To the Graduate Council:

I am submitting herewith a dissertation written by Alan B. Cady entitled "Mechanisms of Coexistence between Two Species of Cliff-Dwelling Spiders, Achaearanea tepidariorum and Coelotes montanus." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

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MECHANISMS OF COEXISTENCE BETWEEN TWO SPECIES OF CLIFF-DWELLING SPIDERS, *ACHAEARANEA TEPIDARIORUM* AND *COELOTES MONTANUS*

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Alan B. Cady

December 1984

ABSTRACT

Results from removal, addition, and enclosure experiments conducted with two spider species inhabiting sandstone cliffs indicate that an interplay of inter- and intraspecific competitive effects shape their coexistence. Reciprocal removal experiments of Achaearanea tepidariorum and Coelotes montanus on similar, noncontiguous cliffs showed that Coelotes populations experienced a competitive release in the absence of Achaearanea. Adult and immature Coelotes increased in number, adults reproduced and weighed more, and the immatures ate more and shifted their use of prey types and microhabitats where Achaearanea had been removed. Addition and enclosure experiments further established that intrspecific territoriality within Achaearanea influences their population levels.

Coexistence of these two species appears to be mediated in part by Achaearanea limiting the number of Coelotes on the cliff through predation and exploitation of food and space. The territorial behavior of Achaearanea may also influence the coexistence of Achaearanea and Coelotes by maintaining spaces on the cliffs which are excluded to use by other Achaearanea. This probably provides areas which are then available to inhabitation by Coelotes. Here is an example of intraspecific territoriality within one species of spider facilitating the coexistence of another.

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CHAPTER I

INTRODUCTION

An ecological community is a dynamic organization of coexisting interdependent populations whose actions and interactions are orchestrated by environmental and biological influences. Environmental factors include the climate and habitat physiognomy, while biological pressures encompass competition, predation, mutualism, disease, and parasitism. These factors shape the overall pattern of distribution and abundance of coexisting species within a community.

Knowledge of the mechanisms by which syntopic community members are able to coexist is important to understanding community structure. Coexistence may occur when vital resources are not limiting or when they are partitioned by the use of different habitat spaces (Connell, 1961; May, 1974; Werner, 1977; Hallet et al., 1983), breeding or activity periods (Linsley et al., 1963; MacArthur, 1972; Istock, 1973; Jaksic et al., 1981), diets (Cody, 1974; Pianka, 1974; Munger and Brown, 1981), or trophic apparatus (Wallwork, 1958; Schoener, 1974; M'Closkey, 1976). These mechanisms promote avoidance of competitive interactions, and may have evolved as a result of past competitive relationships (Price, 1975; Schoener, 1982, 1984). If sufficient divergence of niche exploitation does not exist, then competitive exclusion of the poorer competitor is the predicted outcome according to the competitive exclusion principle (Grinnell, 1917; Gause, 1934). However, recent ideas have proposed that this principle is a

theoretical construct, and cannot explain natural examples of coexistence among ecologically similar species (Peterson, 1975; Jacobs, 1979; Lawton and Strong, 1981; Wise, 1981(a); Kareiva, 1982; Tinkle, 1982). This apparent contradiction of the competitive exclusion principle may be related to its operation within an evolutionary time scale, while coexistence is an empirical fact and operates on an ecological time scale. Because of this, parallel or convergent evolution of competing organisms could explain examples of competitive coexistence that are observed today (Connell, 1980; Ghilarov, 1984). Community structure may be greatly influenced by competition between coexisting species, in the past or present (MacArthur and Levins, 1967; Cody, 1974; Schoener; 1982, 1984).

Predators add much to the complexity of ecological systems because they interact with organisms at a greater number of trophic levels than nonpredatory community members (Pianka, 1983). Exploring the mechanisms that allow coexistence among predators may thus yield substantial insight into community structure. Spiders are invertebrate predators, and as such, represent a group which may add considerable information concerning the mechanics of community organization. Spiders are one of the major predators of arthropods in terrestrial ecosystems (Clarke and Grant, 1968; Moulder and Reichle, 1972), and have numerous and varied links with different tiers of food webs. They often constitute a "trophic node," which is a focal point of many links between and within trophic levels. Thus, spiders are a major point of energy exchange within a community, and share an array of interactions with their community cohabitants.

