyrtus fimicolus* Mari Mutt, *Folsomia similis* Bagnall, *Hypogastrura (Hypogastrura) essa* Christiansen and Bellinger, *Onychiurus (Protaphorura) encarpatus* Denis, *Proisotoma (Ballistura)* sp. A, and *Onychiurus (Onychiurus) folsomi* Schäffer. Population increase in monocultures was monitored and graphed for a three-month period for each species. Although the natural log increase of collembolan species fell into three rate categories (high, medium and low), the rates during the mid-period differed little. Differences in rates of increase occurred primarily in the initial period and plateau period. Results indicated that temperature, humidity, diet, and substrate conditioning affect the numbers attained and their variability. An additive design of pairwise combinations was made for a two-month period, and the majority of the combinations experienced a significant decrease in one or both of the species

when compared to its respective control. A ranking was developed indicating the extent to which each species was affected by the presence of another species

and not necessarily its dominance in combination. A second ranking obtained from the frequency of dominant groups in pairwise combinations was roughly equivalent to the monoculture ranking for rate of increase. Two trials were done involving substrate conditioning, and the results are discussed in relation to microorganisms and semiochemicals in the culture habitat.

INTRODUCTION

The study of community relations with Collembola has been done by utilizing field studies, microcosms and laboratory pairwise studies. Field studies give the most accurate information about communities, but are complicated to analyze. At the other extreme, pairwise studies as used in this investigation are easier to control, but their relationship to the community is difficult to interpret. Regardless of how Collembola are studied, their distributions will be aggregated. The aggregations serve to protect against desiccation (Joosse, 1970) and to enhance reproductive success (Joosse, 1970; Schaefer, 1991) and microbial processes (Schaefer, 1991). Species specific, weakly volatile pheromones have been suggested as being responsible for aggregation, and the failure of Collembola with amputated antennae to aggregate supports this proposal (Verhoef, Nagelkerke and Joosse, 1977). Studies involving the effect of such chemical factors, along with direct interactions, were done as a Master's dissertation at California State University Northridge by Marlon Van Cott (1982) and subsequently by Christiansen, Doyle, Kahlert and Gobaleza (1992).

In his dissertation, Van Cott studied interspecific competition defined as depressed fitness or a "reduced intrinsic rate of natural increase or reduced carrying capacity of the environment" (Van Cott, 1982). Van Cott used five species of Collembola (*Entomobrya (Entomobryoides) guthriei* Mills, *Cryptopygus thermophilus* Axelson, *Pseudosinella sexoculata* Schött, *Sinella (Sinella) curviseta* Brook, and *Proisotoma (Ballistura) schoetti* Dalla Torre) in his laboratory study of population growth in collembolan cultures of single species, paired species, and single species in culture dishes with the substrate conditioned by another species. Van Cott also made comparisons of egg laying,

duration until hatching, and noted the absence of egg predation by other species in the study.

In the Christiansen *et al.* (1992) study of four species of Collembola (*Folsomia candida* Willem, *Xenylla grisea* Axelson, *Sinella caeca* Schött and *Pseudosinella violenta* Folsom), the authors reviewed previous investigations of interspecific interactions between paired collembolan species in culture, including the work of Van Cott. Christiansen *et al.* noted that the interactions between species of Collembola in culture may stimulate or inhibit their growth and may change with conditions in the culture. Consequently, Christiansen *et al.* took care not to label the type of interactions between paired species as competition, but referred to these as interspecific interactions. Furthermore, in addition to investigating the direct interactions between paired species and the effect of conditioning the substrate by another species, Christiansen *et al.* added a third component to their investigation: airborne factors. Christiansen *et al.* prepared dual chambers separated by screen-covered holes that allowed airborne chemicals, but not individuals, to pass between the two sides.

The initial concept of this work was to do similar trials with collembolan species as Van Cott (population growth in cultures of single species, paired species, and single species in culture dishes with the substrate conditioned by another species), with the addition of the airborne factors in the work of Christiansen, *et al.* The trials of single and paired species population growth were done, but when these were analyzed, the type of the substrate conditioning trial was changed. The airborne factor trial has not been done for reasons explained in the discussion.

MATERIALS AND METHODS

Species Used

All species used in this work, with the exception of one of the *Lepidocyrtus* species, were isolated from avocado leaf litter collected in Ventura County by Marlon Van Cott in September, 1993. The sole species of *Lepidocyrtus* not from Ventura County was a darker, banded one identified as *Lepidocyrtus fimicolus* Mari Mutt by Christiansen (personal communication, 1995). This species was collected from compost in Northridge, California and is also referred to in this work as *L.* sp. #2 or Group #2. It was similar in appearance to the *Lepidocyrtus* species from Ventura County, which was lighter in color and not as distinctly banded. The Ventura species is referred to as *L*. sp. #1, or Group #1, and was also identified by Christiansen (personal communication, 1995) as *Lepidocyrtus* sp. J. A preliminary test of whether the two species would interbreed was made with twelve individuals of each species reared in individual 1 oz. containers with plaster/charcoal (as described below) and then coupled in the same container as same or different species.

Other species collected and used in this work were identified as: *Folsomia similis* Bagnall, *Hypogastrura (Hypogastrura) essa* Christiansen and Bellinger, *Onychiurus (Protaphorura) encarpatus* Denis, *Proisotoma (Ballistura) laticauda* Folsom, and *Onychiurus (Onychiurus) folsomi* Schäffer. The *Ballistura* species was subsequently noted to differ from *B. laticauda* in having a smaller eye, shorter unguicular filaments, and no ungual tooth. There were also differences in thoracic and abdominal chaetotaxy. It is referred to subsequently as *P. (Ballistura)* sp. A (Christiansen, personal communication, 1996). All the species were referenced by numbers in experimental trials. As mentioned previously, the

two *Lepidocyrtus* species were numbered 1 and 2. The other species were numbered respectively as 3, 4, 6, 7, and 9. These numbers were not entirely sequential because there were several other species with which this work started that were not included. These were not as hardy as the above species under the culture conditions and were lost during a hiatus caused by the Northridge Earthquake in January, 1994. Only the cultures in lidded baby-food-jar containers survived this period. The lost species were tentatively identified as *Isotoma (Desoria) notabilis* Schäffer, *Isotomurus (Isotomurus) tricolor* Packard, *Sphaeridia pumilis* Krausbauer and possibly a new, unnamed species of *Brachystomella* Agren.

Culture Methods

Specimens were separated into a container with cured and remoistened plaster of paris/charcoal under a Tullgren funnel over which an incandescent lamp was placed just above the sample. The soil fauna collected in this manner were floated in water, then removed immediately from the surface of the water and placed in culturing containers also containing moistened plaster of paris/charcoal in a 9 to 1 ratio. A small loop about the size of a 3 mm inoculating loop was fashioned from an insect pin, inserted in a wooden handle, and used to remove individuals from the surface of the water. This method was preferred to either aspiration or transfer with a brush. Often the Collembola would jump from a brush during transfer, but would remain on the film of water within the loop during the process and were then transferred into the culture container with a flick as if to remove an ash from a cigarette. After attempting aspiration by mouth for manipulating soil organisms, it was determined that this was a most insalubrious method. For later work, a suction device was made from a Stansport

brand bellows foot pump on which a glass eyedropper tube with the larger end covered with nylon mesh was attached to the tubing that is supplied with the pump. The culture containers used initially were either finger bowls (3.5 cm x 10 cm) of the sort used by Van Cott or baby food jars, the bottom of which were filled with 1 cm of hardened 9:1 plaster/charcoal. These containers were either covered with 0.5 mil plastic wrap affixed with a rubber band or, in the case of some of the baby food jars, covered with the jar lid. The charcoal used in the mixture was 50% animal bone black (Spectrum) and 50% activated charcoal. The dry powder was mixed thoroughly and then heated to 120 degrees Celsius for one hour and cooled. Bottled distilled water was boiled and cooled and mixed with the dry mixture in an approximate ratio of 2 parts dry ingredients: 1 part liquid by volume so that the consistency was that of a thick milkshake. An Eberhard Faber brand Pink Pet™ rubber eraser (11 mm in thickness) was used not only to gauge the height for filling containers but also as a focusing point for adjusting a camera to photograph culture surfaces. Once hardened, culture dishes were placed under a UV germicidal lamp for several hours and then stored for a minimum of 48 hours. Prior to use, containers were moistened with distilled water until they would not readily absorb additional moisture, but no liquid was apparent on the surface.

The Collembola were fed on Fleischmann brand active dry baker's yeast (*Saccharomyces cerevisae*) in the approximate ratio of one granule per twenty individuals, except in trials of another food source. The yeast was added dry with a V-shaped, stainless micro-spatula (No. 9008 Arthur H. Thomas Company, Philadelphia, PA). Cultures were watered weekly to maintain humidity. Cultures were also kept in larger storage containers with transparent fronts that could be closed or propped open to adjust humidity. Moldy food and dead individuals were removed prior to feeding by gently scraping the surface of the plaster. An

implement was fashioned for this purpose from a flattened jumbo size wire paper clip that had been inserted into a small rigid tube cut from the plastic shaft of a cotton swab. The tip of this scraper was dipped into 91% isopropyl alcohol and then heated in a flame prior to cleaning the culture. A 0.15% solution of methylparabin mold inhibitor (Carolina Biological) was applied to the substrate to control mold but was discontinued when these cultures did not thrive after application. Glass squares made from 2 mm window glass cut to 10 cm lengths were used singly as a cover during maintenance of cultures or observation under the stereomicroscope. A set of ten glass covers was made so that clean covers could be used for each culture to insure that this was not a means of contamination between cultures. In addition, when Collembola were picked up by aspiration, the glass eye dropper tube on the suction device was dipped in boiling water between use on different species or after handling a contaminated culture. Starting in 1995, a Honeywell brand enviracaire^{r} HEPA portable air cleaner model 10500 was used in the room with the cultures to reduce airborne contamination. The air filter was on a 12 hour on/off timing cycle along with an incandescent lamp to provide diffuse lighting to the cultures during this period. The lighting was used so that conditions would be more uniform because the room that contained the cultures was also used as an office, workroom and laboratory.

Experimental Containers

The experimental containers used for most work were 2 oz. polystyrene Iris® brand souffle cups and lids. These cups have tapered sides for viewing from above and are about 57 mm in diameter at the top, a size comparable to that of containers used by other researchers. These are also inexpensive. Their

disadvantages are that they hold a considerable static charge if handled when dry and that they lose moisture more rapidly than some other containers. Evaporation from the 2 oz. souffle cups was tested by filling a number of cups with 10 ml of water and measuring these during subsequent weeks. The static is greatly reduced by spraying the backs with Static Guard^{TM} brand static spray. This treatment, however, was not used on the experimental containers. With careful handling and moistening, the static was not an insurmountable problem.

A special pheromonal/allomonal container was designed for the airborne portion of this work. This container was to consist of two equally sized, clear polystyrene boxes with lids, made by Amac Plastic Products, Sausalito, CA., which were square in the base and rectangular on the sides. A 9.5 mm hole was drilled on the center-line of one side of each box 28.5 mm from the base. Nylon mesh with 90 micrometer openings in the mesh was to be cut to a size larger than the holes and sandwiched between the two boxes that were to be held together with acrylic cement. Control boxes were to be prepared in exactly the same manner except for the drilled holes. This design was intended to produce a container with closely fitting removable lids along with a mesh-covered airway between the two sides. Boxes 30 mm at the base were selected initially, but upon the suggestion of Dr. K. Christiansen, a larger box with 41 mm base was purchased for construction by the CSUN Biology Shop. Materials for this project were given to the Shop prior to the Northridge Earthquake. These boxes were drilled by the CSUN Science Shop in August 1996, but the finished boxes have not been constructed, so no trials with these boxes can be included here. Preliminary work with single boxes is described in the results.

Photographic Methods

Macro photographs were taken with a Canon FT QL 35 mm manual

camera with Fujichrome ASA 100 positive film . The camera body was equipped with a Kiron 70-150 mm f/4 macro lens preceded by a 35 mm extension tube for focusing at approximately 70 cm from the surface. Dual Vivitar #283 flash units with white cloth diffusers placed 40 cm from the surface were used for lighting, and most photographs were taken at f/16 at 1/30th second. Microphotographs were also made to show the features of the Collembola. Stereomicrophotographs were made at 30X total magnification on a Nova stereomicroscope using a Cabisco #60-3310 adapter on the Canon FT. At first, the uncovered Vivitar flash units were angled at 45 degrees approximately 20 cm from the specimen. A fiber optic illuminator was used subsequently, as the exposure could be determined through the lens with this type of illumination. Kodak EPT 160 film was used when photographing with the fiber optic illuminator.

Counting Trials

Initial observations of cultures were made by transferring 20 adults of each species into 2 oz. souffle cups prepared with cured and moistened plaster/charcoal medium and then counting the number of individuals every week for three months. Several methods were used initially to count Collembola:

1) Counting small numbers with a hand magnifier;
2) Counting random fields of view through the stereomicroscope;
3) Counting numbers from macrophotographs;
4) Counting numbers within an ocular grid in the stereomicroscope;
5) Counting numbers in a 12 mm square placed in the ocular of the stereomicroscope.

In addition, counts were tried at ambient temperature, at ambient temperature with CO_2 anesthesia, and at lowered temperatures to reduce

movement. The method selected for later work was the fifth method listed above at ambient temperatures. The rationale for choosing this method is in the discussion. All living Collembola were counted as individuals, as distinctions between instars were difficult to make and sex differentiation could not be done easily with living Collembola under the stereomicroscope. McMillan (1980) did describe a method for sex determination in living Collembola. On account of the large number of Collembola used in this study and the fact that McMillan did not supply any controlled survival data after treatment, this method was not used and Collembola were not sexed.

A second trial was made with an additional replicate of each culture using the chosen counting method in order to get an indication of variance.

Additional trials were done to determine the effect of a change in the medium, food source, or container on the increase of Collembola. Potato dextrose agar (Acumedia No. 7149) with the mycoparasite *Coniothyrium minitans* obtained from North Dakata State University Plant Pathology was used as a food source in Petri dishes, 2 oz. souffle cups, and also with agar covering plaster/charcoal in the 2 oz. cups. Fleischmann's yeast was also grown on potato dextrose agar (PDA) in order to determine whether growing yeast colonies were a suitable substrate and food source for these Collembola. In addition, an agar medium for algae, Modified Knop's Solution (Morholt, Brandwein, and Joseph, 1966) was used to culture *Chlorella pyrenoidosa* (Carolina Biological bacterial-free). A trial was done for comparison to the 2 oz. cups in single Amac 41 mm boxes with an amount of plaster/charcoal equivalent to the 2 oz. cups. Other than the type of container, this trial was done in the same manner as the second trial. Lastly, a trial with five replicates per species was done using the 2 oz. souffle cups, plaster/charcoal and yeast as was done in the second trial. Subsequent work was done using this preparation method.

Direct Interactions

Direct interactions were tested by combining five replicates started with 10 individuals each of seven species. One of the groups of five replicates was a control; another group had 10 individuals of the same species added for comparison to the control group started with 10. Subsequent groups of five replicates had 10 individuals of each of the other species added until all the combinations were made. Because of the number of containers, these could not be counted regularly, so the numbers were counted at the end of two months.

Preconditioning

Finally, a test was made comparing the increase of cultures that had been preconditioned prior to adding individuals as compared to control containers prepared as described. The preconditioned containers were selected at random from the control group and the substrate “conditioned” by the addition of a small amount of food, fecal pellets and plaster/charcoal (frass) removed from cultures that had Collembola of the same species for a previous six month period. Both the preconditioned and control group consisted of 12 containers each started with 25 individuals of *Lepidocyrtus* sp. J and *Hypogastrura essa*. A third group was prepared in the same way with *Onychiurus folsomi* except that each container was started with 30 individuals. The culture container positions were rotated to allow for environmental differences. These containers were counted after Week 1 for number of eggs and after Weeks 3, 4, 6, and 8 for number of individuals.

A second preconditioning trial was done with *Lepidocyrtus* sp. J using culture containers without excess frass. In this trial, the surface of the plaster/charcoal was scraped, and the scraping was moistened and smeared on the surface of a newly prepared culture container. This group was compared to a group prepared in the same manner except that a newly prepared culture container was used as a control for conditioning rather than a culture container that had previously contained Collembola of the same species. A second set of unconditioned containers was prepared at the same time. One portion of these was used as a control for the previous two treatments. The second portion of these was used to test an additional variable: food source. The three previous groups were fed Fleischmann's active dry yeast, but this last group was fed with this same yeast after it had been heat-killed. These groups were counted every week for four weeks.

RESULTS

Species Used

The interbreeding trial with the two *Lepidocyrtus* species resulted in the reproducing of only one pair of *Lepidocyrtus* sp. J. None of the pairs of *L. fimicolus* reproduced, nor did any of the combinations of both species.

Culture Methods

Trials with a food source other than Fleischmann's active dry yeast resulted in fewer numbers as compared to the yeast-fed cultures. In fact, in the case of *Coniothyrium minitans* cultured on potato dextrose agar and *Chlorella pyrenoidosa* cultured on agar with Modified Knop's Solution, the numbers of Collembola declined either immediately or gradually until at the end of two months there were few or no Collembola remaining. Furthermore, when active dry yeast was allowed to grow on potato dextrose agar prior to the introduction of Collembola, the Collembola died within days of being introduced. A trial with a layer of potato dextrose agar inoculated with *Coniothyrium minitans* over plaster/charcoal was also done. Those containers which contained the greatest numbers of individuals with *C. minitans* as a food source were those in which the Collembola had produced a hole in the agar covering and had contact with the plaster/charcoal layer. The comparisons of the two *Lepidocyrtus* species (Group 1 and 2), *H. essa* (Group 4), *Proisotoma* (Group 7), and *O. folsomi* (Group 9) are shown graphically in figures 1 to 5.

Figure 1. Increase in numbers by week comparing *Lepidocyrtus* sp. J (Group #1) cultured on potato dextrose agar (PDA) poured over plaster/charcoal and inoculated with the mycoparasite *Coniothyrium minitans* as compared to the increase in numbers of the same species cultured on plaster/charcoal and fed yeast.

Figure 2. Increase in numbers by week comparing *Lepidocyrtus fimicolus* (Group #2) cultured on potato dextrose agar (PDA) poured over plaster/charcoal and inoculated with the mycoparasite *Coniothyrium minitans* as compared to the increase in numbers of the same species cultured on plaster/charcoal and fed yeast.

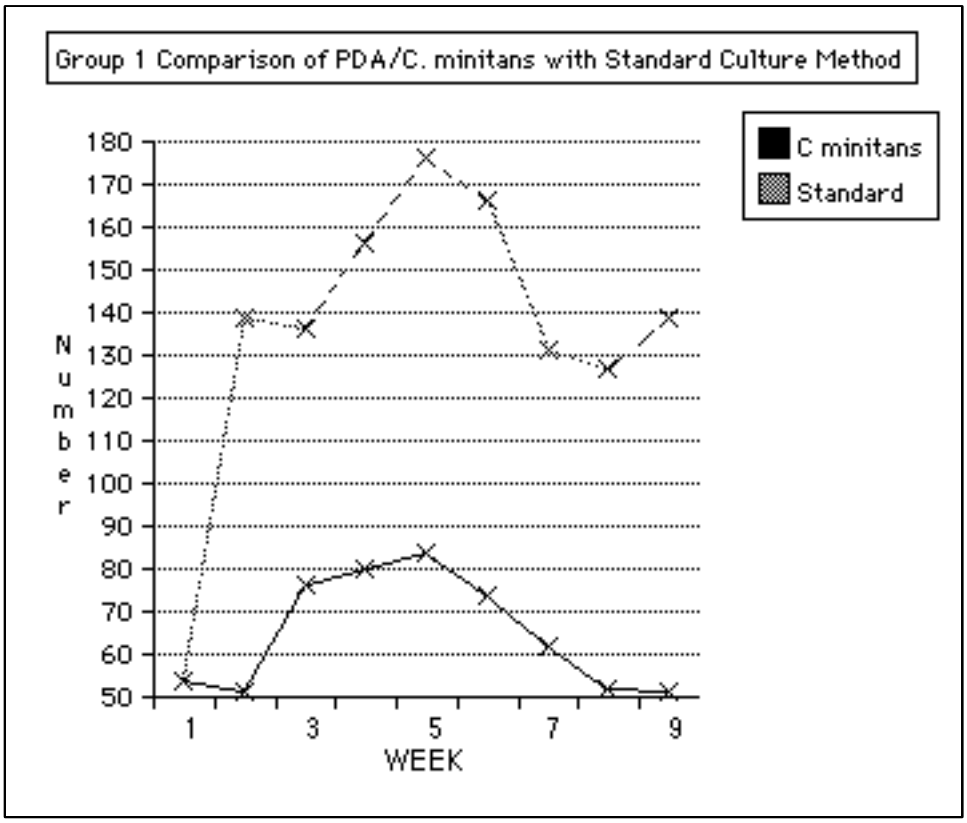

Figure 1

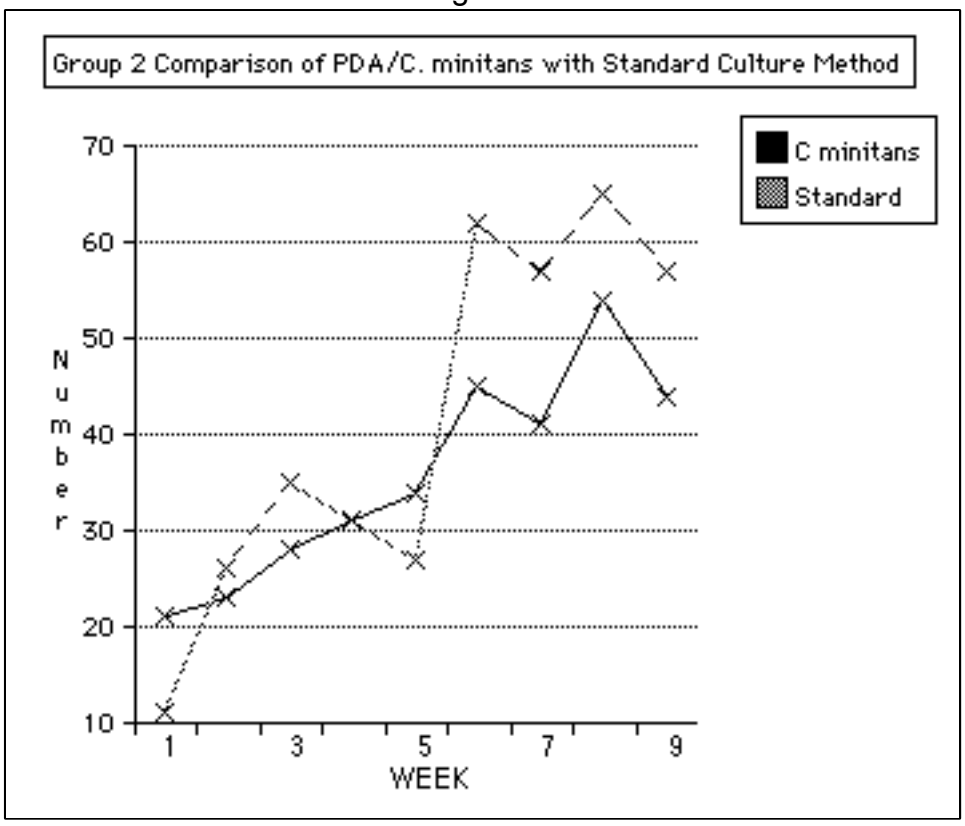

Figure 2

Figure 3. Increase in numbers by week comparing *Hypogastrura essa* (Group #4) cultured on potato dextrose agar (PDA) poured over plaster/charcoal and inoculated with the mycoparasite *Coniothyrium minitans* as compared to the increase in numbers of the same species cultured on plaster/charcoal and fed yeast.

Figure 4. Increase in numbers by week comparing *Proisotoma* sp. A (Group #7) cultured on potato dextrose agar (PDA) poured over plaster/charcoal and inoculated with the mycoparasite *Coniothyrium minitans* as compared to the increase in numbers of the same species cultured on plaster/charcoal and fed yeast.

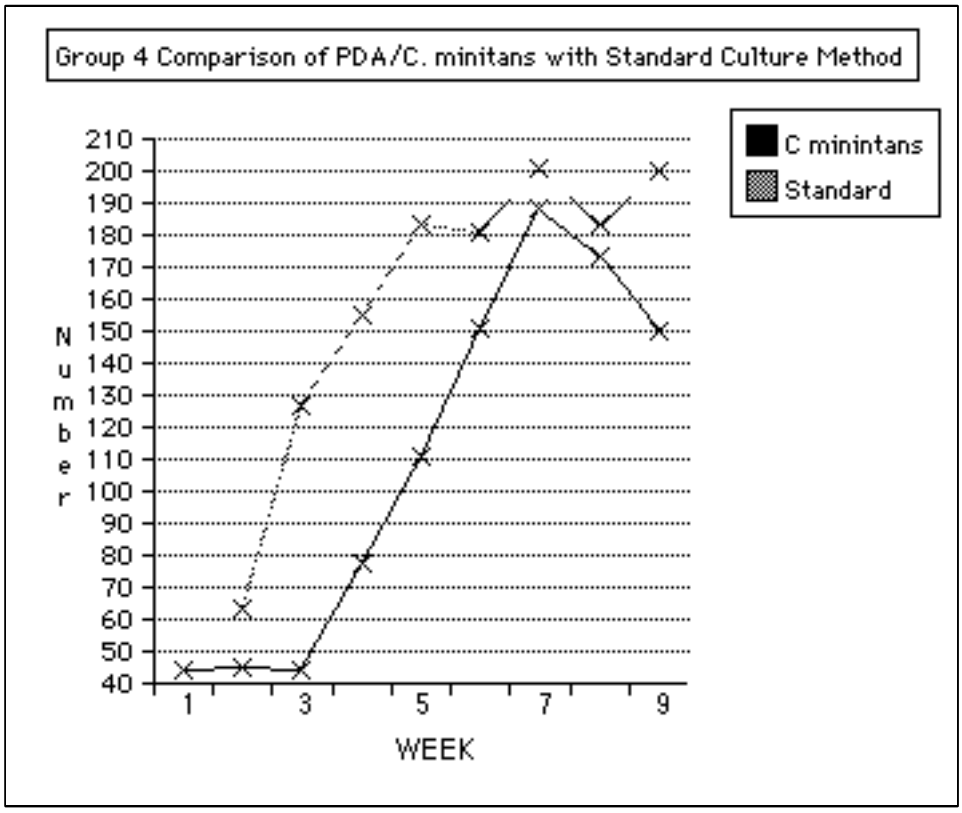

Figure 3

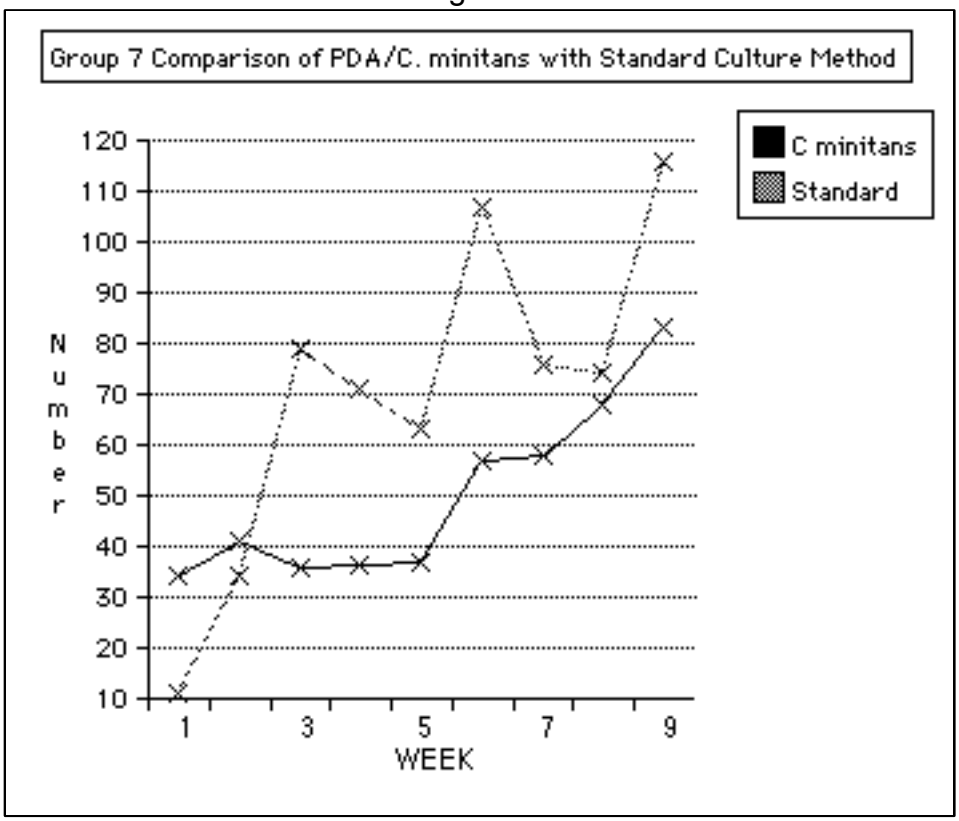

Figure 4

Figure 5. Increase in numbers by week comparing *Onychiurus folsomi* (Group #9) cultured on potato dextrose agar (PDA) poured over plaster/charcoal and inoculated with the mycoparasite *Coniothyrium minitans* as compared to the increase in numbers of the same species cultured on plaster/charcoal and fed yeast.

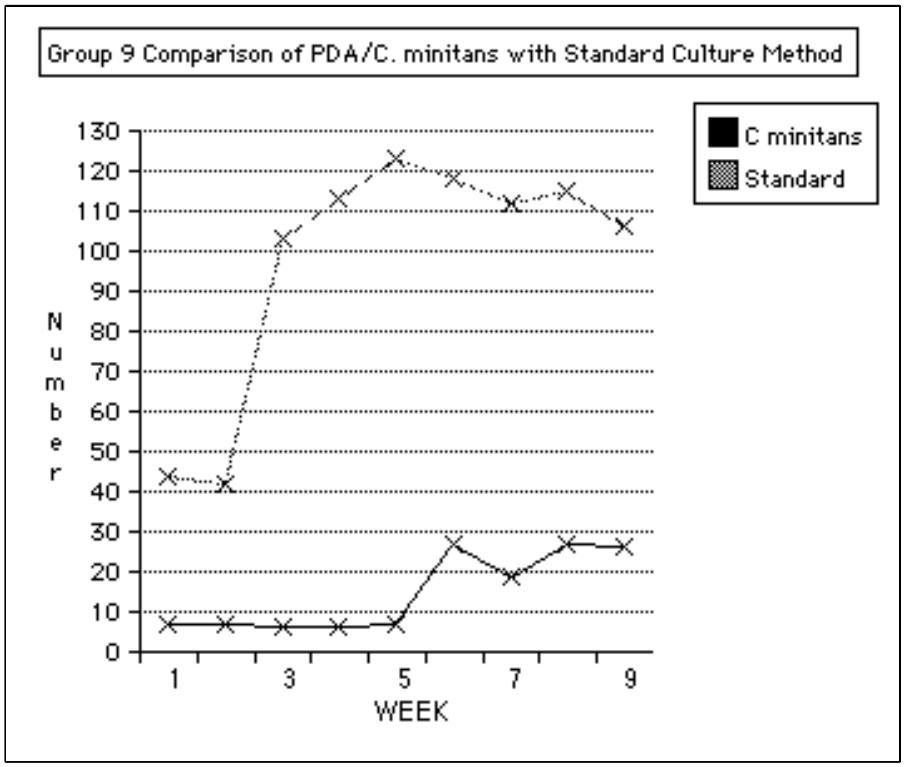

Figure 5

Experimental Containers

A trial compared the evaporation rate of distilled water from the thinner polystyrene 2 oz. souffle cups to the thicker Amac containers. The evaporation from the souffle cups was at approximately twice the rate as from the other containers. Results of counts for Collembola cultured at about the same time of year in both containers for most of the species seemed lower for the souffle cups. However, these did not differ significantly, as is shown in the results of the next section.

Counting Trials

Mean numbers of Collembola were determined by week and plotted in

figures 6 through 12 for each species along with the standard error. The data for all of the species are shown together in figure 13.

Because of the considerable variance shown in the mean numbers of these counts, the data were examined further by date and plotted in figures 14 through 20. The month in which each of the counts was begun was May, August, April and February for the lines indicated respectively as 1, 2, 3, and 4 in each of the figures. The regression lines for each of the nine counts for the four starting dates for each group were compared by ANCOVA using the statistics program Statex 1.6.1 from Dinan Software, Clinton, IA. These data required a natural logarithmic transformation of the numbers; consequently, in subsequent mention of count comparisons these will be based on transformed numbers rather than actual numbers. The slopes of the regression lines for these starting dates within all the species groups differed significantly. When the counts that were started in August were removed from the analysis of Groups 7, 1, 6, and 2, however, the slopes of the remaining counts for each species group did not differ significantly in slope at alpha = 0.05. The results for this are shown in Table 1. These groups rank first through fourth in the magnitude of their slope. The regression lines for the remaining three groups differed so greatly that counts in addition to the August ones were removed from the analysis in order to reach the alpha = 0.05 level. Those removed included the August counts and one or more other counts for Groups 3 and 9, but in the case of Group 4, one of the August counts did not differ significantly from the others.

Reviewing Figure 13 and Table 1, there appear to be three levels of rates of increase: High as in Group 7; Moderate as in Groups 1, 2, 4, 6, and 7; and Low as in Groups 3, and 9. In order to determine whether these differences in rates resulted from differences in the onset of oviposition, differences in the

Figure 6. Mean number of *Lepidocyrtus* sp. J (Group #1) by week. Counts were made during four time periods and each mean represents nine counts. The vertical lines represent standard errors of the means.

Figure 7. Mean number of *Lepidocyrtus fimicolus* (Group #2) by week. Counts were made during four time periods and each mean represents nine counts. The vertical lines represent standard errors of the means.

Lepidocyrtus sp. #1 Mean ° Standard Error

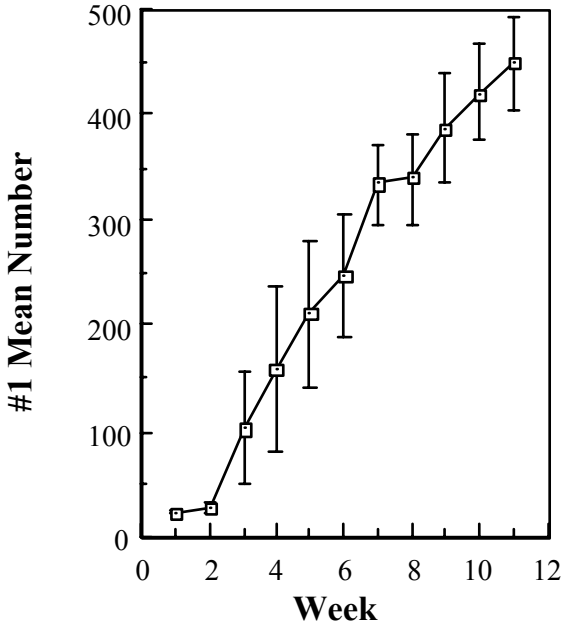

Figure 6

Lepidocyrtus sp. #2 Mean ° Standard Error

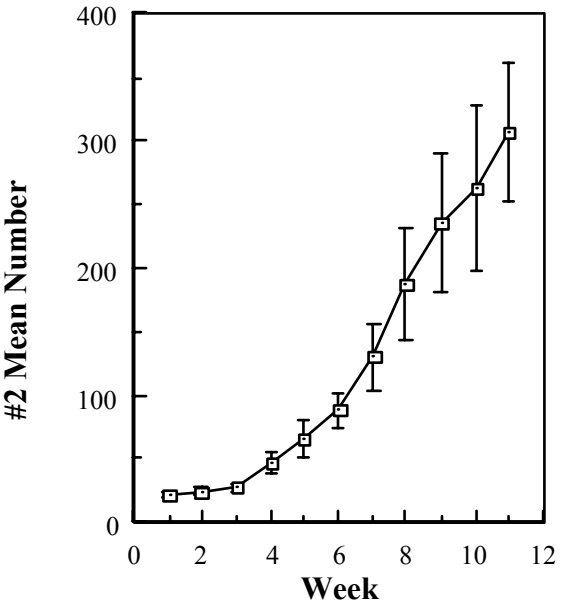

Figure 7

Figure 8. Mean number of *Folsomia similis* (Group #3) by week. Counts were made during four time periods and each mean represents nine counts. The vertical lines represent standard errors of the means.

Figure 9. Mean number of *Hypogastrura essa* (Group #4) by week. Counts were made during four time periods and each mean represents nine counts. The vertical lines represent standard errors of the means.

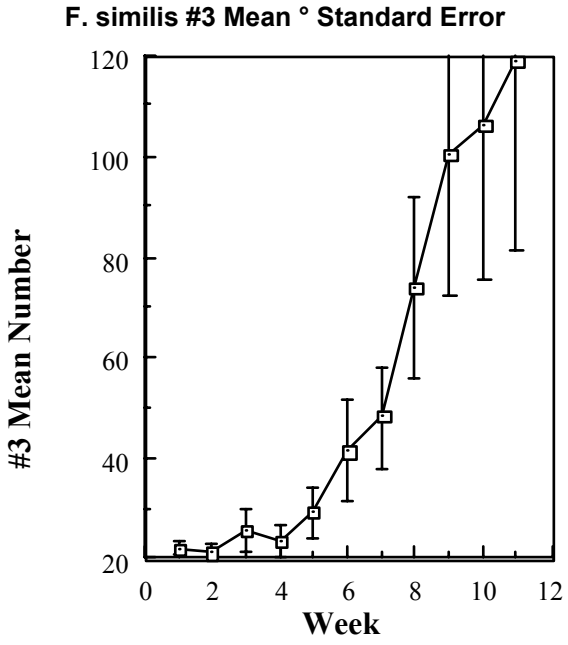

Figure 8

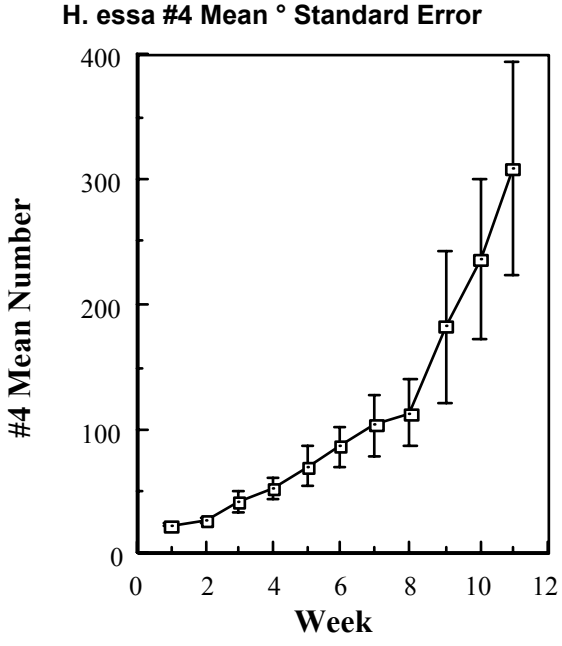

Figure 9

Figure 10. Mean number of *Onychiurus encarpatus* (Group #6) by week. Counts were made during four time periods and each mean represents nine counts. The vertical lines represent standard errors of the means.

Figure 11. Mean number of *Proisotoma* sp. A (Group #7) by week. Counts were made during four time periods and each mean represents nine counts. The vertical lines represent standard errors of the means.

O. encarpatus #6 Mean ° Standard Error

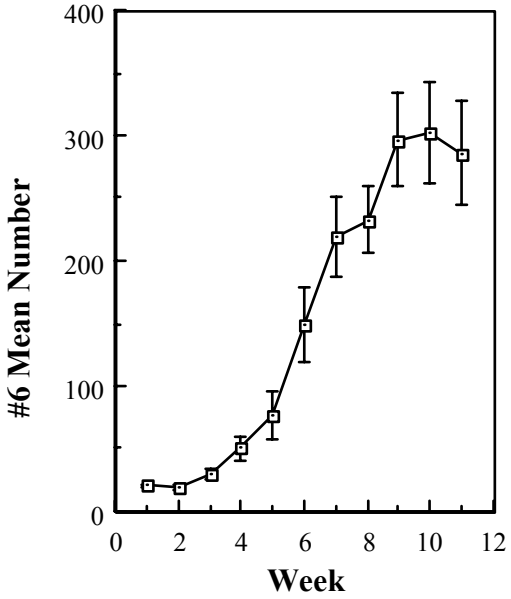

Figure 10

Proisotoma #7 Mean ° Standard Error

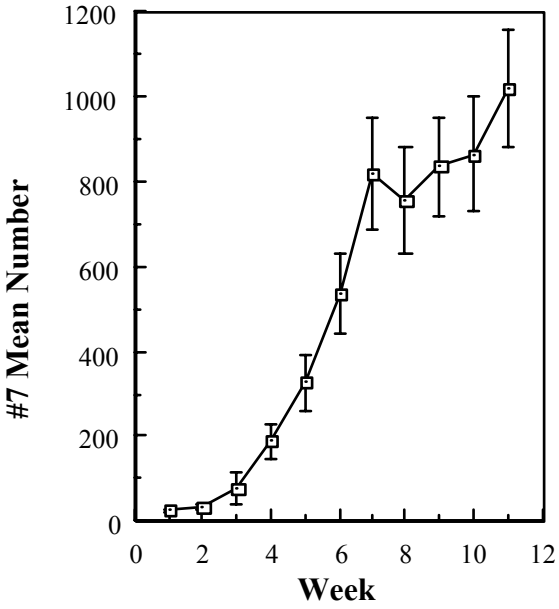

Figure 11

Figure 12. Mean number of *Onychiurus folsomi* (Group #9) by week. Counts were made during four time periods and each mean represents nine counts. The vertical lines represent standard errors of the means.

Figure 13. The data for the seven species from Figures 6 to 12 are shown together. For the sake of clarity, the vertical standard error lines from Figures 6 to 12 are not shown.