The observed coexistence of spider community members has been attributed to the differential use of space and habitat structure (Turnbull, 1966; Enders, 1974; Post and Riechert, 1977; Uetz, 1976, 1979; Turner and Polis, 1979; Robinson, 1981; Bultman and Uetz, 1982; Abraham, 1983), time of activity (Edgar, 1971; Dondale et al., 1972; Kiritani et al., 1972; Gertsch and Riechert, 1976), breeding periods (Berry, 1971; Uetz, 1977), and prey size (Luczak, 1963; Enders, 1976). Thus, resource partitioning among spider species has been shown to operate as a proximate mechanism allowing coexistence of ecologically similar species.

Competition has been theorized to be one of the ultimate driving forces for divergent uses of potentially limiting resources (MacArthur and Levins, 1964, 1967; Diamond, 1978; Price, 1975). This idea has led to numerous investigations which have attempted to discover, describe, and interpret competitive interactions among different (interspecific) and within the same (intraspecific) coexisting spider species.

Interactions within conspecific spider species may influence community organization by altering the intensity and probability of interspecific contests for limited resources. For example, intraspecific competition may explain the lack of observed interspecific interactions among adult spiders (Riechert, 1978a, 1981). Territoriality in adult spiders is well documented, and often arises from contests over websites, mates, or food (Plett, 1962; Rovner, 1968; Riechert, 1978a, 1978b, 1979, 1981; Schaefer, 1978). Intraspecific territoriality may decrease the levels of interspecific competition by

limiting population levels to below the carrying capacity of the habitat. Thus, resources of possible contention do not become limited and ecologically similar species may coexist. Interspecific territoriality has yet to be demonstrated in spiders.

Interspecific interactions among many different sets of syntopic spider species have been studied, but the overall extent to which between species competition affects coexistence is not well defined. Schaefer (1972, 1974, 1975) determined that distributions of lycosid spiders on a seacoast were influenced more by endogenous factors than by interspecific competition, even though there was a significant potention for competition among species. Although prey levels may have influenced the egg production of two forest orb-weavers, subsequent experiments showed no evidence of interspecific competition (Wise, 1979, 1981a, 1983). Where the densities of two species of old-field orb-weavers were manipulated, evidence of intraspecific competition was uncovered for only one species (Horton and Wise, 1983). However, Spiller (1984) found evidence of exploitative and interference competitive effects between two species of orb-weavers.

Riechert and Cady (1983) determined the extent of overlap in resource use among four syntopic spider species living on sandstone outcrops. Three of the species were found to overlap significantly on temporal, food, and spatial niche axes. Further investigation indicated that space was a potentially limiting factor while prey availability was not. The probability for the operation of interspecific competition within this system was substantial since only one of four

dominant species had niche parameters separated enough from the others to indicate resource partitioning. When all but one species of potential competitors were removed from selected cliffs in an effort to find evidence of competitive release, no changes in population density, egg production, or microhabitat use were found. It was concluded that interspecific competitive effects were not observed because they may have been masked or offset by the operation of other effects. Removal of all other spiders also removed an important source of food for the remaining ones. Potentially limiting intraspecific competitive effects may also have been present. Therefore, there appeared to be no clearly defined mechanism(s) of coexistence operating among three spider species.

The present investigation seeks to unravel how two of these ecologically similar species, Achaearanea tepidariorum (C. L. Koch) and Coelotes montanus (Emerton) coexist on the cliffs. A detailed three year investigation of the two species was undertaken which closely measured not only individual adults throughout their reproductive lives, but also included diet and spatial relations of immature Achaearanea and Coelotes. Experiments were devised to test for the presence of inter- and/or intraspecific competitive effects, and to delineate how different types of competition may affect the coexistence of Achaearanea and Coelotes.

I.1 Hypotheses and Experiments

The initial investigation of Riechert and Cady (1983) showed no clear evidence of resource partioning by Achaearanea and Coelotes, and

although the removal experiments showed no evidence of competitive release (niche shifts, increased densities or reproduction), this result was suspect. The presence of intraspecific competition and/or the impact that removal of all other spider species had upon the food supply of the remaining spiders could be possible explanations. The present study concentrated on investigating the following hypotheses.