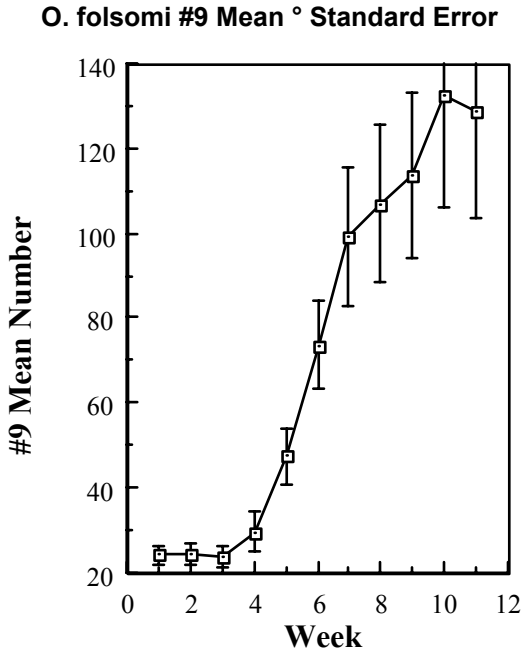

Figure 12

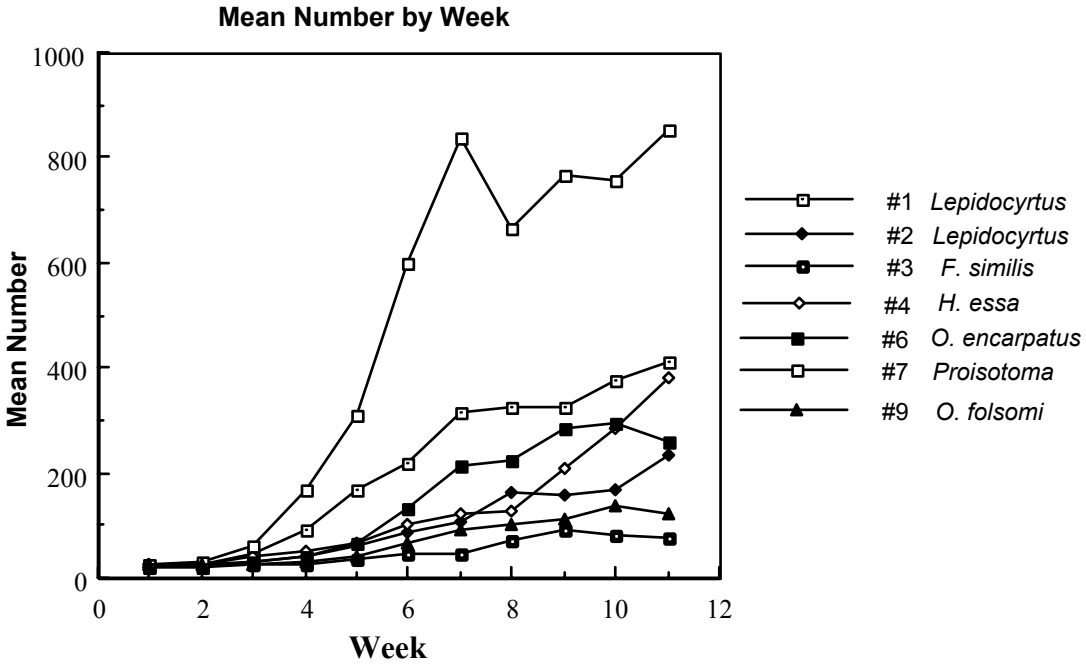

Figure 13

Figure 14. Mean numbers of *Lepidocyrtus* sp. J (#1) plotted according to the months in which the counts were begun. Lines indicated as 1, 2, 3, and 4 were begun respectively in the months of May, August, April and February.

Figure 15. Mean numbers of *Lepidocyrtus fimicolus* (#2) plotted according to the months in which the counts were begun. Lines indicated as 1, 2, 3, and 4 were begun respectively in the months of May, August, April and February.

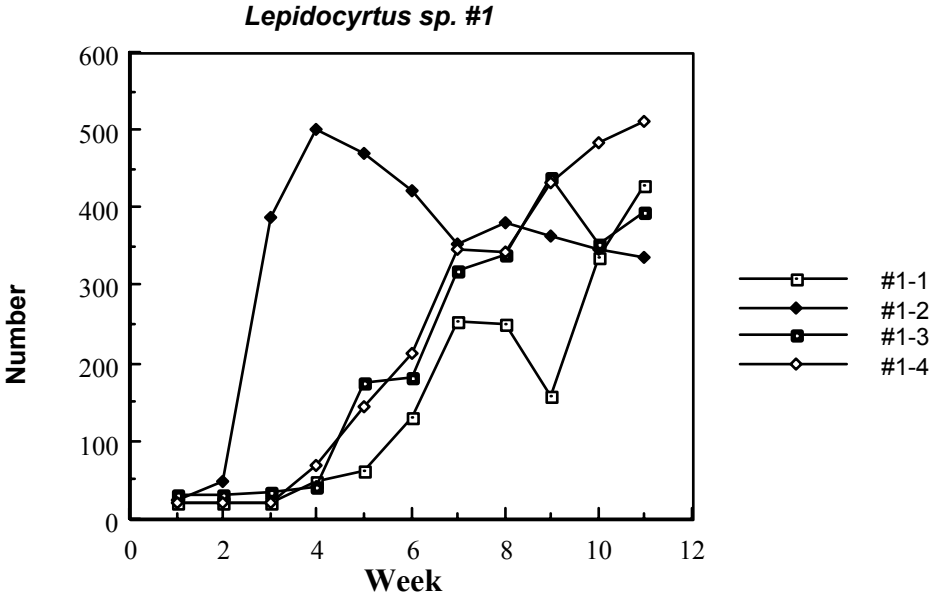

Figure 14

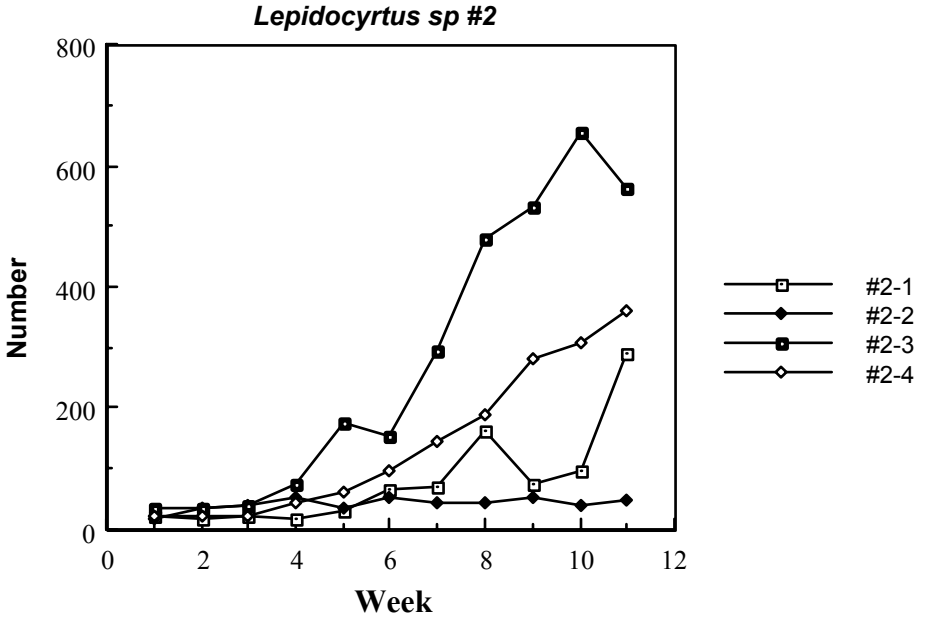

Figure 15

Figure 16. Mean numbers of *Folsomia similis* (#3) plotted according to the months in which the counts were begun. Lines indicated as 1, 2, 3, and 4 were begun respectively in the months of May, August, April and February.

Figure 17. Mean numbers of *Hypogastrura essa* (#4) plotted according to the months in which the counts were begun. Lines indicated as 1, 2, 3, and 4 were begun respectively in the months of May, August, April and February.

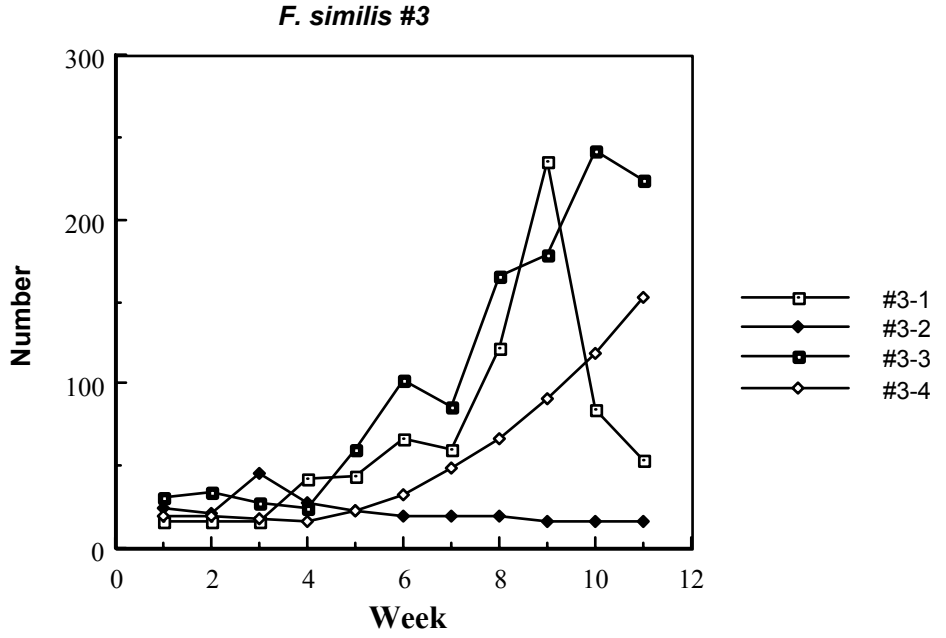

Figure 16

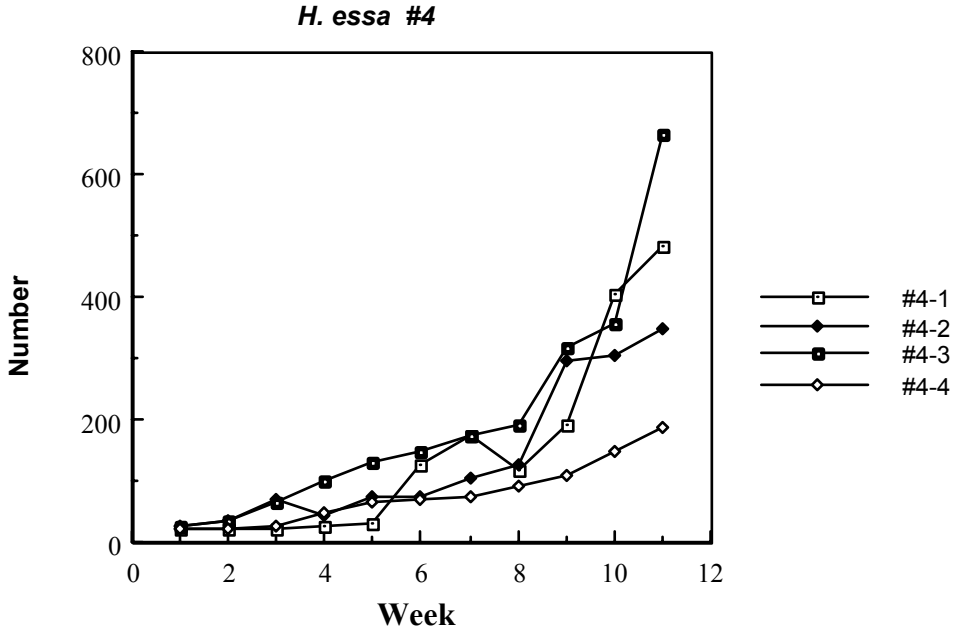

Figure 17

Figure 18. Mean numbers of *Onychiurus encarpatus* (#6) plotted according to the months in which the counts were begun. Lines indicated as 1, 2, 3, and 4 were begun respectively in the months of May, August, April and February.

Figure 19. Mean numbers of *Proisotoma* sp. A (#7) plotted according to the months in which the counts were begun. Lines indicated as 1, 2, 3, and 4 were begun respectively in the months of May, August, April and February.

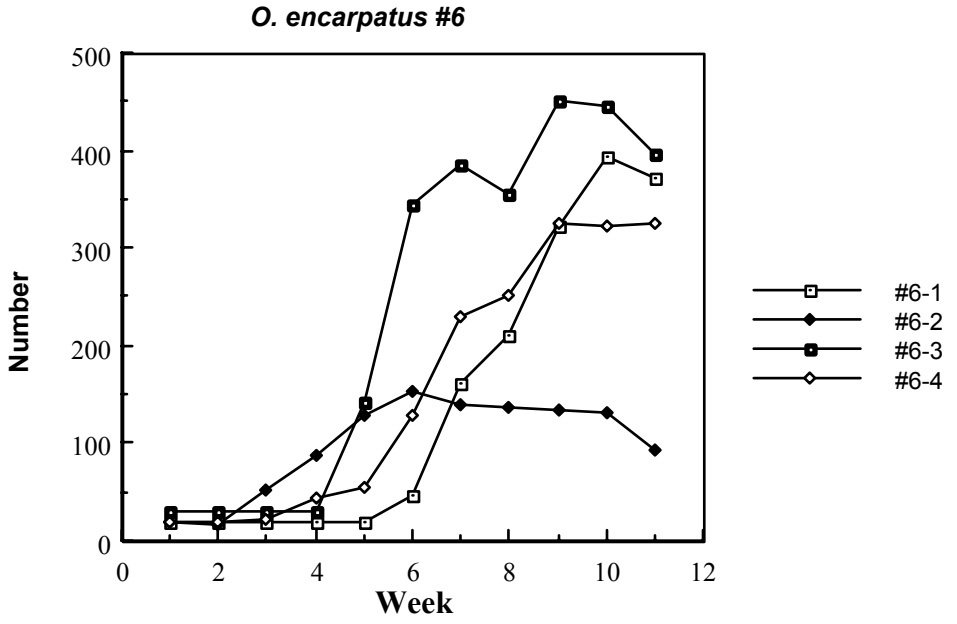

Figure 18

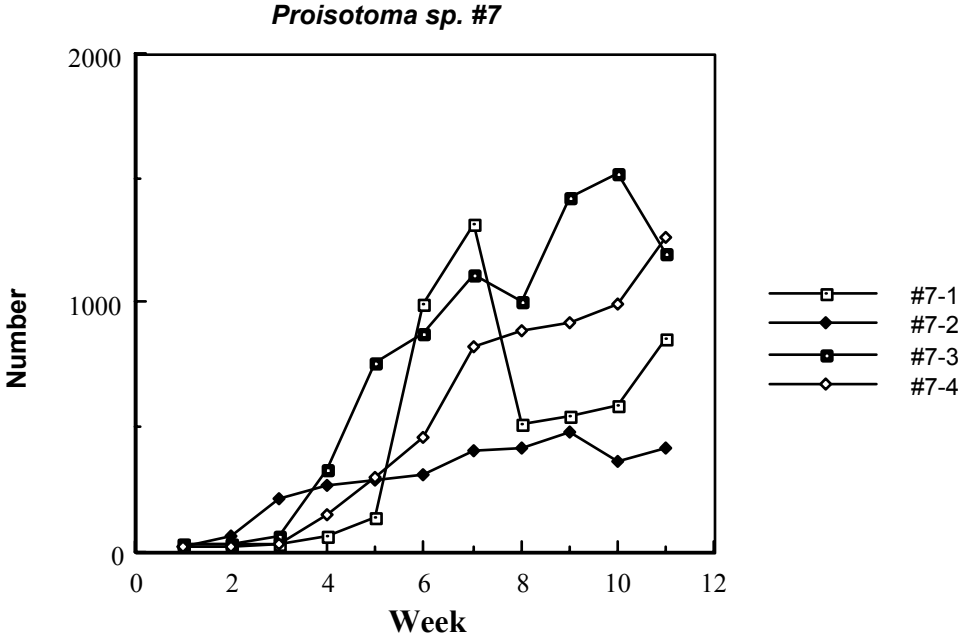

Figure 19

Figure 20. Mean numbers of *Onychiurus folsomi* (#9) plotted according to the months in which the counts were begun. Lines indicated as 1, 2, 3, and 4 were begun respectively in the months of May, August, April and February.

Table 1. The data for the groups shown in Figures 14 to 20 were transformed to their natural logarithm and tested by ANCOVA. Trials were numbered according to starting date and a key for this is shown at the bottom of the table. The numbered trials which were deleted from the analysis in order to reach a significance level of 0.05 for equality of slope were indicated, and the common slopes for each of the groups were ranked from highest to lowest.

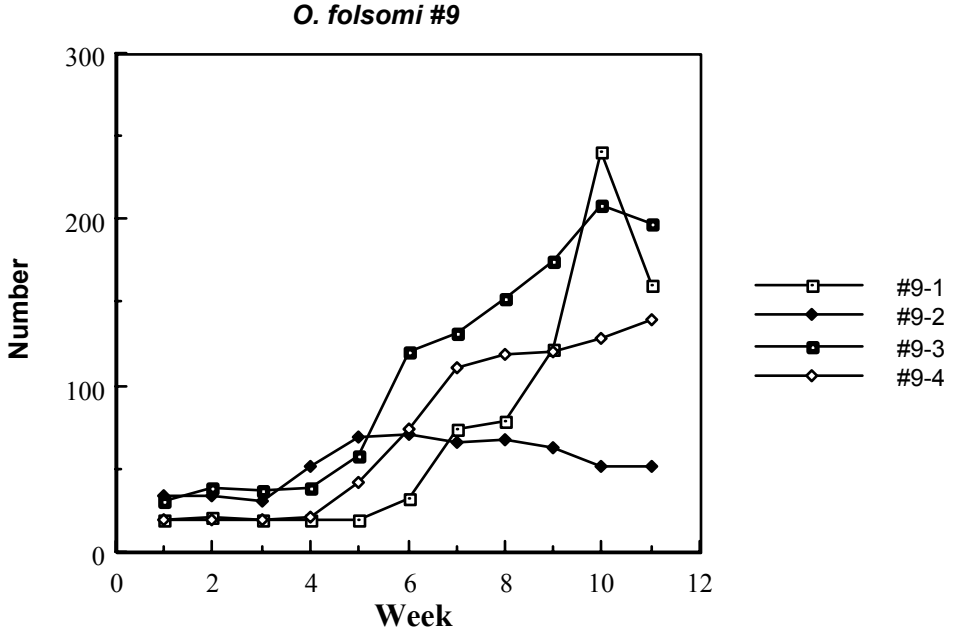

Figure 20

ANCOVA Selected Trials of ln (Number) by Week				
Group	Trial Removed	Common Slope	Equality of Slope Significance	Rank of Slope
Lepidocyrtus #1	7 & 8	0.365	0.205	2
Lepidocyrtus #2	7 & 8	0.321	0.155	4
F. similis #3	1, 2, 4, 7, & 8	0.252	0.049	7
H. essa #4	1, 2, 3, 4, 7, 9	0.31	0.245	5
O. encarpatus #6	7 & 8	0.346	0.992	3
Proisotoma #7	7 & 8	0.442	0.936	1
O. folsomi #9	2, 7 & 8	0.256	0.199	6
Key: 1 to 5 started Feb.; 6 started May; 7, 8 started Aug.; 9 started April				

Table 1

Figure 21. Graph of the means for the natural logarithm-transformed trials of *Onychiurus encarpatus* indicated in Table 1 compared to the linear regression and the line segments generated from the common slopes of the ANCOVAs for the same trials for each of three periods: Weeks 1-3, Weeks 4-7, and Weeks 8-11.

Table 2. Table 2 shows the common slopes derived from ANCOVA for each of the species groups for the three periods: Weeks 1-3, Weeks 4-7, and Weeks 8-11. The rank for each of the slopes within each period is also shown.

Table 3. The 95% Confidence Interval was calculated after Sec. 17.4 Zar (1984) at the 8th week time period for each of the species groups. The L1 and L2 intervals calculated are shown on Figure 22 to Figure 28 as horizontal lines.

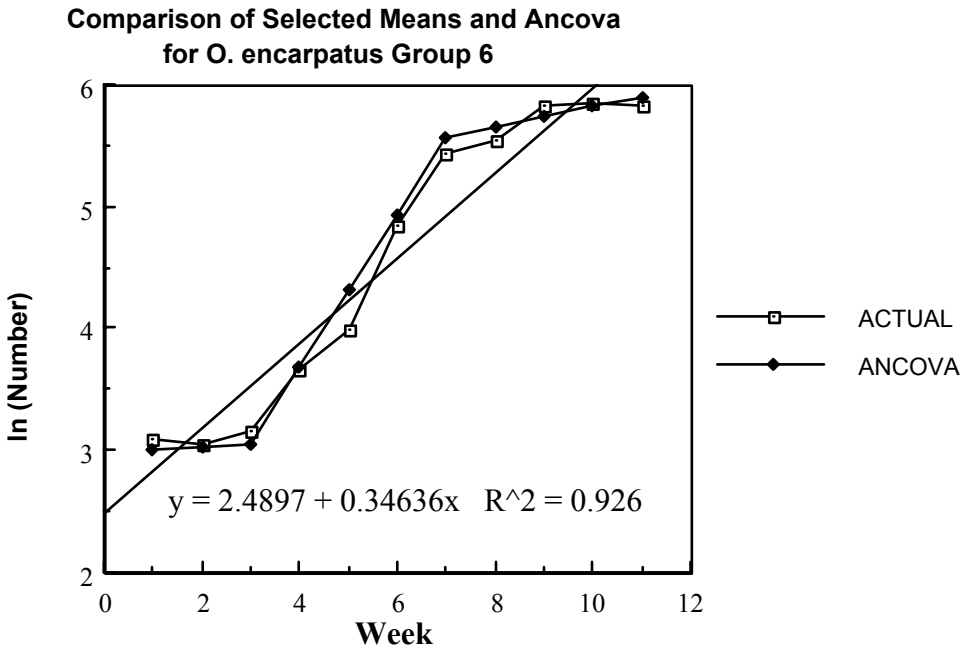

Figure 21

ANCOVA of Selected Means by Period						
Group	Slope Weeks 1-3	Rank of Slope	Slope Weeks 4-7	Rank of Slope	Slope Weeks 8-11	Rank of Slope
Lepidocyrtus #1	-0.01	5	0.551	4	0.131	3.5
Lepidocyrtus #2	0.038	3	0.408	5	0.187	2
F. similis #3	-0.023	7	0.362	7	0.089	6
H. essa #4	0.339	1	0.379	6	0.355	1
O. encarpatus #6	0.029	4	0.628	2	0.083	7
Proisotoma #7	0.22	2	0.643	1	0.131	3.5
O. folsomi #9	-0.014	6	0.557	3	0.097	5

Table 2

Calculation of 95% Confidence Interval after Sec. 17.4 Zar(1984) for 8th week Numbers			
Group	Statistic	L1	L2
Lepidocyrtus #1	312	256	381
Lepidocyrtus #2	122	101	148
F. similis #3	49	40	60
H. essa #4	164	131	198
O. encarpatus #6	208	175	246
Proisotoma #7	693	560	858

Table 3

maximum rates of increase, or a difference in the carrying capacity, the data for each group shown in Table 1 were analyzed again by ANCOVA for each of three periods: Weeks 1 to 3; Weeks 4 to 7; and Weeks 8 to 11. Figure 21 is a graph of the selected means for *O. encarpatus* showing the linear regression line as well as the connected line segments generated from the three ANCOVA slopes.

Table 2 shows the common slopes for each of the groups for the three periods. For Weeks 1-3, *H. essa* Group 4 and *Proisotoma* Group 7 had greater slopes than other groups and the slopes of these two groups were not significantly different. The other groups (1, 2, 3, 6, and 9) had relatively flatter slopes which did not differ significantly from one another. For Weeks 4 to 7, the slopes for all species were not significantly different, with a common slope of 0.524. The *Proisotoma* Group 7 had a higher initial slope within this period, but ended in a dip which lowered the slope of the regression. For Weeks 8 to 11, *H. essa* Group 4 continued at a higher slope. Group 2 (*L. fimicolus*), although lower in slope than Group 4, did not differ significantly from it . The slopes of the regression lines for Groups 1, 7, 3, 6, and 9 for Weeks 8 to 11 differed significantly in slope at alpha = 0.05, but only marginally with a probability of 0.046.

Direct Interactions

In this section, results of direct interactions are reported. The data are based on counts made at eight weeks. For comparison to the counts of the previous section, 95% confidence intervals were computed from the monoculture data according to the method of Zar (1984) section 17.4. This information in shown in Table 3. The count data for each of the combinations recorded after two

months were analyzed by single factor analysis of variance (ANOVA) after a square root transformation using a statistics program SchoolStat from WhiteAnt Occasional Publishing, West Melbourne, Australia. Multiple comparisons were made subsequently by comparing the control mean to each of the treatment means using Dunnett's test according to Zar (1984) section 12.4. Results for each of the species groups are graphed showing the means and standard errors for each treatment with the same or other combination of species in Figures 22 through 28. Each combination with a mean differing significantly from the control mean at an alpha level of 0.05 is marked with an asterisk. The 95% confidence levels obtained from the counts of single species are shown as horizontal lines for comparison to prior monoculture trials. Results of the ANOVA and Dunnett's tests are shown in Table 4.

Table 5 shows all the pairwise interactions and summarizes the results of Dunnett's tests for each pair. Each pair is indicated by number for each species and a symbol as to whether there was a positive difference from the mean of that species (+); no difference (0); or a negative difference (-).

In figures 29 through 35, the mean total number of individuals and standard error for each combination are shown as a stacked column graph. Once again, the groups that differ from the control mean are indicated with an asterisk, although these calculations are not very meaningful in the case of the mean of a slower reproducing species combined with a faster one. A ranking of dominance is shown in Table 7.

As fungal contamination could be a confounding variable, notation was made during counts of groups containing fungal growth. One group examined for differences between containers with mold and those without was Group 1:4. When counts of cultures containing fungal growth were compared to those

Figure 22. Column graph showing mean numbers of *Lepidocyrtus* sp. J (Group 1) control (:0) and combinations with itself (double control) and each of the six other species at eight weeks. The asterisks represent groups which differ significantly from the control mean by Dunnett's test. The vertical lines represent the standard error of the mean and the horizontal lines indicate the 95% confidence interval shown in Table 3.

Figure 23. Column graph showing mean numbers of *Lepidocyrtus fimicolus* (Group 2) control (:0) and combinations with itself (double control) and each of the six other species at eight weeks. The asterisks represent groups which differ significantly from the control mean by Dunnett's test. The vertical lines represent the standard error of the mean and the horizontal lines indicate the 95% confidence interval shown in Table 3.

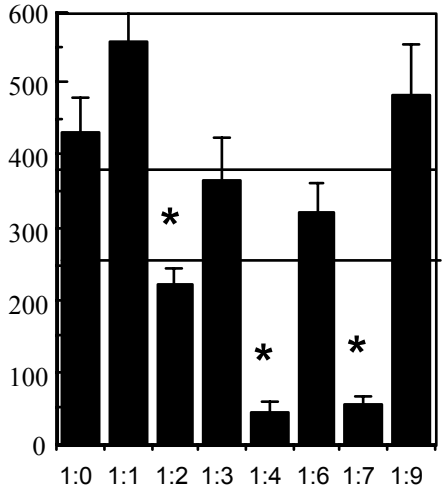

Figure 22

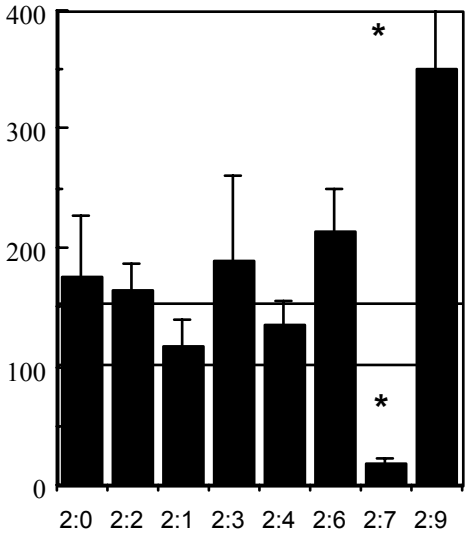

Figure 23

Figure 24. Column graph showing mean numbers of *Folsomia similis* (Group 3) control (:0) and combinations with itself (double control) and each of the six other species at eight weeks. The asterisks represent groups which differ significantly from the control mean by Dunnett's test. The vertical lines represent the standard error of the mean and the horizontal lines indicate the 95% confidence interval shown in Table 3.

Figure 25. Column graph showing mean numbers of *Hypogastrura essa* (Group 4) control (:0) and combinations with itself (double control) and each of the six other species at eight weeks. The asterisks represent groups which differ significantly from the control mean by Dunnett's test. The vertical lines represent the standard error of the mean and the horizontal lines indicate the 95% confidence interval shown in Table 3.

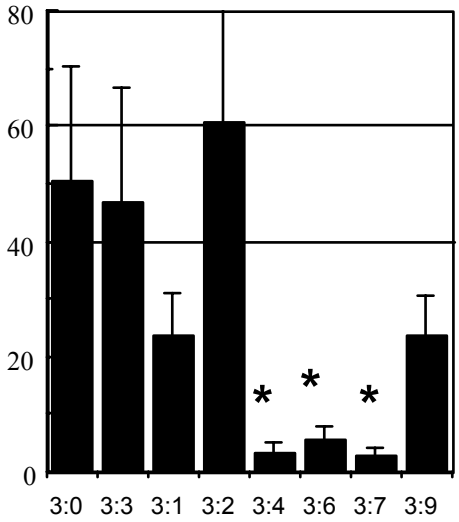

Figure 24

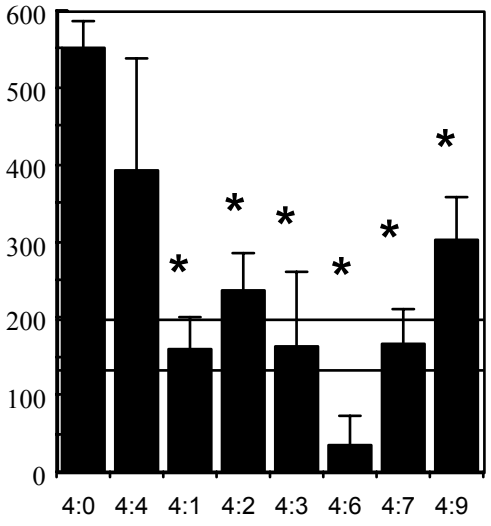

Figure 25

Figure 26. Column graph showing mean numbers of *Onychiurus encarpatus* (Group 6) control (:0) and combinations with itself (double control) and each of the six other species at eight weeks. The asterisks represent groups which differ significantly from the control mean by Dunnett's test. The vertical lines represent the standard error of the mean and the horizontal lines indicate the 95% confidence interval shown in Table 3.

Figure 27. Column graph showing mean numbers of *Proisotoma* sp. A (Group 7) control (:0) and combinations with itself (double control) and each of the six other species at eight weeks. The asterisks represent groups which differ significantly from the control mean by Dunnett's test. The vertical lines represent the standard error of the mean and the horizontal lines indicate the 95% confidence interval shown in Table 3.

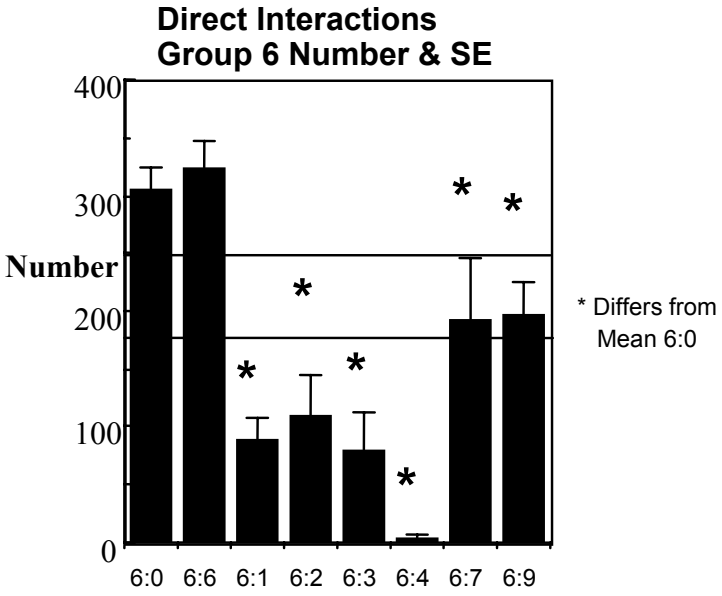

Figure 26

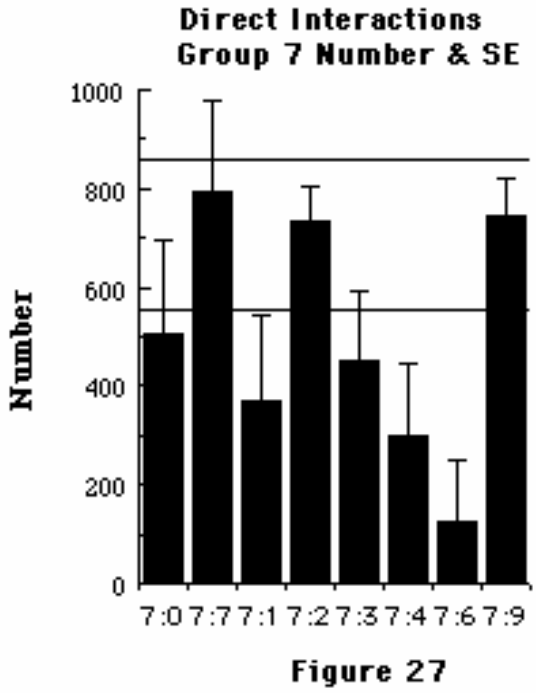

Figure 27

Figure 28. Column graph showing mean numbers of *Onychiurus folsomi* (Group 9) control (:0) and combinations with itself (double control) and each of the six other species at eight weeks. The asterisks represent groups which differ significantly from the control mean by Dunnett's test. The vertical lines represent the standard error of the mean and the horizontal lines indicate the 95% confidence interval shown in Table 3.

Table 4. ANOVA for each of the groups of Figure 22 to 28 was done and the F and p values and those groups which differ significantly from the control mean according to Dunnett's test are shown. A ranking indicating the least to greatest frequency of differences determined by Dunnett's test is shown at the bottom of the table.

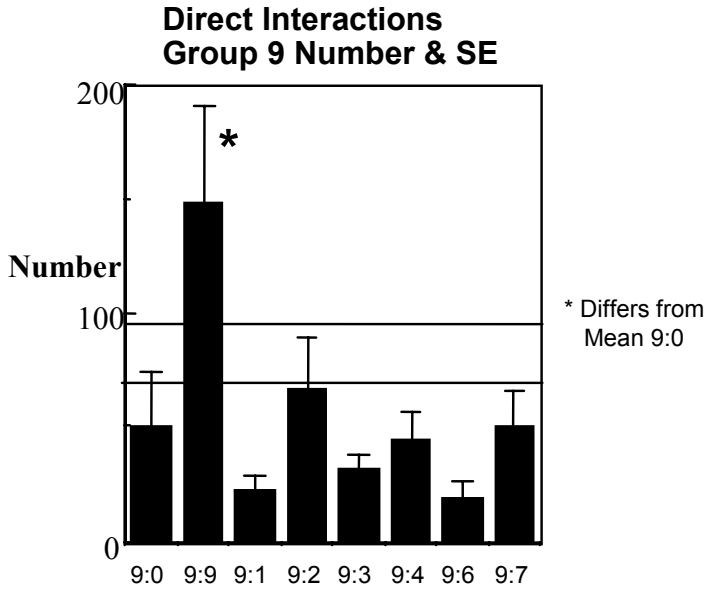

Figure 28

ANOVA for species groups and Differences from Control Mean			
Group	**ANOVA**		**Differ by Dunnett's test**
Lepidocyrtus #1	F=29.0956	p=.0000	1:2,4,7
Lepidocyrtus #2	F=6.5586	p=.0001	2:7,9
F. similis #3	F=4.3047	p=.0019	3:4,6,7
H. essa #4	F=4.9864	p=.0007	4:1,2,3,6,7,9
O. encarpatus #6	F=15.0329	p=.0000	6:1,2,3,4,7,9
Proisotoma #7	F=2.7114	p=.0252	No Group
O. folsomi #9	F=3.8742	p=.0037	9:9
	alpha level = 0.05		
RANKING: (indicating number of differences) **Group #7, #9, #2, #1 & #3, and #4 & #6**			

Table 4

Table 5. This table shows all combinations at two-months time. The numbers indicate the species groups and the symbols “-”, “0”, or “+” indicate whether the numbers were reduced, not significantly different, or increased for each pairwise combination. The frequency of each type of result is tallied at the bottom-left side of the table. Groups are listed by category on the bottom-right side of the table.

Table 6. Five of the pairwise interaction groups were analyzed within each group by t-test according to whether or not there was fungal growth.

Table of Pairwise Interactions at 2 month
Using Dunnett's Test for Difference from Control

	1	2	3	4	6	7	9
1	0	1 (-), 2(0)	1(0),3(0)	1(-),4(-)	1(0),6(-)	1(-),7(0)	1(0),9(0)
2	2(0),1(-)	0	2(0),3(0)	2(0),4(-)	2(0),6(-)	2(-),7(0)	2(+),9(0)
3	3(0),1(0)	3(0),2(0)	0	3(-),4(-)	3(-),6(-)	3(-),7(0)	3(0),9(0)
4	4(-),1(-)	4(-),2(0)	4(-),3(-)	0	4(-),6(-)	4(-),7(0)	4(-),9(0)
6	6(-),1(0)	6(-),2(0)	6(-),3(-)	6(-),4(-)	0	6(-),7(0)	6(-),9(0)
7	7(0),1(-)	7(0),2(-)	7(0),3(-)	7(0),4(-)	7(0),6(-)	0	7(0),9(0)
9	9(0),1(0)	9(0),2(+)	9(0),3(0)	9(0),4(-)	9(0),6(-)	9(0),7(0)	+

Analysis:	**Listing**
Groups with Both Groups Increased: O	
Groups with One Group Increased: 2	*2:9, 9:9
Groups with No Difference: 5	1:3, 1:9, 2:3, 3:9, 7:9
Groups with One Group Decreased: 11	*1:2,1:7,2:7,3:7,4:2,4:7,4:9,6:1,6:2,6:7,6:9
Groups with Both Groups Decreased: 4	1:4, 3:4, 3:6, 4:6
	*Group that is increased or decreased shown first

Table 5

T tests Comparing Within Interaction Test Groups with No Fungal Growth to Test Groups with Fungal Growth

GROUP	t value	Probability	Result at alpha = 0.05
1:4	1.8862	0.0779	Accept Null Hypothesis
4:1	3.1372	0.0259	Reject Null Hypothesis
2:0	0.311	0.3881	Accept Null Hypothesis
2:3	6.48	0.0037	Reject Null Hypothesis
3:2	1.3742	0.1315	Accept Null Hypothesis

Table 6

Figure 29. Stacked column graph for *Lepidocyrtus* sp. J (Group 1) with combined mean numbers for all of the pairwise combinations for the group and standard errors of the means for the combined totals. Each combination is indicated by number. The standard error of the mean is shown as the uppermost, finely-striped portion of the column. The mid-portion represents the mean of the second species in the pair.

Figure 30. Stacked column graph for *Lepidocyrtus fimicolus* (Group 2) with combined mean numbers for all of the pairwise combinations for the group and standard errors of the means for the combined totals. Each combination is indicated by number. The standard error of the mean is shown as the uppermost, finely-striped portion of the column. The mid-portion represents the mean of the second species in the pair. The asterisks indicate significant differences from the control group as analyzed by Dunnett's test.

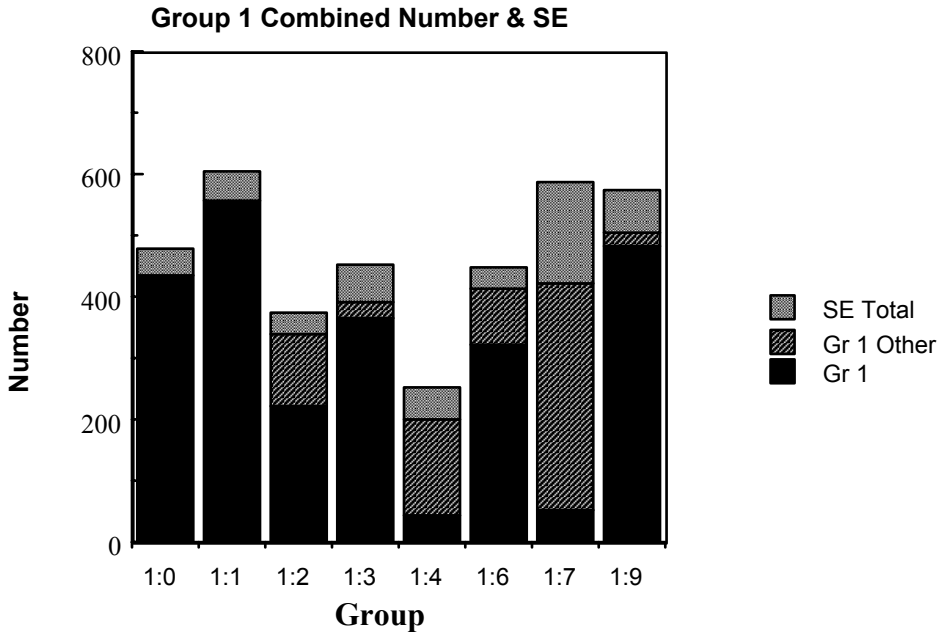

Figure 29

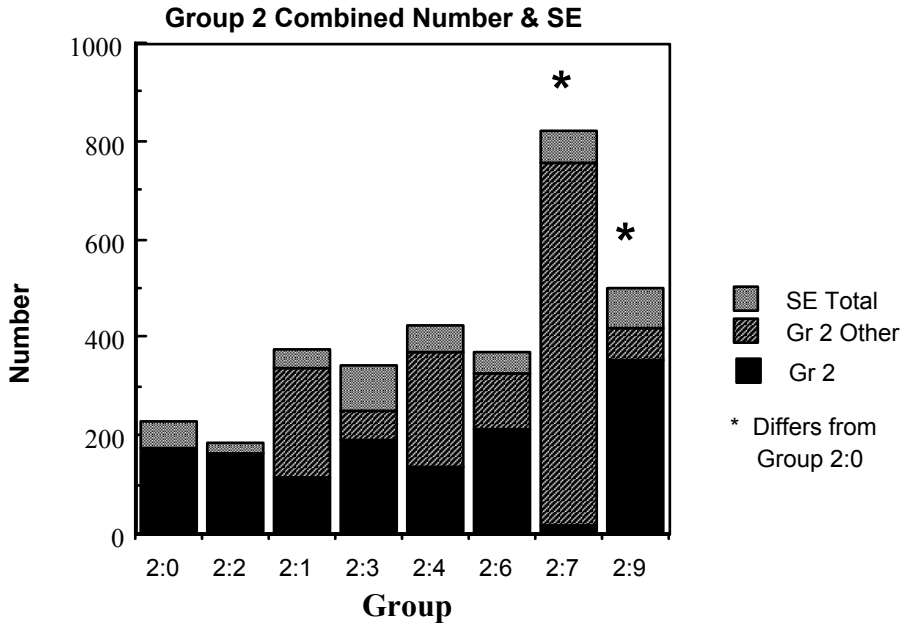

Figure 30

Figure 31. Stacked column graph for *Folsomia similis* (Group 3) with combined mean numbers for all of the pairwise combinations for the group and standard errors of the means for the combined totals. Each combination is indicated by number. The standard error of the mean is shown as the uppermost, finely-striped portion of the column. The mid-portion represents the mean of the second species in the pair. The asterisks indicate significant differences from the control group as analyzed by Dunnett's test.

Figure 32. Stacked column graph for *Hypogastrura essa* (Group 4) with combined mean numbers for all of the pairwise combinations for the group and standard errors of the means for the combined totals. Each combination is indicated by number. The standard error of the mean is shown as the uppermost, finely-striped portion of the column. The mid-portion represents the mean of the second species in the pair. The asterisks indicate significant differences from the control group as analyzed by Dunnett's test.