1. Interspecific competition is a possible mechanism facilitating the coexistence of Achaearanea and Coelotes.

The first step toward the testing of this hypothesis was the initiation of single species removal experiments. Only Achaearanea or Coelotes were removed from designated cliffs, while all other spider species were allowed to remain. Removal of only one species at a time circumvented the problem encountered by Riechert and Cady (1983) where the deletion of other spider species eliminated an important food source for the remaining spiders. If Achaearanea and Coelotes were competing, then changes may become apparent in one or both of the populations due to competitive release. This experiment tested for the existence of both inter- and intraspecific competitive effects, and also allowed a closer inspection of possible resource partitioning.

If competitive effects were evident, then specific resource(s) of contention needed to be identified. Since Riechert and Cady (1983) found that food was not a limiting factor and that cliff space was, (and that Achaearanea and Coelotes overlap in microhabitat use), an addition experiment was planned (contingent upon the results of the removal experiment) to determine the extent to which the adults of

Achaearanea and Coelotes compete for microhabitat structures which provide websites. A cliff would be saturated with adult female Achaearanea by introducing them in four release groups over a 31 day period. Coexisting Coelotes would then be removed, and two more groups of Achaearanea added to the cliff. If Coelotes and Achaearanea were competing for space, the second additions of Achaearanea (after saturation of the cliffs and removal of Coelotes) might persist on the cliff longer than the previous innoculations. This is because those spiders in the second release group may move into the spaces opened by the deletion of Coelotes. Achaearanea was first designated as the spider to be added due to its numerical dominance and ease of manipulation. Adult female Coelotes were less abundant and more difficult to capture and handle. In addition, intraspecific interactions among Achaearanea were expected to be frequent during this experiment. Information concerning direct intraspecific contests over limited websites could then be monitored. If only intraspecific competition among Coelotes was detected from the removal experiments, then the experiment would involve additions of Coelotes and removal of Achaearanea.

In the event that intraspecific competition was found to exist within one of the species, a third experiment was devised in order to explore the possible effects of hunger on spider spacing within the habitat. An enclosure was built on a cliff to allow manipulation of prey levels and subsequent observations of spider dispersal patterns. Two feeding treatments (sated, deprived) were applied to adult females, and the movements and dispersion of the spiders belonging to each feeding level within the enclosures were monitored.

In summary, the hypothesis of competitive coexistence operating between Achaearanea and Coelotes was tested by the removal experiment (evidence of: competitive release, inter- vs. intraspecific competition) and addition experiment (further details of inter- vs. intraspecific competition).

2. Intraspecific competition allows coexistence.

Operation of intraspecific competition (e.g., territoriality) may maintain a population below average carrying capacity of the habitat. Riechert, for instance, has delineated energy-based territoriality in a desert spider (Agelenopsis aperta) which serves to space individuals such that a limited resource (food) is not overexploited (Riechert, 1978a, 1978b, 1981, 1982). Because intraspecific competition may keep species numbers at levels below the average carrying capacities, resources that could otherwise be potentially limiting are not in short supply. As a result, species with similar life histories would be expected to coexist. This hypothesis will be tested by the removal experiment (general resource utilization of cohabitants), and more specifically by the addition (spatial co-utilization) and enclosure (relation of hunger to territoriality) experiments.

3. Interpredation permits coexistence.

Interpredation (between species or within guild predation) may regulate populations of one or both species to levels where interspecific competion is less intense (Slobodkin, 1961), and thus allow coexistence of two potentially competing species. Spiders (Turnbull, 1966; Edgar, 1969a, 1969b, 1970; Hagstrum, 1970; Hallander, 1970) and

scorpions (Polis, 1980) are well known for their within-guild predation, and will feed on any animals of the appropriate size. Thus, it is likely that predation of one spider species upon another may influence their coexistence and community structure. This hypothesis was investigated by the removal experiment (possible release from predation) and continuing observations of the two species during the study.