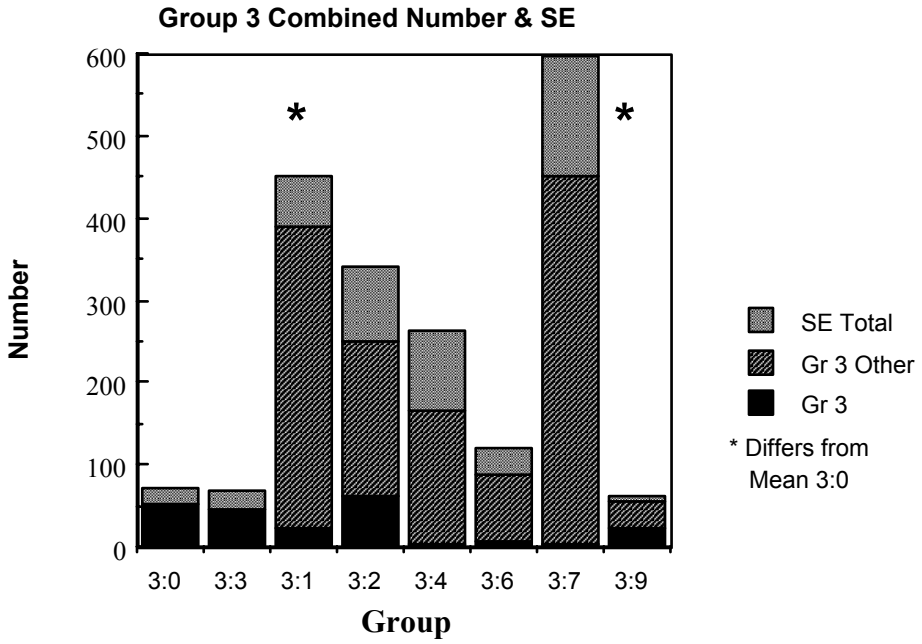

Figure 31

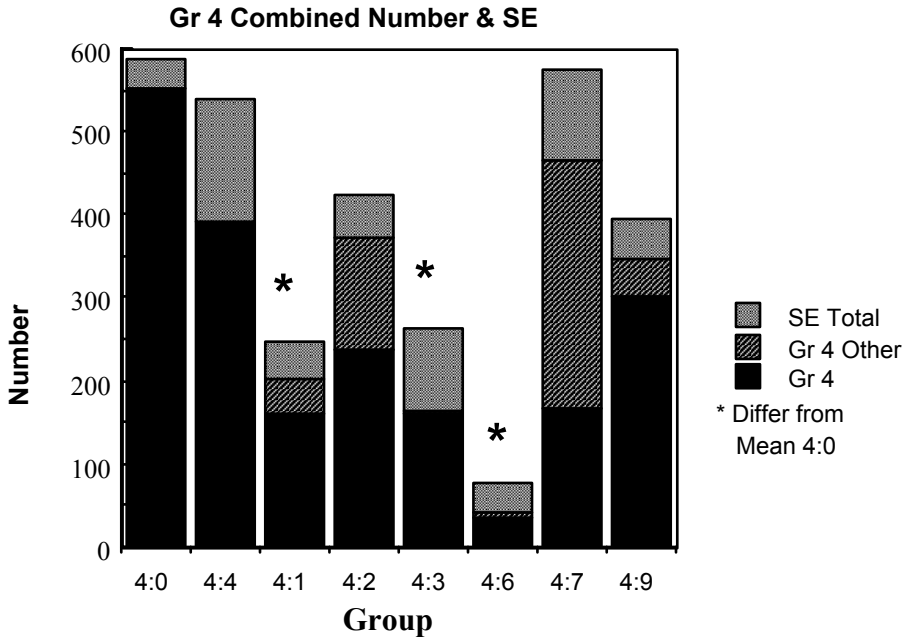

Figure 32

Figure 33. Stacked column graph for *Onychiurus encarpatus* (Group 6) with combined mean numbers for all of the pairwise combinations for the group and standard errors of the means for the combined totals. Each combination is indicated by number. The standard error of the mean is shown as the uppermost, finely-striped portion of the column. The mid-portion represents mean of the second species in the pair. The asterisks indicate significant differences from the control group as analyzed by Dunnett's test.

Figure 34. Stacked column graph for *Proisotoma* sp. A (Group 7) with combined mean numbers for all of the pairwise combinations for the group and standard errors of the means for the combined totals. Each combination is indicated by number. The standard error of the mean is shown as the uppermost, finely-striped portion of the column. The mid-portion represents the mean of the second species in the pair.

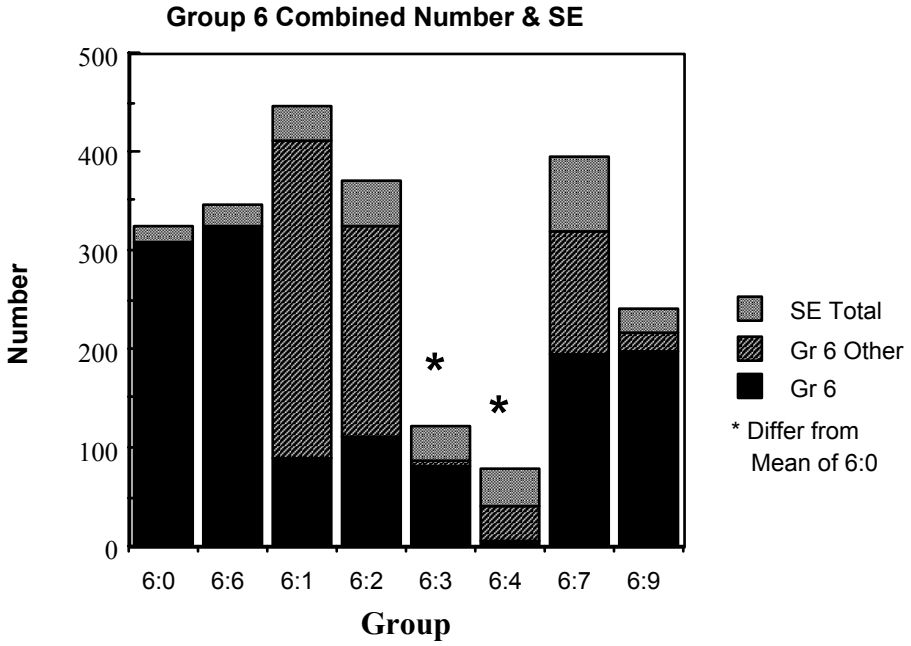

Figure 33

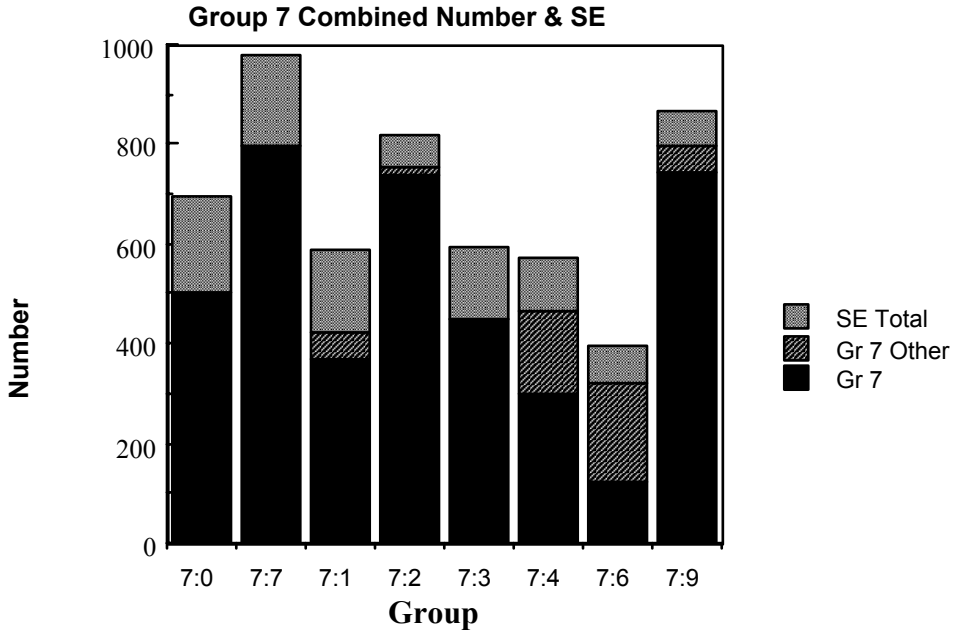

Figure 34

Figure 35. Stacked column graph for *Onychiurus encarpatus* (Group 6) with combined mean numbers for all of the pairwise combinations for the group and standard errors of the means for the combined totals. Each combination is indicated by number. The standard error of the mean is shown as the uppermost, finely-striped portion of the column. The mid-portion represents the mean of the second species in the pair. The asterisks indicate significant differences from the control group as analyzed by Dunnett's test.

Table 7. Results are tabulated according to the frequency of combinations in which the indicated group had greater numbers than the other pairs in the combinations. The frequency of these, which are noted as dominant combinations, are noted for all the groups and compared to the ranking determined for monoculture in Table 1. Pairwise groups in which the dominance was inconsistent with the monoculture ranking are listed at the bottom of the table.

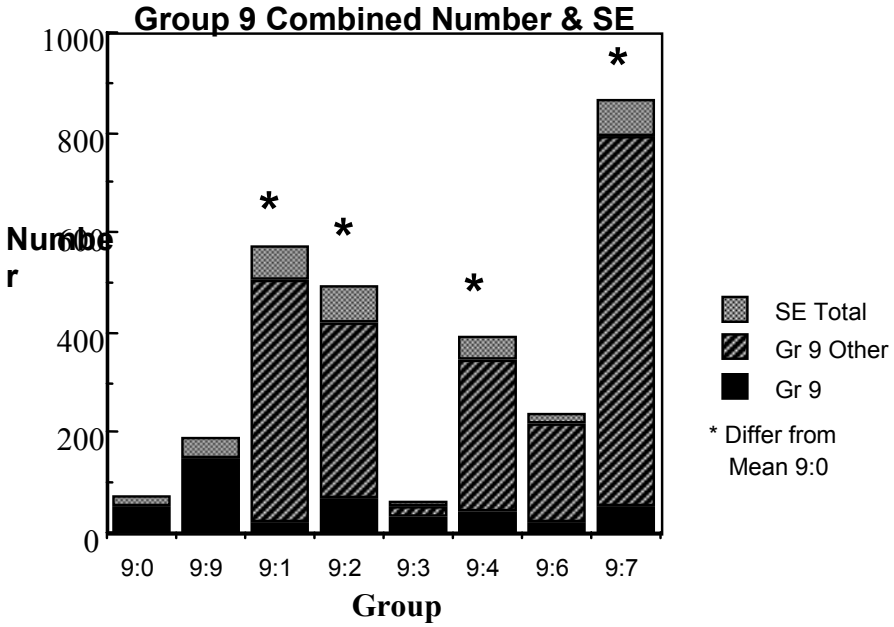

Figure 35

Frequency of Dominant Groups for Figures 29 to 35		
Group Number	Number of Dominant Combinations	Monoculture Ranking
Group #7	5 Combinations	Group #7
Group #4	5 Combinations	Group #1
Group #1	4 Combinations	Group #6
Group #6	3 Combinations	Group #2
Group #2	3 Combinations	Group #4
Group #9	1 Combination	Group #9
Group #3	0 Combinations	Group #3
Inconsistencies: Groups 1:4, 2:4 (and 4:1 and 4:2), 4:6 (and 6:4), 2:6 (and 6:2), and 6:7 (and 7:6).		

Table 7

Figure 36. Graph of the increase in numbers by week for 11 control populations of *Lepidocyrtus* sp. J (#1).

Figure 37. Graph of the increase in numbers by week for 11 treatment populations of *Lepidocyrtus* sp. J (#1). Treatment consisted of the addition of frass from another culture container of the same species prior to the addition of starting numbers of Collembola.

Lepidocyrtus #1 Pre-Conditioning Control

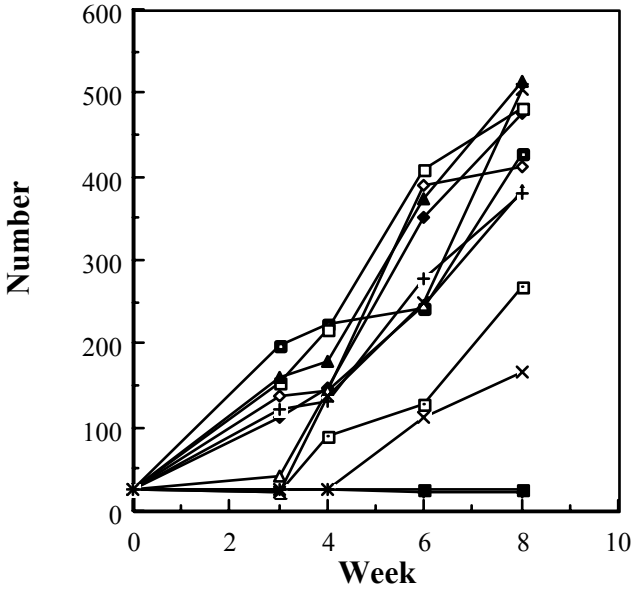

Figure 36

L. #1 Pre-Conditioning Treatment

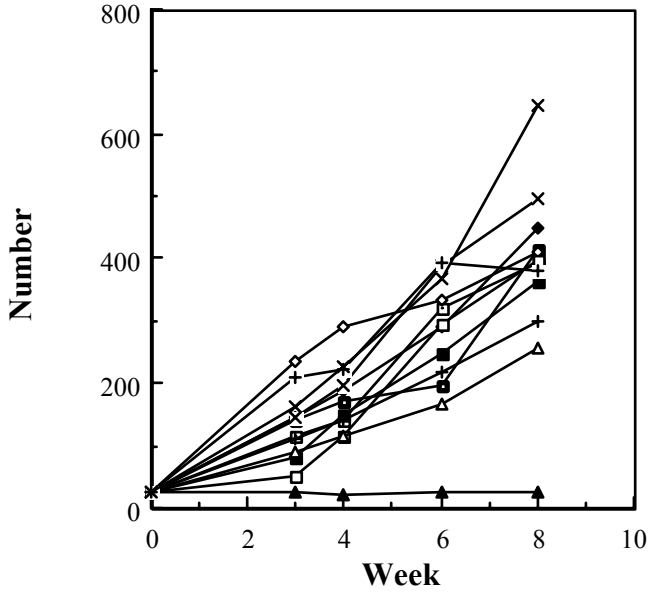

Figure 37

Figure 38. Graph of the increase in numbers by week for 11 control populations of *Hypogastrura essa* (#4).

Figure 39. Graph of the increase in numbers by week for 11 treatment populations of *Hypogastrura essa* (#4). Treatment consisted of the addition of frass from another culture container of the same species prior to the addition of starting numbers of Collembola.

H. essa #4 Pre-Conditioning Control

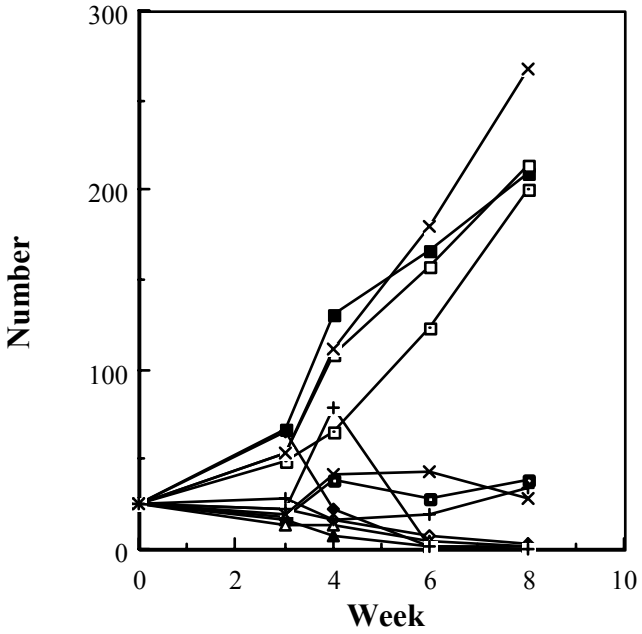

Figure 38

H. essa #4 Pre-Conditioning Treatment

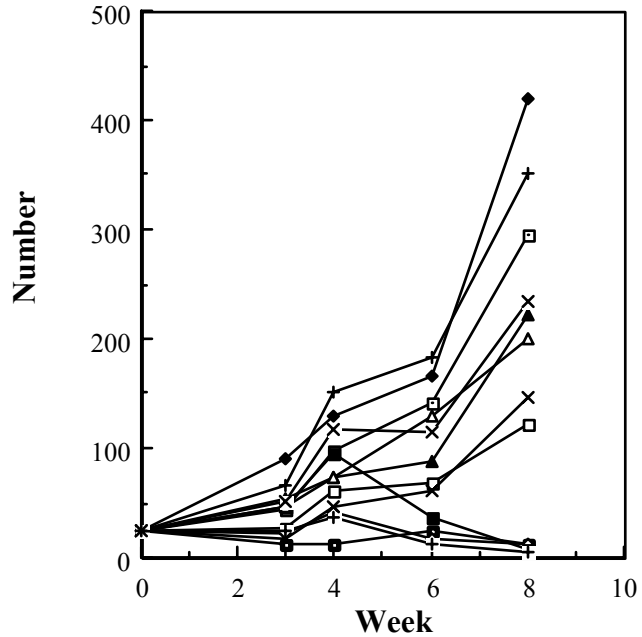

Figure 39

Figure 40. Graph of the increase in numbers by week for 11 control populations of *Onychiurus folsomi* (#9).

Figure 41. Graph of the increase in numbers by week for 11 treatment populations of *Onychiurus folsomi* (#9). Treatment consisted of the addition of frass from another culture container of the same species prior to the addition of starting numbers of Collembola.

O. folsomi #9 Pre-Conditioning Control

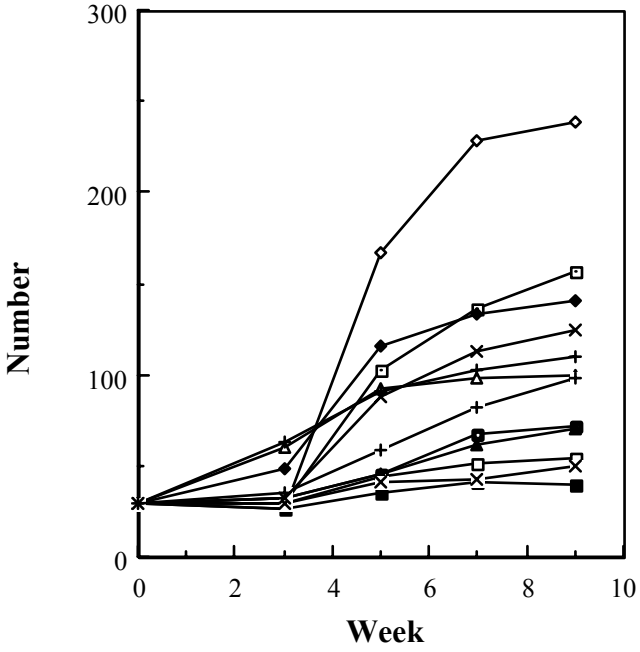

Figure 40

O. folsomi #9 Pre-Conditioning Treatment

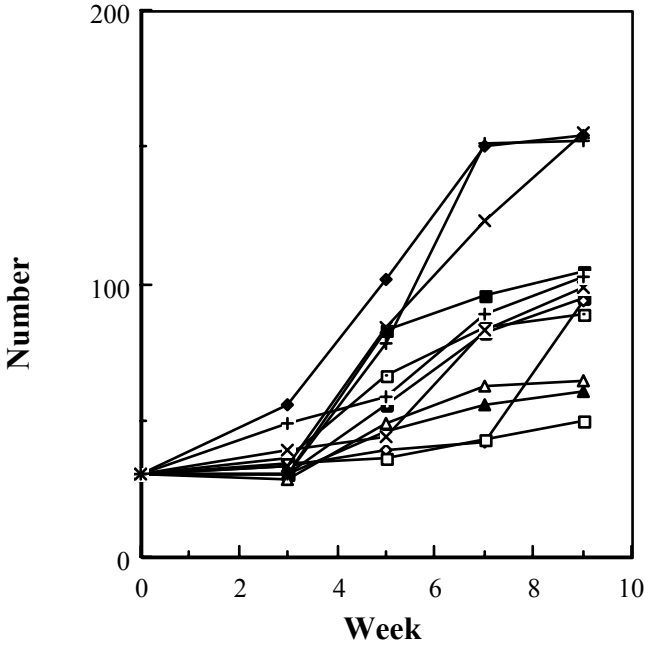

Figure 41

without and analyzed with a t-test, the *H.essa* Group 4 had t=3.1372 and p=.0259; whereas the *L.* sp. J had t=1.8862 and p=.0779. Consequently, there was a significant difference in the counts for those containing fungus and those without for *H.essa* but there was not a significant difference in the counts for the same containers for *L.* sp. J. Results of this are shown in Table 6.

Preconditioning

Counts of individuals in the control and treatment group were compared and are shown graphically for each species in Figures 36 through 41. These graphs will be mentioned further in the discussion. Table 8 shows t -Tests comparing the control and treatment means for numbers of each species for the final week of the trial. These do not differ significantly in any of the three species.

Initial numbers of eggs oviposited in each container for the first preconditioning investigation were noted and the association between treatment and control was examined by the chi-square test and shown in Table 9. The treatment was the preconditioning by transfer of “frass” from another culture container of the same species. The chi-square value for the *L.* sp. J group was 5.04 with a critical value of 3.84 at an alpha level of 0.05 as per table 14 of Rohlf and Sokal (1981). For this species, there was a relationship between the treatment and egg production, with the treatment group having the greater percentage of initial egg production. For *H. essa* Group 4, there appeared to be an early relationship as in *L.* sp. J, but by the time egg numbers were observed for chi-square analysis, there was not. For *O. folsomi* Group 9, there was no relationship between the treatment and egg production. Chi-square values for *H. essa* and *O. folsomi* were 0.67 and 1.51 respectively.

Table 8. Table with results of t-tests to examine null hypotheses for Preconditioning I trials of three species at end of trial period.

Table 9. Table with results of chi-square test to determine whether the initial ovipositing of treatment groups differed significantly from the control groups in terms of the percentage of containers with eggs after two weeks.

Table 10. Table with results of ANOVA testing whether the initial number of eggs oviposited in each of four groups of *Lepidocyrtus* sp. J (#1) differed significantly according to treatment. As there was no significant difference between the groups, the mean number of eggs and the variance are shown for each of the groups.

For the second preconditioning investigation using *L.* sp. J, initial oviposition was compared in Table 10 showing number and variance. Numbers of individuals and variance for the four groups are shown in Table 11. ANOVA testing for initial ovipositing resulted in an F = 1.316 and p=0.2865 at an alpha = .05. ANOVA testing for numbers in week 3 and 4 gave F = 0.74, p = .536 and F= .4984, p=.686 respectively. An analysis of covariance for the means of the regression lines also indicated acceptance of the null hypothesis and these results are shown in Table 11. Consequently, neither initial ovipositing nor numbers differ significantly in the four groups.

Preconditioning I t-test Comparing Means of Three Species for Final Week of Trial

Species	t-Value	Probability	Result
L. sp J #1	0.4241	0.3921	Accept Null Hypothesis
H. essa #4	1.554	0.1398	Accept Null Hypothesis
O. folsomi #9	0.156	0.4602	Accept Null Hypothesis

t-test Critical Value for 22 df = 2.074, Table 12 Rohlf and Sokal (1981)

Table 8

Initial Oviposition Preconditioning I

Group	Chi-Square Value	Result
L. sp. J #1	5.04	Treatment>Control
H. essa Group #4	0.67	Accept Null Hypothesis
O. folsomi #9	1.51	Accept Null Hypothesis

Chi-Square Critical Value = 3.84 at alpha=0.05 from Table 14 of Rohlf and Sokal (1981)

Table 9

Initial Oviposition Preconditioning II

Lepidocyrtus sp. J #1

Group	Number	Variance
Control	71.1	1064.6
Plaster	47.9	1149.4
Scraped	48.0	498.0
Killed Yeast	48.7	888.3

ANOVA: F = 1.316, p=0.2865 at alpha = 0.05
Accept Null Hypothesis of No Difference between Groups

Table 10

Table 11. Table showing results of ANCOVA for Preconditioning II trial with *Lepidocyrtus* sp. J (#1). As there was no significant difference between the regression lines for the four groups, the mean numbers and variances for each of the weeks are shown.

Figure 42. Maximum and minimum laboratory temperatures in ˚Celsius are shown by month for 1995.

Number, Variance and Regression Coefficient
Preconditioning II Lepidocyrtus sp. J #1

Group	Week1 Number	Week1 Var.	Week2 Number	Week2 Var.	Week3 Number	Week3 Var.	Week4 Number	Week4 Var.	Regression Coefficient
Control	21.7	15.0	46.7	483.0	63.3	963.5	59.9	620.9	13.1
Plaster	20.8	57.4	49.6	699.3	65.7	881.8	72.2	1325.9	17.0
Scraped	19.6	6.3	46.2	625.9	51.6	304.3	60.9	1484.4	13.3
Killed Y.	19.8	3.2	40.3	234.0	70.2	931.4	76.2	1381.2	19.9
ANCOVA:		Fvalue	Signif.						
Equality of Means		0.76	0.451	Accept Null Hypothesis that Regression Lines					
One Regr. Line		0.773	0.387	Do Not Differ Between Treatments					

Table 11

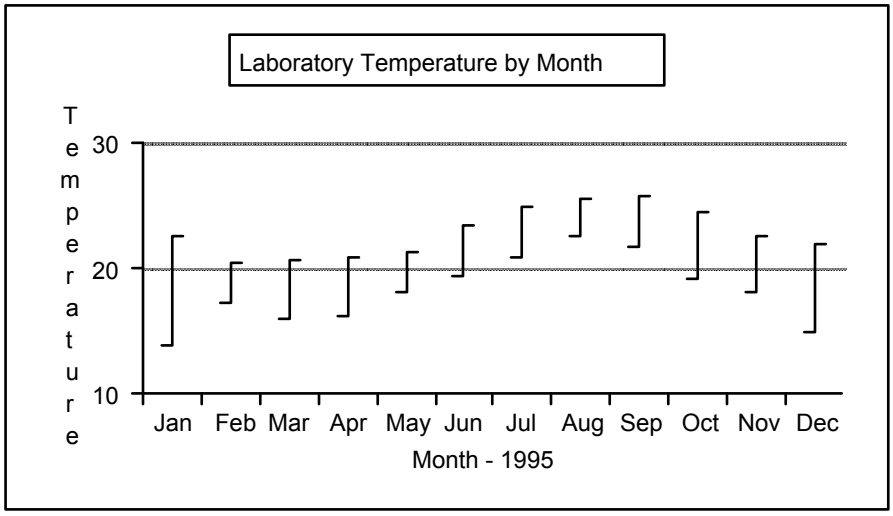

Figure 42

DISCUSSION

Species Used

An obvious first step in any study is the correct identification of the organisms used. This is sometimes easier to state than to accomplish. A case in point is *Lepidocyrtus* #1, identified as *Lepidocyrtus* sp. J. As of this writing, it has not yet been determined whether this is an introduced species or a new species. On account of an initial uncertainty over the identification of this and *Lepidocyrtus* sp. #2 (*L. fimicolus*) as different *Lepidocyrtus* species, the interbreeding trial was performed as described in the methods and results. As there was reproduction in only one of the containers of *Lepidocyrtus* sp. J, it was difficult to conclude anything with certainty, but there was the suggestion that perhaps *L.* sp. J reproduces more readily than *L. fimicolus* under the culture conditions; there was also no evidence of interbreeding.

It is noteworthy that none of the species used in this study were the same as those used by Van Cott (1982) even though litter samples were collected by the same individual in the same geographic area. One *Proisotoma (Ballistura)* species used in this study, *P.(B.)* sp. A, is within the same subgenus as a species used by Van Cott, *P.(B.) schoetti*. These differ most noticeably in the number of eyes and number of dental setae (Christiansen and Bellinger, 1980). The other species are no closer than within the same family or subfamily of Isotomidae or Entomobryidae Subfamily Entomobryinae. Van Cott's work did not include any species from the families of Hypogastrurinae or Onychiuridae as does this work. Van Cott did mention having *Onychiurus (Onychiurus) folsomi* Schäffer from San Diego in culture. The *O. folsomi* was the same species as

the #9 species in this work. He also mentioned collecting and culturing a *Lepidocyrtus* sp. from compost at California State University Northridge. This species was probably the same as *L. fimicolus* in this work. Both projects had *Brachystomella* and *Sphaeridia* species in cultures for a time, but could not maintain these successfully for long. One species that seems to be commonly found, *Isotoma (Desoria) notabilis* Schäffer, was not mentioned by Van Cott.

It is certain that the species used represent those that are able to survive and reproduce under the culture methods used. These may or may not represent any of the core species (Argyropoulou, Stamou and Latrou, 1994) for the habitat and may not be a particularly inclusive list of species found there. Muzzio (1984), for example, collected 43 species of Collembola from second growth *Sequoia sempervirens* Coast redwood forest. Temperate deciduous forest soils normally contain more than 30 species of Collembola (Chen, Snider and Snider, 1995). It is quite possible that after collecting, preserving, and identifying the species found in the area of collection for this work, at least 20 or more species would be identified in this litter. A collembolan list of species with records for southern California as well as possible other species is given in Appendix 1. The identification of species found in the avocado litter habitat and their relative numbers over the year would help with the analysis of the results of this work in the context of the community.

Culture Methods, Containers and Census Methods

The culture method most often used and quoted in the literature is that of Goto (1961), who used a smooth plaster/charcoal substrate in a stoppered container. Goto stressed that the surface “should be as smooth and as free from bubble-craters as possible because any small cracks or pits which are

present are very frequently found to house egg batches, early instars or cast skins which may thus be overlooked." An attempt was made during these investigations to use smooth and consistent substrates for experimental containers. As it seemed that the conditions required by the investigator were somewhat contrary to the nature of the organisms, this practice was not used exclusively. For culturing containers, for example, the surface was normally scored initially prior to adding Collembola to offer oviposition sites. Hale (1965) also noted that oviposition is common in holes left in the plaster surface. Gist, Crossley, and Merchant (1974) made grooves in the substrate of their culture dishes. Although eggs were observed in this work to have been oviposited in the crevices thus formed on the substrate of culture dishes, it was questioned after obtaining the results of the Preconditioning II study as to whether there was an actual benefit to this practice. The results in Table 9 indicated that initial ovipositing was not significantly different on a smooth control substrate as compared to one with a roughened, plaster slurry instead of grooves. Testing by controlled experiment is probably the best way to make decisions on each method to be used.

A number of studies have found that the abiotic conditions influence population growth and interspecific interactions. The most important abiotic factors are temperature and humidity. This work was carried out under fluctuating temperature as indicated in Table 42 showing mean monthly maximum and minimum laboratory temperatures over the year 1995. A temperature range from 15˚ to 26˚C has been shown to be a range in which Collembola will oviposit (Argyropoulous and Stamous, 1993). The growth rate, however, will not always be linear throughout this range (Johnson and Wellington, 1980) and, in addition, with spermatophore production declining with temperature for *Orchesella cincta*, the optimal temperature will be below

the maximum temperature (Joosse, Brugman and Veld, 1973). The effect of higher temperature is suggested by figures 14 to 20 for each of the species. Cultures begun in August are indicated by the second group (symbolized by the solid diamond points) in each of the figures. Generally, there was a higher initial increase followed by a decline with mean numbers at 11 weeks below that of other period trials in all cultures except *H. essa*.

Humidity has also been noted as an important abiotic factor (Verhoef, 1977; Joosse, 1981). The humidity fluctuated in the containers starting at nearly 100% after watering and then declining over the week until cultures were next tended. The rates of evaporation differed between the 2 oz. souffle cups and the Amac containers, with the evaporation rate in the souffle cups being approximately double that of the other container. In figures 14 through 20, the third group (symbolized by the solid square points) in each figure was cultured in the Amac containers. Although these data for the most part do not differ significantly from the data derived from souffle cups, the counts in the Amac containers are in almost every case generally higher. This difference was most noticeable in *L. fimicolus* collected from compost . On the other hand, Figure 14 for *Lepidocyrtus* sp. J groups indicated little difference between the two types of containers. The *L.* sp. J groups were similar in numbers with the exception of the higher temperature August culture. It appears that the *L.* sp. J was more tolerant to humidity changes but was influenced by temperature changes. On the other hand, *L. fimicolus* was influenced by both humidity and temperature changes within the abiotic range of this study. This suggests that these species could respond differently to the abiotic conditions used.

In addition to the abiotic factors, the availability of food resources is also of primary importance. In this study, food was supplied weekly as the containers were watered. This period for keeping containers unopened was to

be used for the airborne factor trial as well as for the other trials. It was selected to maximize the possible effects of airborne factors within the containers. Other investigators have changed food as frequently as every day or as infrequently as every week or more (Waldorf, 1971, three days; Van Cott, 1982, weekly; Longstaff, 1976 and Christiansen *et al. ,* 1992, every two weeks). The presence of fungal growth in a number of containers could also provide nutrition to a greater or lesser extent than the yeast, as well as possibly make unpalatable any yeast overgrown with fungal contamination. Consequently, as other fungi have grown on the yeast supplied as food in a number of the containers with a weekly feeding period, a four day period between feedings is recommended for further work to minimize this problem as well as to provide maximum nutrition for the Collembola.

There were several reasons for trying food sources other than active baker's yeast: 1) Whipps (1993) found that the mycoparasite*Coniothyrium minitans* was a food source that equaled baker's yeast in quality for*Folsomia candida.* Whipps (1993) also found little contamination in*C. minitans* - fed cultures of *F. candida* as compared to the yeast-fed cultures over a three year period. Supporting these results showing that a high inoculum of one fungal species will inhibit the growth of contaminating fungal species is the microcosm work of Parkinson, Visser and Wittaker (1979). When*C. minitans* was used as a food source in this work, all of the species trials on a solid lawn of*C. minitans* grown on PDA did not survive for long. On the other hand, the five species tried on PDA with*C. minitans* over plaster/charcoal (Figures 1 to 5), survived reasonably well, particularly when the Collembola had grazed through the PDA growth medium to the plaster/charcoal. The effect of a change of substrate on fungal preference in Collembola has been noted by Leonard (1984) and more recently by Kaneko, McLean and Parkinson (1995). The first method of

preparing a fungal lawn was hoped to provide a culture condition that could not only be left untended for an extended period, but also could have a lesser amount of contamination than yeast-fed cultures. The greater success of the second method of pouring PDA over plaster/charcoal suggests that either surface contact is required or the microhabitat on the *C. minitans* lawn is unsuitable, possibly on account of lower relative humidity or the presence of metabolites. Perhaps using a method of placing plugs of *C. minitans* grown on agar onto the surface of plaster/charcoal would produce results equal to those of yeast-fed cultures, but the amount of handling of the cultures would be no less than with active yeast. Consequently, this approach was not continued.

2) Waldorf (1971) determined that yeast byproducts inhibit oviposition of *Sinella curviseta*. In this study, yeast metabolites are quite able to reduce collembolan numbers when baker's yeast is actively growing on PDA. Collembola placed in Petri dishes with baker's yeast growing on PDA did not survive for more than several days. It is not known whether the mortality resulted from the presence of volatile metabolites, such as acetone, ethyl alcohol, and methyl alcohol (Waldorf 1971) or from excess CO_2. If response to volatile compounds is any indication of their effect, Bengtsson, Erlandsson and Rundgren (1988) mention that volatile compounds produced from yeasts could potentially attract or repel Collembola. Their study did not, however, find any evidence in which Collembola were repelled by fungi.

The results of the second preconditioning study are shown in Tables 9 and 10. In the single trial performed, containers of *Lepidocyrtus* sp. J fed on heat-killed yeast had a somewhat, but not significantly, lower initial oviposition as compared to active-yeast-fed controls. By the fourth week, however, numbers in containers fed on killed yeast were higher, but not significantly so, than the control, and the regression coefficient for increase in numbers was

also greater. Once again, the differences are not significant, so no definite conclusion can be made for the use of killed yeast over active yeast.

3) The algal *Chlorella pyrenoidosa* cultures were also prepared with the hope of providing a culture that could be left untended for an extended period. The *C. pyrenoidosa* could not be used as a single food source for long because it was so readily contaminated by fungal growth. Algae have been used as food for Collembola for both tree-dwelling and litter-dwelling species. Verhoef, Prast and Verweij (1988) found that the epedaphic species *Orchesella cincta* grew better on fungi than on algae and that hemiedaphic species also fed on green algae. Both Verhoef *et al.* (1988) and Bakonyi, Dobolyi and Thuy (1995) recommend a mixed diet of fungi and algae for Collembola. Also using a combined diet, Zettel (1982) was able to avoid cannibalism on yeast-fed *Hypogastrura manubrialis* by feeding cultures the oligochaete *Tubifex* as well as yeast.

Another issue relating to feeding is whether to attempt to synchronize molting in the individuals used in the trials by a period of starvation (Joosse and Testerink, 1977). Such a practice would have the added benefit of allowing the test subjects to void fungal spores that are contained in their guts. Although test animals in this work were normally maintained for 24 hours without food prior to being allocated to test containers, this is probably the minimum time for food to pass through the digestive system and not the starvation period of a week used by Joosse and Testerink (1977). Parkinson, Visser and Wittaker (1979) found that field-collected Collembola held for 48 hours without food only had fungal colonies germinating on 5% of the plated specimens and it was concluded that the spores producing this germination were from the cuticle and not the feces. After noting the reduced viability of fungal propagules after passing through the collembolan gut, Visser, Parkinson, and Hassall (1987) also concluded that

collembolan dispersal of fungi was mainly from the cuticle rather than through feces. On the other hand, Visser *et al.* (1987) found that approximately 50% of collembolan fecal pellets from field collected specimens when plated produced fungal growth, although these were similar to the species found on the cuticle. It is quite possible that a two-day period without food would be more effective than one day in clearing the gut; however, a percentage of the populations would probably still become contaminated from cuticular spores. Aggregation pheromones are reduced during starvation, but production of pheromones is stopped neither during starvation nor molting (Verhoef, 1984), so starvation should not completely interfere with aggregation. It would be interesting for the future to compare results obtained with the species used in this work when these are fed and starved prior to trials to determine whether there is any difference.

This section concludes with a few comments on census methods. A number of methods were tried initially for counting Collembola and these were listed previously in Materials and Methods in the section “Counting Trials”. These methods are discussed here as they appear listed in the Materials and Methods section: 1) While counting individuals with a magnifier is suitable for the larger Collembola when numbers are few, this method cannot be used when Collembola are small in size or many in number. 2) Counting random fields of view has been used by other researchers. Van Cott (1982) for example, counted a third of the substrate surface for cultures with large numbers. Christiansen *et al.* (1992) also counted a portion of the substrate surface when numbers of Collembola were large. They used a grid of up to 16 sections, made four counts and multiplied by four. On account of the more aggregated distributions (Joosse and Verhoef, 1974) of some of the species in this study, this method could not be uniformly relied upon, particularly without

statistical analysis. 3) Macrophotographs were made and counting results compared to other methods. Although photographic counting methods have been used successfully by others (Longstaff, 1976), these were not adequate here for these reasons: i) The 35 mm film size and 100 ASA film grain size did not adequately allow living Collembola to be distinguished in all cases from cadavers, exuviae, and imperfections on the substrate. ii) Some genera (*Lepidocyrtus*) inhabit the sides of the container when numbers become greater and some genera (*Hypogastrura*) sometimes form aggregates on the sides of the containers. These cannot be counted easily by photography. iii) Collembola go into holes in the surface or spaces between the medium and the sides of the container. iv) Finally, *H. essa* aggregates to such an extent that individual Collembola are difficult to count from a photograph. 4) An ocular grid was also tried for counting sections of the substrate until the entire surface was counted. Although the movement of Collembola while being counted was found to be of assistance, movement of Collembola outside the grid was found to be distracting. Consequently, a low-tech solution, (5), was to prepare a 12 mm square window from black construction paper and use this in the ocular of the stereomicroscope instead of the ocular grid. This window could be positioned to view subsequent sections of the culture surface so that the entire surface could be counted. This method was checked against counts made with a magnifier until it could be done with accuracy and then was used in the remainder of this work.

Analysis of population curves

Some discussion of the pure-culture population growth has already been mentioned in the section above on culture methods. Table 1 was already

described in the Results section. It is noteworthy that the species which required additional removal of groups from the ANCOVA analysis so that the equality of slope significance was at least 0.05 were those with the lower ranks of common slopes (*H. essa,* 5th; *O. folsomi*, 6th; and *F. similis* , 7th in rank). It is possible that these are slower reproducing species. On the other hand, culture conditions may have not suited these species. Support for this conclusion is given by Sharma and McKevan (1963). They found that *F. similis* required both baker's yeast and decaying leaves in order to reproduce. In addition, *H. essa* reproduced in greater numbers during the direct interaction trials at higher temperatures.

In addition to comparing the linear regression slopes for each of the species over the entire eleven weeks, this same period was also broken into three linear segments consisting of an initial oviposition stage, increase stage, and plateau stage. Correspondence of actual natural logarithm-transformed data to the three regression lines is best shown for *O. encarpatus* in Figure 21. The data used were the remaining selected data after removal of the groups indicated in Table 1. The three periods correspond respectively to Weeks 1 -3, Weeks 4-7, and Weeks 8-11. Table 2 shows the slopes and ranks for these three periods for all of the species.

Using Table 2 with reference to *O. encarpatus* indicated that this species has a moderately flat initial stage and plateau, but the increase stage is ranked 2nd, giving this species an overall rank of 3rd over the entire period. *P.* sp A has a somewhat steeper initial period, the highest slope of increase, and a moderately high plateau slope, giving this species an overall rank of 1st over the period. *Lepidocyrtus* sp. J, on the other hand, has an almost flat initial period, a moderate increase and a plateau slope equivalent to *P.* sp. A , giving this species an overall rank of 2nd over the period. *H. essa*, on the other hand,

has an initial slope which ranks 1st, an increase slope ranking 6th and a plateau slope ranking 1st. In other words, the three slopes for *H. essa* are closer to being linear over the entire period than for any other species examined. Although this species had an overall rank of 5th for the period, given the extent of aggregation and steep slope of the "plateau" for this species, it is reasonable to expect this species eventually to outstrip other species whose increases had become more inhibited. Finally, *F. similis* with ranks of 7, 7, and 6 for the three periods and an overall rank of 7 is clearly the slowest reproducing species and mention is again made of the possibly inadequate diet (Sharma and McKevan, 1963).

Interactions

Park's (1948) study of *Tribolium* beetles is a classic example of pairwise studies. Park found that temperature as well as a sporozoan parasite, *Adelina*, could alter the results of competition between two species of *Tribolium , T. confusum* and *T. castaneum* . The influence of both abiotic and biotic factors in pairwise studies of *Collembola* has also been an issue. One approach to the study of the biotic factors is to construct a ranking such as that built for *Drosophila* by Gilpin, Carpenter, and Pomerantz (1986). An attempt to construct a ranking was performed here. The approach used was to determine first the monoculture growth in numbers by week and to use these data to determine the week when numbers begin to plateau. This was considered the optimal time to note differences between populations when making a single count. The preparation of the 175 containers consisting of 5 of each combination, as well as being time consuming to count, was a logistical challenge for a single worker and did not allow proper controls for bias. After

performing this work, it was concluded that smaller scale studies of each species in turn would allow greater numbers in each group, allow for control for bias and also be more consistent with the statistical analysis applied.

Table 3 shows the results of calculations of 95% confidence intervals for the number of each species at the eight week time period. These intervals are shown on Figures 22 through 28 for each of the species. It is noted that a number of the control groups as well as some of the interaction groups are greater in number after eight weeks than the 95% confidence interval obtained from previous monoculture population counts. This could have occurred because the interaction study took place during the months of June and July at higher than average temperatures.

In each of the Figures 22 through 28, there are two control groups. Controls for the first group, for example, are numbered 1:0 and 1:1. The first group was started with 10 individuals and the second group was started with 20 individuals. Keddy (1989) described two types of pairwise experiments. The first is the substitutive design in which the mixtures have half as many individuals of one species as do the controls, but the total number of individuals in the mixed cultures and the controls are the same at the outset. Van Cott (1982) used this design for competition experiments. The second is the additive design in which the mixtures have the same number of individuals of one species as do the controls so that the mixed cultures are started with a total of twice the initial numbers as the control containers.

The design used for direct interactions in this study was the additive design. The null hypothesis statement was: “The addition of an equal number of the same or another species has no effect on the resulting numbers after eight weeks.” The F values and probabilities for the ANOVAs are shown in Table 4,

and these indicate that the alternative hypothesis must be accepted in each case.

As controls with twice the number of the mixtures (double controls) were also included in this study, it could easily be analyzed as a substitutive design. These were included not primarily for this reason, but as a measure of whether there were sufficient starting numbers with 10 individuals of that species in single controls. Some of the groups had double controls with a lower number than the single controls (Groups #2, #3, and #4), but none of these differed significantly. On the other hand, some of the groups had double controls with a greater number than the single controls (Groups #1, #6, #7 and #9) but only the double control of Group #9 (*O. folsomi*) differed significantly from the single control. Perhaps *O. folsomi* required more than 10 individuals at the start for numbers to increase at a greater rate as shown in the double control. Mertens and Bourgoignie (1975) found for *Hypogastrura viatica* that the initial aggregation on a newly prepared substrate was the same when started with 16 or 32 individuals, but decreased substantially when started with eight or less. Usher and Hider (1975) also noted that aggregation of *F. candida* only occurred when sufficient numbers were present. Having a sufficient starting number for aggregations could be important for reproduction if a primer pheromone responsible for reproductive synchrony is subsequently elicited (Verhoef, 1984). On the other hand, Draheim and Larink (1995) found that singly maintained *F. candida* produced more eggs than *F. candida* maintained in groups of ten. Other factors, such as temperature, could have affected reproduction of *O. folsomi* because numbers of the double control were above the 95% confidence interval for the population counts also started with 20 individuals.

Using figures 22 through 28, an interaction ranking was constructed by counting the number cases for each species that are significantly reduced from the control group. After doing so, the following order was obtained and noted at the bottom of Table 4 showing from lowest to highest number of cases: Group #7, #9, #2, #1 & #3, and #4 & #6. It was not surprising to find Group #7, *P.* sp. A, first in the ranking, as this group reproduced most prolifically when compared to the other groups. Group #9, *O. folsomi* , on the other hand, was surprising. Although *O. folsomi* ranked 6th in comparison for the slope of the natural log for numbers in monocultures, it was apparent that this species was not greatly affected by the presence of another species in pairwise combinations. At the other extreme, Groups #4 (*H. essa*) and #6 (*O. encarpatus*) were in the penultimate and ultimate position in terms of the extent to which these cultures were affected by interactions and were at somewhat mid-range positions in the ranking for monocultures. In other words, this ranking indicated the extent to which a population of each species was affected by additional numbers of the same or other species as stated in the hypotheses for the ANOVA testing and not necessarily which species was more dominant in numbers.

A further comment is made here on Group #6, *O. encarpatus.* Longstaff (1976) found that another species,*Onychiurus armatus* (Tullberg), did well in monoculture but not in combination with the other species tested. Observations with *O. encarpatus* were somewhat similar. This species tolerated small numbers of *Lepidocyrtus* sp. in culture without obvious effects, but when the numbers of *Lepidocyrtus* increased, the numbers of *Onychiurus* declined. Such a decline in numbers was not observed to such a great extent, however, in combination with *Onychiurus folsomi* or with *Proisotoma* sp. A, and the numbers of *O. encarpatus* in these combinations were even greater than the other species. In combination with *Folsomia similis*, *O. encarpatus* was

dominant in numbers, but both species were reduced significantly in numbers as compared to their respective controls. The results of starting test populations with different ratios, as did Longstaff (1976), for these species would be of interest for future study.

In order to summarize the results of the combinations as pairs, Table 5 was prepared showing significant differences from controls, either negative (-) or positive (+), as well as with no significant difference (0). The possible outcomes were that both groups increased, one group increased, there was no difference, one group decreased, or both groups decreased as compared to their respective controls. After tallying numbers of groups in each category excluding the double controls (0, 1, 5, 11, and 4 respectively), it was apparent that the most frequent consequence of pairwise combination was that one of the species was significantly decreased in numbers as compared to its control (52% of the combinations). In approximately 19% of the combinations, both groups were decreased. Longstaff (1976) considered that when both groups are depressed with steadily decreasing totals, there is competition between the species. As the counts in this work were not done over a time period and there were also fungal contamination in some of the combinations, no conclusion about competition is made here. Furthermore, Christiansen *et al.* (1992) concluded that they were unable to identify the interactions between species of Collembola as competition and simply referred to these as interspecific interactions.

In 45% of the combinations in which one group decreased, the second group was *P.* sp. A (Group #7). In combinations in which both groups decreased, Groups 3, 4 and 6 (*F. similis*, *H. essa*, and *O. encarpatus*) were prominent. Groups which had no significant difference were combinations with Group #9, or Group #3 combined with Group #1 or #2 (the two *Lepidocyrtus*

species). Groups which increased involve only combinations with Group #9 (*O. folsomi*).

The above results indicating that one species or both are reduced in pairwise combinations in direct interactions are consistent with the results of other studies. Van Cott (1982) found that either one or both species are reduced in pairwise competition and did not note any cases in which one species stimulated another as was noted by Christiansen (1967). Hägvar (1995) in citing Nygard and Solberg (1985) noted that this study found paired species of Collembola to have reduced numbers when compared to monocultures. This work supports reduced numbers, as compared to controls, in 71% of the combinations, with 52% having one species reduced and 19% having both species reduced (as previously noted). Close to 24% had no significant difference in numbers and the remaining 5% had an increase in numbers. Longstaff (1976), Christiansen (1967) and Christiansen *et al.* (1992) noted situations in which one species stimulated another. This work indicates that pairwise combination of two species results in a majority of cases in a reduction of one or both species as compared to its control, but in a small percentage of cases could result in an increase of one of the species.

Keddy (1989) has described pairwise interactions as being to a greater or lesser extent symmetric or asymmetric. On one side of the interaction continuum, symmetric interactions, the two populations have equal effects on each other; whereas, at the other extreme, asymmetric interactions, one of the population is dominant over the other. Consequently, it is necessary to consider the interaction in pairs as well.

Christiansen (1967) described three possibilities for dominance in pairwise interactions: type 1) one species is dominant for the entire period; type 2) dominance switches from the first species to the second; and type 3) neither

species is dominant. Because the direct interaction data was taken at one period, it is not possible to say which of the pairs, if any, switched dominance during the period of the trial. In addition, the comparisons made in developing Table 5 were made for each individual species and did not examine the interactions occurring within the pairwise combinations. Christiansen *et al.* (1992) reviewed the results of all prior direct interaction studies and concluded that 76% were type 1, 12% were type 2 and 12% were type 3. Furthermore, the type 1 interactions were consistent in 73% of the pairing, whereas the type 2 and 3 results were consistent in only about half of the pairs. Usher (1985) also concluded that: "Competition between soil arthropods is generally asymmetrical." In this study, containers were examined six months after counting and observations made on the condition of the cultures. In the combination between *O. encarpatus* (Group #6) and *P.* sp. A (Group #7), for example, after this six-month period, *O. encarpatus* was dominant in four out of five containers. This dominance was essentially the same when counted after two months. On the other hand, *O. folsomi* (Group #9) paired with *L. fimicolus* (Group #2) after six months had one container in which *O. folsomi* was dominant. At two months, the *Lepidocyrtus* species was dominant. At three months in this container, the two species were equal in numbers. At six months, however, *O. folsomi* was clearly dominant in this one container. Although this example does represent a type-2 change for this container, the interaction between these two species cannot be considered to be type 2 because the other containers for this combination had *Lepidocyrtus fimicolus* as dominant.

The discussion for Table 5 considers the pairwise combinations with reference to their controls and not with reference to a paired species. Figures 29 through 35, on the other hand, shows the combined numbers for each of the pairwise combinations graphed as stacked column graphs by group. Although

asterisks on these graphs indicate a significant difference from the single control by Dunnett's test, this has little meaning when the combination was with a prolific species, such as combinations with *P.* sp. A (Group #7). These graphs allowed comparison of mean relative numbers of each combination and a comparison to the rank order of slope for monocultures determined in Table 1.

For comparing pairs of species, the only data available were population numbers. The frequency of dominance for each combination was tabulated by group after inspection of figures 29 through 35. If the portion of the column graph which was solid was greater than the portion which was striped, then the species represented by the solid portion of the column graph was considered dominant. Group 1 for *L.* sp. J, for example, in figure 29 had four dominant combinations. Table 7 summarizes the number of dominant combinations for each species. At the extremes of this ranking, probably Group #7 (*P.* sp. A) is closest to dominance and Group #3 (*F. similis*) is closest to subordinance.

Such an ordering was expected if the magnitude of decrease (or increase) resulting from interactions was considerably less than the magnitude of the numbers for monocultures, the difference between them, or if the change was symmetrical. With the exception of Group #4 (*H. essa*), this order was the same as Table 1 for monocultures. This comparison is shown in Table 7. It was apparent in Figure 13 and Table 2 for monocultures that *H. essa* (Group #4) increased at a higher rate than other groups during Week 8 through Week 11. A possible explanation for this change in position during the direct interaction studies was that the higher temperatures of June and July allowed a greater increase for *H. essa* by Week 8 and resulted in this difference in position. Furthermore, if the numbers of the controls from the direct interaction study are used instead of the initial monoculture data, the position of Group #4 (*H. essa*) would be shifted to the 2nd position, which is consistent with this ranking.

When the individual combinations were examined for their consistency with the monoculture ranking, the following inconsistencies were apparent: Groups 1:4, 2:4 (and their reciprocal 4:1 and 4:2), 4:6 (and 6:4), 2:6 (and 6:2), and 6:7 (and 7:6). The higher reproductive rate of Group #4 (*H. essa*) during the direct interaction trials explains to some extent the inconsistencies for the combinations in Groups 1:4, 2:4, and 4:6. With regard to the other combinations, it appears that Group #2 (*L. fimicolus*) was more dominant in combination with Group #6 (*O. encarpatus*), and that Group #6 (*O. encarpatus*) was more dominant in combination with Group #7 (*P.* sp. A) in four out of five containers. Groups #4 and #6 (*H. essa* and *O. encarpatus*) were already noted as being in the penultimate and ultimate position in terms of the extent to which these cultures were affected by interactions as compared to their respective controls. With reference to the inconsistencies in numbers mentioned above, the predominance of groups #4 and #6 (*H. essa* and *O. encarpatus*) also suggests that factors other than the rate of reproduction could be involved in the outcome of combinations of some species.

In conclusion, except for several specific exceptions, the number in monoculture at two months was an approximate prediction of dominance in combination. This dominance ranking differs from the ranking built from the effect on the numbers of each individual species in combination as compared to its control as shown in Table 4. This dominance ranking supports Usher's (1985) conclusion that the attributes of the life-history which determine the rate of increase of a collembolan species may be as crucial as the interactions between species for the outcome of which species is dominant. As the pairwise combination study was continued for only two months and not for three or more months, or to the point of the exclusion of one of the species, the results are not entirely comparable to those of others. For example, the direct interaction study

of Christiansen *et al.* (1992) was continued for three months and the study of Van Cott (1982) was continued for up to six months.

Preconditioning

One of the difficulties in comparing trials with Collembola is obtaining results which are not so variable within a group so as to not differ significantly from other groups. This problem arises when some cultures reproduce very well and others not at all. Christiansen (1967) found some consistency in this variability in that about 25% to 38% of cultures did not reproduce. Given this consistency and high percentage of type-1 interactions in which one species dominates from the start (Christiansen *et al.*, 1992), it was tempting to study only the initial weeks in combination trials to examine this variability rather than to wait two to three months for results. Tables 10 and 11 give results of the Preconditioning II investigation over a four-week period for one species, *Lepidocyrtus* sp J. Table 10 shows initial oviposition. Although these results were not significantly different, the control group did have the highest egg count, but the scraped group had the lowest variance of all the treatments. In Table 11 showing weekly counts of collembolan numbers, however, this initial situation changed (though not significantly so), and by the end of four weeks, the treatment with the killed yeast had the highest numbers and the control had the least variance. As these results were inconclusive, a longer-term, two-month trial which includes the period of increase occurring in the second month would be preferred for future work in order to demonstrate any differences between treatments.

The motivation for doing the Preconditioning II trial was to test two assumptions regarding chemical factors. Instead of using a preconditioned new

containers, Van Cott (1982) performed substrate conditioning by transferring Collembola into previously occupied containers from which the culture surfaces were cleaned but maintained intact. Van Cott found inhibition in containers conditioned by the same species, particularly in the case of *S.(S.) curviseta*. Van Cott, however, did not conclude whether the observed inhibition resulted from self-inhibition from substrate conditioning or from inhibition from yeast byproducts (Waldorf, 1971). That pheromones may be waterborne was previously shown by Mertens, Blancquaert and Bourgoignie (1979) for the aggregation of *Orchesella cincta* on preconditioned filter paper. The results here with *Lepidocyrtus* sp. J do not help to support either conclusion as there were not significant differences between the groups. The results of Christiansen *et al.* (1992) with other species did not support self-inhibition as being stronger than interspecific inhibition, but did support interspecific inhibition through substrate conditioning in most of the combinations studied. No interspecific inhibition trials were done in this study.

In another preconditioning study in this work, three of the species were counted for eight or nine weeks and control containers were compared to treatment containers preconditioned with conspecific frass rather than a slurry of plaster/charcoal scraped from the surface. Verhoef (1984) found evidence for pheromones in the fecal pellets of three species of epedaphic entomobryid Collembola. Figure 37 for *Lepidocyrtus* sp. J appears to have a greater central tendency than the control Figure 36. Although Figure 39 for *H. essa* has approximately 1/3 of the containers non-reproducing, this is almost the reverse of the control in Figure 38 in which only 1/3 are reproducing and 2/3 are non-reproducing. The control Figure 38 is clearly bimodal. The distribution for *O. folsomi* in Figure 41 is somewhat more uniform with 50% of the counts clustered around the medium and an equal number of high and low counts as compared to

the control in Figure 40 with an almost equal spread for all but one high count. The graphs in Figure 36 through Figure 41 indicate that the tendency for results to be bimodal with reproducing and “non-reproducing” containers could be modified to some extent by the treatment method. These results also suggest that deleting containers with low reproduction during the testing of treatment methods may possibly give a false picture of results. When a group has bimodal results due to methods or culture conditions, the elimination of the lower counts from analysis will result in the other group with greater central tendency as appearing inhibited in comparison. Table 8 shows that t-tests on the means for treatment and controls for the final week of the trial were not significantly different. The significant difference in early oviposition in one of the groups shown in Table 9 indicates that this treatment had some effect at least initially with one of the species. Most likely there is more than one factor which could affect the stadia differently. Finding the appropriate methods to reduce the variance between control cultures is a necessary first step if any significance is to be shown between controls and treatment groups. Previously, Christiansen (1967) investigated the effect of changes of abiotic conditions in laboratory culture. Although having cultures of *Folsomia candida* at constant or fluctuating temperature altered the proportion of reproducing cultures for Christiansen (1967), Christiansen *et al.* (1992), determined that in interactions with other species, “Varying temperature or light seldom had any significant impact on outcome.”

Contamination by Other Organisms

A number of authors have mentioned the difficulty in maintaining collembolan cultures free of fungal contamination. The experience here was

essentially the same as that of Goto (1961). Even though the dry culture medium was heat sterilized, boiled distilled water used for moistening the medium, and UV sterilized after setting, contamination still occurred. Booth and Anderson (1979) were unable to keep containers of *Folsomia candida* sterile and noted growth of fungi even in containers without food. They noted also that fungi will differ in food quality depending upon the species and growth conditions for that fungi. Van Cott (1982) mentioned for maintaining cultures: “Excessive mold was removed where possible.” Van Cott (1982) also noted that “mold was found on many of the eggs...” of several species in his work, including *Sinella curviseta* , and that hatching percentage for this species was lower than that found by other researchers. Van Straalen (1985), on the other hand, noted that the egg stage is not very vulnerable to fungal attack and that hatching approached 100% even when laboratory cultures are contaminated with fungi; however, mortality after hatching was high and is also variable and could be a key factor in collembolan population fluctuation. Although Van Cott mentions that “competitive interactions might be changed by changing the food type” in relation to fungal feeding and that “toxification” could be one “mechanism of competitive interaction”, he did not suggest that fungal contamination could alter the results of pairwise interactions. Walsh and Bolger (1993) do indicate that changing fungal diets of mixed collembolan cultures can change the type of outcome, which suggests that fungal contamination could have an impact on results.

Contamination from several as yet unidentified fungal-like microorganisms occurred in this study. First observed in *L. fimicolus* was a cottonball-like fungal growth on the yeast and upon which this species would feed. Noted initially in *H. essa* cultures, a carpet-like weft of fungal growth would cover much of the substrate and *H. essa* would be observed under or on the growth. Hyphae were observed growing from cadavers of this species. Mills &

Sinha (1971) noted of another species of *Hypogastrura* , *H. tullbergi* , that this species preferred fungi in low mats. Noted in *F. similis* and *O. encarpatus* was a crust-like fungal growth on the surface of the yeast, much like mold on cheese. This must have been unpalatable, because *O. encarpatus* would eat inside the yeast granules with mold on the outside, but were not observed feeding on the outside where mold was present.

Because the organisms were not sampled for microorganisms at the outset, it is not known whether these fungi were associated with the gut or surface of these Collembola when collected or were from contamination which entered the cultures subsequently. Hassall, Visser and Parkinson (1986) have noted that a collembolan species, *O. subtenuis*, in a particular site was capable of carrying the spores of 120 different fungi. Although contaminating organisms carried inside or upon the collembolan species used was a possible source of this contamination, the fungi observed could also be opportunistic species whose spores entered the cultures during feeding and watering and which were able to thrive because of suitable conditions and absence of other fungal species.

Containers with fungal growth were noted during these studies and some of these were analyzed by t-tests. The results are shown in Table 6. Numbers of *H. essa* (species #4) in the containers of Group 1:4 of the direct interaction study with fungal growth were significantly lower than in those without fungal growth. In these same containers, those with and those without fungal growth did not differ significantly for the other species (*L.* sp. J, species #1). The significantly lower result for numbers of *H. essa* which was associated with fungal contamination did lower the mean for this group which was indicated with an asterisk as significantly lower than the control in Figure 25. However, the containers without fungal contamination were also significantly lower than the control. *L.* sp J, which was not significantly reduced in groups with and without fungal contamination,

also had a significantly lower mean for combination 1:4 in Figure 22. A similar situation was noted for group 2:3: Containers with fungal growth have numbers of *L. fimicolus* (Group #2) significantly less than numbers in containers without fungal growth. On the other hand, numbers of *F. similis* (Group #3) in these same containers with and without fungal growth did not differ significantly. Comparison of the means for Group 2:3 with their respective controls indicated that this combination did not differ from these controls. Although neither example was associated with a change in dominance, these results suggest that fungal growth in cultures in combination with other factors could be associated with asymmetrical results in pairwise studies.

Hawksworth (1991) considers the diversity of fungi to be second only to that of insects. Their long evolutionary history offers the possibility of many relationships including the co-evolution of mutualism. A collembolan preference for feeding on spores over hyphae and greater frequency of ovipositing on more preferred fungi are suggested as evidence for mutualism (Moore, Ingham and Coleman, 1987). Fungi may have a negative relationship with Collembola through predation, such as *Arthrobotrys* (Christiansen, 1964) or through pathogenesis. Fungal entomopathogens, such as *Beauveria bassiana* , have narrow host ranges and susceptibility could be related to differences in the surface of the cuticle (Federici and Maddox, 1996; Lussenhop, 1992). *B. bassiana* was found in 22% of the Collembola sampled by Visser, Parkinson and Hassall (1987), but the frequency of this insect pathogen in the soil layer sampled was only 7%, so Collembola do not avoid this species. On the other hand, *Trichoderma* species are much more frequent in the same soil layer, but are infrequently isolated from Collembola. Visser *et al.* (1987) concluded that *Trichoderma* species could be toxic to some Collembola. Walsh and Bolger (1990) determined that two *Trichoderma* species were the least preferred fungal

species in 45 tests, but one of the Collembola studied had the greatest survivorship on one of these least preferred species. Results of Shaw (1988) also indicate that Collembola often increase more successfully on species other than the most preferred species. Soil arthropods are also in contact with facultative pathogens. Lussenhop (1992) mentions *Aspergillus flavus* and *Fusarium* species as examples of these. Lussenhop (1992) estimates the extent of entomopathogenic fungal disease in collembolan populations by citing Purrini (1983): "...only 0.7% of the Collembola in European forests were infected with fungi; another 0.7% were infected with bacteria, and 2% with microsporidia... 24% Collembola...carried no inoculum.... Collembola are flexible and are able to remove surface spores. The elaborate cuticular sculpture and setation of euedaphic Collembola may be an adaptation to minimize contact with fungi." Fungal pathogens may not be toxic at all stages of development. Sabatini and Innocenti (1995) determined that Collembola tested on a fungal cereal pathogen, *Bipolaris sorokiniana* , were able to feed on *B. sorokiniana* conidia, and that many of the conidia were able to germinate from the collembolan feces. The mycelia which grew became toxic only after two days and the hyphae repelled the Collembola tested. At least 12 hours of contact with the toxic metabolites were required for a lethal dose. Collembola also have age-specific susceptibility to fungal attack, with young stages being particularly susceptible (Christiansen, 1964; Keller and Zimmermann, 1989).

Fungi could have a positive relationship with Collembola as an important food source, but food preference differs by species (Walsh and Bolger, 1990). The availability of food, rather than overcrowding, has been shown by Usher, Longstaff, and Southall (1971) to be the limiting resource for the rate of growth and maximum density of *Folsomia candida.* Takeda (1987), in studying collembolan community structure in forest soils, concluded that numbers also

responded to changes in resources. If unpalatable fungi were to cause the yeast in the experimental containers to become limiting, it is possible that resource competition would cause one of the species of a pair to be competitively displaced if its equilibrium resource requirement (R*) is larger than that of the other species (Tilman, 1982). The same situation could also arise in the event of insufficient supply of yeast or too infrequent feedings. On the other hand, Draheim and Larink (1995) found the egg production of *Folsomia candida* in groups of ten to be between 100 and 120 eggs, but the egg production of singly maintained *F. candida* to be between two and four times higher (200 to 500 eggs). Green (1964) and Hutson (1978) previously suggested that crowding reduced fecundity in *Folsomia candida*. If both food and space are limiting resources for Collembola, then the analysis of competition becomes more complicated. This would be difficult to study, however, unless cultures could be maintained without other contamination. Furthermore, direct and indirect interactions other than resources could impact numbers. Christiansen *et al.* (1992) concluded from their studies that: "... there were, in most if not all cases, several mechanisms at work at once."

Beyond what has already been mentioned about contamination, volatiles from fungi have been shown by Bengtsson, Hedlund and Rundgren (1991) to be associated with the searching, arresting and feeding behavior of Collembola and food discrimination. Any relationship, however, between these volatile compounds and the pheromonal/allomonal compounds of Collembola has not been established. Leonard and Bradbury (1984), however, have cautioned those doing long-term food preference studies that semiochemicals produced by Collembola will produce aggregations around the conditioned areas.

The observation made during the population studies in this work that fungal hyphae are not frequently observed growing on collembolan frass prompts

speculation. Borkott and Insam (1990) suggest that bacteria are mutualistic with *Folsomia candida* and that as this Collembola feeds on chitin, the bacteria increase. Hale (1967) also notes that *Bacillus* species in the guts of some Collembola allow them to ingest the cuticle of exuviae and possible chitin remnants of arthropods. Christiansen's speculation on intraspecific coprophagy in Collembola is also appropriate to mention at this point: "...it is more than probable that digestion, at least in soil Collembola, is a cooperative venture; food material passes through the digestive tracts of many individuals, and under the influence of bacteria, fungi, and the several sets of digestive enzymes becomes more and more utilizable. At every passage in this chain, some nutriment is yielded" (Christiansen, 1964). Lussenhop (1992) mentions the long evolutionary history of Collembola with bacteria and fungi and because of this long co-occurrence, interaction should be expected. Lussenhop (1992) also mentions collembolan feeding on dietary clay in relation to adsorbed bacterial enzymes. On the other hand, Harasymek and Sinha (1974) in studying *Proisotoma minuta* and *Hypogastrura tullbergi* on a number of single bacterial diets concluded that, "...bacterial species found in the soil are toxic to Collembola, and probably have little nutritive value to permit survival." Furthermore, Simonov and Dobrovolskaya (1994) found that Collembola have little influence on bacteria in the soil.

Another possible explanation for what seems to be reduced fungal growth in collembolan frass could be collembolan pheromones in fecal pellets (Verhoef, 1984). Blum (1996) notes examples in other insect groups in which insect pheromones have antifungal properties. A further explanation could be the reduced viability of fungal spores which have passed through the collembolan gut, as noted by Visser *et al.* (1987). It is also possible in the field that volatile oils from plants present in the soil could favor the growth of bacteria over fungi (Vokou, Margaris and Lynch, 1984).

Although contaminating organisms could alter the outcome of pairwise interactions to some extent, the importance of the life-history attributes already mentioned in the Interactions section must be stressed. A number of factors could affect the rate of increase for a culture: 1) the age and condition of the culture used; 2) culture methods; 3) starting numbers; 4) presence or absence of contaminating organisms; and 5) other factors involving interactions between Collembola. Christiansen *et al.* (1992) reviewed these other factors and their impact on pairwise interactions in Collembola.

Other factors

Christiansen *et al.* (1992) categorized these factors in their study into direct interactions, substrate conditioning, and pheromonal/allomonal factors. Direct interactions could include interference with feeding, interference with oviposition, oophagy, and destruction of spermatophores (Christiansen *et al.* , 1992; Van Cott, 1982; Hedlung, Gunnarsson and Svegborn, 1990). When doing direct interaction pairwise trials, it was not possible to determine the extent of the influence of substrate conditioning and airborne chemical factors because these factors could not be separated in such trials from those involving direct contact. Studying substrate conditioning and airborne chemical factors is important for gauging the influence of pheromonal/allomonal factors in pairwise trials. It was felt, however, that prior to studying chemical factors, those factors responsible for the “irregular and indeterminate results” (Christiansen, 1967) should first be investigated and ameliorated.

Other reports have shown that chemical factors are evident. One example of these is the toxic haemolymph of the Onychiuridae. Christiansen (1964) cited autohaemoragy in the genera *Hypogastrura* and *Onychiurus.* Bauer and

Christian (1987) noted that the Onychiurid, *Tetrodontophora bielanensis* (Waga), released volatile warning alkaloids that deter predators and were antimicrobial as well (Blum, 1996). Blum (1996) has reviewed semiochemicals in arthropods and noted the parsimony of volatile compounds such as 2-heptanone in some insects that serves both as an alarm pheromone eliciting aggregation, a defense allomone, and an antifungal agent. Aggregation pheromones in *Heteromurus nitidus* were found by Krool and Bauer (1987) to be sexual pheromones secreted after maturity. Tempering the suggestion of parsimony, however, were the results of Christiansen *et al. '*(1992) that 75% of the airborne pheromonal effects were negative, whereas 75% of the airborne allomonal effects were positive or neutral. Christiansen *et al.* (1992) inferred from these results as well as others that "there were different mechanisms at work in substrate mediated interaction, airborne chemical mediated interaction and at least sometimes in direct interactions."

It is apparent in this study, however, that except for several exceptions mentioned previously in the Interactions section, these factors do not have a greater impact on numbers than the life-history attributes.

It is suggested for the future that if such work is to be related to the community, a particular site or habitat be selected for long-term study, the Collembola contained there be identified, their frequency or dominance be calculated, and the microorganisms on or in the Collembola selected for culture be identified at the outset. Furthermore, constant temperature and humidity conditions for culturing also would be of assistance by allowing more consistent conditions from one trial to the next and possibly more consistent results.

The suggestion that other organisms, such as fungi or bacteria, could have an impact on the results of pairwise studies makes the analysis of these collembolan species solely in pairs perhaps too narrow a focus to produce a

clear view of these interactions. It is unfortunate that there were not merely three species to consider in pairwise combinations of Collembola as for Park's (1948) work on *Tribolium*. With a number of contaminating species that may serve as food and/or pathogen, an analysis of interspecific interactions becomes complex. This is probably best stated by quoting Thompson (1994): "Studies of pair-wise interactions alone are insufficient for understanding the evolution of interactions in general and the coevolutionary process in particular. We have enough studies now to know that the interpretation of interactions between pairs of species can be terribly misleading when separated from the community, and sometimes geographic context in which the interaction takes place. Detailed studies of the mechanisms of competition between pairs of species, for instance, are important, but only when analyzed in the context of how those mechanisms affect individuals in the context of the communities in which they operate."

Conclusions

1) Although increase of collembolan species fell into three rate categories (high, medium and low), the rates during the mid-period of increase differed little. Differences in rates of increase occurred primarily in the initial period and plateau period. Results indicated that temperature, humidity, diet, and substrate conditioning affect the numbers attained and their variability.

2) When species were combined in pairwise combinations, the majority of the combinations experienced a significant decrease in one or both of the species when compared to its respective control. The ranking developed from this comparison indicated the extent to which each species was affected by the presence of another species and not necessarily its dominance in combination.

3) A second ranking obtained from the frequency of dominant groups in pairwise combinations was roughly equivalent to the monoculture ranking for rate of increase. Consequently, the relative rates of increase are of major importance to the outcome of pairwise combinations at two months' time. Because this study was of less than three or more months' duration, it is not entirely comparable to those studies done for longer periods.

4) This outcome of pairwise combinations is complicated by other factors which are evidenced by the inconsistent groups when pairwise dominance and monoculture rates are compared. This work was unable to pinpoint any single factor, but direct interactions between species, semiochemical factors, and presence or absence of other organisms may impact the pairwise outcome in addition to the relative rates of increase.

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APPENDIX 1

Following is a list of collembolan species that are either recorded for Southern California or are probable for occurrence in the area. This list was

compiled from a World List of Collembola by P. Bellinger and K. Christiansen with the assistance of Dr. P. Bellinger. Notations are indicated as follows: "yes" if there are records from the southern counties and "bracketed" if there are records from northern and Baja California. For species recorded from California but not south of the Tehachapis, the closest county or locality is noted. Also, those species with either obscure or recent records occurring in this area may also be noted by location.

Hypogastruridae

Ceratophysella Börner, 1932

boletivora Packard, 1873	Yes
denticulata Bagnall, 1941	Yes
gibbosa Bagnall, 1940	Yes
guthriei Folsom, 1916	Yes
pratorum Packard, 1873	Yes
pseudarmata Folsom, 1916	Yes
scotti Yosii, 1962	? ("Buena Vista, CA")

Hypogastrura Bourlet, 1839

assimilis Krausbauer, 1898	Yes - see pannosa
bulba Christiansen & Bellinger, 1980	Yes
christianseni Yosii, 1960	Lancaster
distincta Axelson, 1902	San Luis Obispo Co.
manubrialis Tullberg, 1869	Yes Riverside
matura Folsom, 1916	Yes Lancaster
oregonensis Yosii, 1960	Yes
pannosa Macnamara, 1922 [=assimilis - Babenko]	Yes(as"essa")
perplexa Christiansen & Bellinger, 1980	Tolumne Co., Kings Co.
viatica Tullberg, 1872	Fresno Co.

Microgastrura Stach, 1922

minutissima Mills, 1934	Fresno Co.

Mitchellania Wray, 1953	
californica Bacon, 1914	Yes
horrida Yosii, 1960	Yes
virga Christiansen & Bellinger, 1980	Yes Colton
Tafallia Bonet, 1947	
robusta Scott, 1961	Yes
Willemia Börner, 1901	
denisi Mills, 1932	Fresno Co.
intermedia Mills, 1934	Yes
Xenylla Tullberg, 1869	
californica Gama, 1976	Sequoia Nat'l Park
christianseni Gama, 1974	Yes
collis Bacon, 1914	Yes
grisea Axelson, 1900	Yes
humicola O. Fabricius, 1780	Yes
paludis Bacon, 1914	Yes
pseudomaritima James, 1933	Yes
welchi Folsom, 1916	Yes
wilsoni	Yes
Pseudostachia Arlé, 1968	
sp.	San Joaquin Valley
Superodontella Stach, 1949	
cornifer Mills, 1934	Yes
ewingi Folsom, 1916	Yes
Xenyllodes Axelson, 1903	
armatus Axelson, 1903	Probably (Baja CA)

Brachystomella Agren, 1903

neomexicana Scott, 1960	Bracketed-Fresno Co.,Baja CA
parvula Schäffer, 1896	Probably (bracketed)

Friesea Dalla Torre, 1895

grandis Mills, 1934	Bracketed
landwehri Christiansen & Bellinger, 1980	Yosemite
wilkeyi Christiansen & Bellinger, 1974	Fresno Co.

Neanuridae, Neanurinae

Morulina Borner, 1906

multatuberculata Coleman, 1941	Yes

Morulodes Cassagnau, 1955

ambiguus Christiansen & Bellinger, 1980	Tulare Co.
serratus Folsom, 1916	Tulare Co.
setosa Canby, 1926	Yes

Neanura MacGillivray, 1893

growae Christiansen & Bellinger, 1980	Fresno Co.
muscorum Templeton, 1835	Yes

Paranura Axelson, 1902

colorata Mills, 1934	Tulare Co.

Sensillanura Deharveng, 1981

barberi Handschin, 1928	Fresno Co.
caeca Folsom, 1916	Yes

Anurida Laboulbène, 1865

maritima Guérin, 1839	Yes (verbal record)
tullbergi Schött, 1891	San Joaquin Co.,Fresno

Protachorutes Cassagnau, 1955

bicolor Christiansen & Bellinger, 1980	Sequoia Nat'l Park

		Pseudachorutinae
Pseudachorudina Stach, 1949		
	ignota Christiansen & Bellinger, 1980	Yes
Pseudachorutes Tullberg, 1871		
	aureofasciatus Harvey, 1898	Yes
	corticicolus Schäffer, 1896	Bracketed
	lunatus Folsom, 1916	Yes
	subcrassoides Mills, 1934	Yes
		Onychiuridae,Onychiurinae
Hymenaphorura Bagnall, 1949		
	californica Coleman, 1941	Yes
	cocklei Folsom, 1908	Yes
Onychiurus Gervais, 1841		
	dentatus Folsom, 1902	Yes
	folsomi Schäffer, 1900	Yes
	opus Christiansen & Bellinger, 1980	Fresno Co.
	pseudofimetarius Folsom, 1917 (Wilkey?)	
Paronychiurus Bagnall, 1948		
	flavescens Kinoshita, 1916	Yes
Protaphorura Absolon, 1901		
	armata Tullberg, 1869	Yes
	debilis Moniez, 1889	Yes
	encarpata Denis, 1931	Yes
	hera Christiansen & Bellinger, 1980	Fresno Co.
	pseudarmata Folsom, 1917	Fresno Co.
		Tullbergiinae
Chaetophorura Rusek, 1976		

anops Christiansen & Bellinger, 1980	Yes (Kern Co.)
collis Bacon, 1914	Yes
duops Christiansen & Bellinger, 1980	Yes
latens Christiansen & Bellinger, 1980	Fresno Co.
Mesaphorura	
iowensis Mills, 1932	Fresno Co.
macrochaeta Rusek, 1976	San Joaquin Co.
pacifica Rusek, 1976	Yes
yosiii Rusek, 1967	Probable

Isotomidae

Anurophorus Nicolet, 1842	
bimus Christiansen & Bellinger, 1980	Yosemite
Appendisotoma Stach, 1947	
aera Christiansen & Bellinger, 1980	El Dorado Co
dubia Christiansen & Bellinger, 1980	Fresno Co.
Archisotoma Linnaniemi, 1912	
interstitialis Delamare, 1954	Yes
laguna Folsom, 1937	Yes
Ballistura Bîrner, 1906	
schoetti Dalla Torre, 1895	Yes
Cheirotoma Bagnall, 1949	
spatulata Chamberlain, 1943	Yes
Clavisotoma Ellis, 1970	
laticauda Folsom, 1937	Yes (Ballistura)
Cryptopygus Willem, 1901	
ambus Christiansen & Bellinger, 1980	Fresno Co.?
aquae Bacon, 1914	Yes

benhami Christiansen & Bellinger, 1980	Fresno Co.
thermophilus Axelson, 1900	Yes
Desoria Nicolet, 1841	
cancellarei Christiansen & Bellinger, 1980	Yosemite
propinqua Axelson, 1902	Sequoia NationalPark
trispinata MacGillivray, 1896	Yes (Kern Co.)
Folsomia Willem, 1902	
candida Willem, 1902	Yes
diplophthalma Axelson, 1902	Yes
elongata MacGillivray, 1896	? (Scott, D., 1956)
nivalis Packard, 1873	Yes
similis Bagnall, 1939	Yes
stella Christiansen & Tucker, 1977	Fresno Co.
Folsomides Stach, 1922	
decemoculatus Mills, 1935	Yes
parvulus Stach, 1922	Yes
Halisotoma Bagnall, 1949	
marisca Christiansen & Bellinger, 1988	Yes
Heteroisotoma Stach, 1947	
carpenteri Arner, 1909	Yes?
Isotoma Bourlet, 1839	
aspera Bacon, 1914	Yes
viridis Bourlet, 1839	Yes
Isotomodes Linnaniemi, 1907	
fiscus Christiansen & Bellinger, 1980	Fresno Co
Isotomurus Bîrner, 1903	
bimus Christiansen & Bellinger, 1980	Fresno Co.

palustris Muller, 1776	Yes
palustroides Folsom, 1937	Fresno Co.
retardatus Folsom, 1937	Yes?
Paranurophorus Denis, 1929	
simplex Denis, 1929	Yes
Parisotoma Bagnall, 1940	
coeca Yosii, 1966	Santa Lucia Mts.?
notabilis Schaffer, 1896	Yes
Proisotoma Borner, 1901	
bulba Christiansen & Bellinger, 1980	Yes (Kern Co.)
immersa Folsom, 1924	?
minuta Tullberg, 1871	Yes
titusi Folsom, 1937	San Luis Obispo Co.
	Entomobryidae Cyphoderinae
Cyphoderus Nicolet, 1842	
similis Folsom, 1927	Bracketed
	Entomobryidae Entomobryinae
Americabrya Mari Mutt & Palacios, 1987	
arida Christiansen & Bellinger, 1980	Baja CA & Arizona
Calx Christiansen, 1958	
sabulicola Mills, 1931	Yes
Coecobrya Yosii, 1956	
caeca Schött, 1896	Probably
communis Chen & Christiansen 1997	Probably
tenebricosa Folsom, 1902	Yes
Drepanura Schött, 1891	
californica Schött, 1891	Yes

Entomobrya Rondani, 1861	
arula Christiansen & Bellinger, 1980	Yes
atrocincta Schött, 1896	Yes
Entomobrya	
clitellaria Guthrie, 1903	Yes
comparata Folsom, 1919	Maybe [CA, no locality]
confusa Christiansen, 1958	Yes
griseoolivata Packard, 1873	Yes
multifasciata Tullberg, 1871	Yes
suzannae Sott, 1942	Yes
triangularis Schött, 1896	Yes Kern, San Luis Obispo
unostrigata Stach, 1930	Yes
washingtonia Mills, 1935	"California", Santa Clara Co., "Arroyo Seco", San Luis Obispo
zona Christiansen & Bellinger, 1980	Fresno Co.
Entomobryoides Maynard, 1951	
guthriei Mills, 1931	Yes
Lepidocyrtus Bourlet, 1839	
pallidus Reuter, 1890	Uncertain
Mesentotoma Salmon, 1941	
laguna Bacon, 1914	Yes
Pseudosinella Schäffer, 1897	
octopunctata Börner, 1901	Yes
rolfsi Mills, 1932	Yes
sexoculata Schött, 1902	Yes
violenta Folsom, 1924	Yes
Seira Lubbock, 1869	

knowltoni Wray, 1953 Yes

reinhardi Mills Yes Imperial Cty.

Sinella Brook, 1882

aera Christiansen & Bellinger, 1980 Fresno Co.

binoculata Schött, 1896 Yes

curviseta Brook, 1882 Yes

quadrioculata Mills, 1935 Yes

sexoculata Schött, 1896 Yes

tecta Christiansen & Bellinger, 1980 Yes?

Willowsia Shoebotham, 1917

nigromaculata Lubbock, 1873 Yes

Entomobryidae, Paronellinae

Salina MacGillivray, 1894

beta Christiansen & Bellinger, 1980 Stanislaus Co.

trilobata Schött, 1896 Baja CA

Oncopoduridae

Oncopodura Carl & Lebedinsky, 1905

mala Christiansen & Bellinger, 1996 Oregon and possibly California

tunica Christiansen & Bellinger, 1980 Tuolumne Co.

yosiiana Szeptycki, 1977 Yes? [apparent local report]

Tomoceridae

Plutomurus Yosii, 1956

californicus Folsom, 1913 Tulare Co.

wilkeyi Christiansen, 1965 Tulare Co., San Luis Obispo

Pogonognathellus Paclt, 1944

celsus Christiansen, 1965 Tulare Co.

flavescens Tullberg, 1871 Yes

Neelidae

Megalothorax Willem, 1900

incertus Börner, 1903	Yes
minimus Willem, 1900	Baja CA

Sminthuridae, Bourletiellinae

Bourletiella Banks, 1899

arvalis Fitch, 1863	Yes
hortensis Fitch, 1863	Yes

Deuterosminthurus Börner, 1901

lurida Snider, 1978	Fresno Co.
validentatus Snider, 1978	Arizona
yumanensis Wray, 1967	Yes

Prorastriopes Delamare, 1947

coalingaensis Snider, 1978	Fresno Co.
lippsoni Snider, 1978	Yes

Dicyrtominae

Ptenothrix Börner, 1906

californica Christiansen & Bellinger, 1981	Fresno Co.
maculosa Schött, 1891	Yes
marmorata Packard, 1873	Yes

Ptenothrix

vittata Folsom, 1896	Yes

Katianninae

Arrhopalites Börner, 1906

amarus Christiansen, 1966	Yes
caecus Tullberg, 1871	Yes

hirtus Christiansen, 1966	Tulare Co.	
Collophora Richards, 1964		
quadrioculata Denis, 1933	Arizona	
Sminthurinus Börner, 1901		
albipes Schött, 1896	"[Baja] California"	
conchyliatus Snider, 1978	Yes	
elegans Fitch, 1862	Yes	
henshawi Folsom, 1896	Fresno Co.	
quadrimaculatus Ryder, 1879	Yes	
		Sminthuridinae
Denisiella Folsom & Mills, 1938		
sexpinnata Denis, 1931	Yes?	
Sminthurides Börner, 1900		
bifidus Mills, 1934	Fresno Co.	
Sphaeridia Linnaniemi, 1912		
pumilis Krausbauer, 1898	Yes	
		Sminthurinae
Sminthurus Latreille, 1802		
eisenii Schött, 1891	Yes	
Sphyrotheca Börner, 1906		
confusa Snider 1978	Yes	