4. Other possible explanations of coexistence.

Environmental effects may also operate to regulate populations below their carrying capacity (Andrewartha and Birch, 1954; Wiens, 1977). The intensity of competition may be variable (Grant, 1972; Conley, 1976), and may be in evidence only at times of environmental stress. As a results, resources are not always in short supply, and coexistence of ecologically similar species may be possible. Although this question was addressed in the present study, the choice of the experimental system made this alternative an unlikely one. These spiders occupy a habitat with less exposure to extreme and rapid environmental variations than those in other temperate areas (see next section). This three year study is a continuation of a previous two year investigation of these spiders, thus providing a relatively long sampling period. If competition does occur on a temporal basis among these two species, the study was of sufficient duration to have a reasonable chance to uncover some evidence of it.

Predation and/or competition by nonspider or nonguild members may also be occurring within this system. Preliminary observations have

indicated that these are probably not significant effects upon Achaearanea and Coelotes. However, their populations were closely monitored during this study in order to determine the severity of predation or competition with other syntopic animals.

The methods and results of each experiment are detailed in its own chapter. These results are then discussed in relation to the hypotheses in the final chapter.

I.2 The Study Site

All fieldwork was conducted on sandstone outcrops in the Clear Creek watershed on the western border of Morgan Co., east Tennessee, U.S.A. (elev. 495 m). Cliffs such as these are common in the Cumberland Plateau and represent the remains of an ancient delta. The cliffs reach 30 m in height, are structurally complex, and afford many features for web attachment. Areas under the large overhangs are usually cooler and more moist than the surrounding environment, and sometimes have a cover of moss, lichens, or vascular plants. Many of the various arthropods brought into contact with the outcrops by air currents fall prey to the spiders inhabiting the rock faces.

These cliffs possess many attributes that make them particularly useful to investigations of spider community structure. The large overhangs protect spiders and their webs from direct contact with rain, shade them from direct insolation in the summer, store warmth in the winter, and moderate strong winds which may damage webs. Severe and rapid fluctuations of temperature and humidity are damped by the large

overhangs and irregular surfaces of the cliffs. Therefore, cliff structure ameliorates and stabilizes environmental extremes, and in doing so, also serves to reduce the confounding environmental variability that is usually inherent in most field studies of community structure.

There are an abundance of cliffs in the study area supporting large populations of spiders. Because most cliffs represent patches of rock face in a forest ecosystem, they are semi-isolated, and migrations of spiders between them were observed to be rare. These attributes facilitate repetitive sampling and controlled experimental manipulation, since removal, addition, and other experimental treatments are possible without disturbing adjacent cliffs. The cliff faces also permit the observation, measuring, and censusing of spiders with less perturbation than in most other habitats. The use of ledges and paths below the cliff surfaces while surveying and censusing reduced disturbance to both the habitat and the webs.

I.3 The Spiders

Achaearanea tepidariorum (C. L. Koch) is a cosmopolitan member of the comb-footed spider family Theridiiadae. The adult female is usually 7 mm long and may weigh up to 130 mg. Achaearanea density on the cliffs was 5.5 (SE±0.67) spiders per square meter, and this species made up 46.2% of all spiders on the cliffs. It builds a "tangled" (scattered line) web usually under an overhanging support. The web may reach 1.5 m in height, and prey are captured by silk strands extending

from a central tangle to the substrate and surrounding structures. Viscid droplets along the final centimeter of these strands stick to prey, which are then lifted off the substrate when the capture strand detaches from its point of attachment. By this method, Achaearanea is capable of capturing prey many times its own weight. It is very fecund, with some females producing over 2000 eggs in one season (Kaston, 1948).

Coelotes montanus (Emerton) is a funnel-web spider (Agelenidae) which may reach 14 mm in length and 250 mg in weight. Its density averages 4.5 (SE±0.67) spiders per square meter, and its population composes 34.2% of all the spiders on the cliffs (Riechert and Cady, 1983). Coelotes are most often found in protected cracks and crevices where it builds a sheet web of non-viscid silk with an attached silken funnel which extends into a crack or crevice. Prey capture occurs when the spider rushes out from the funnel to grab prey which tread across the sheet or signal threads radiating out from the periphery of the sheet. The spider spends most of its time in the funnel, where it consumes prey and places its egg sacs which contain approximately 125 eggs.

I.4 The Study Cliffs

Five cliffs were used in this study. They were all within 0.5 km of each other and had the same southeast exposure. None of them were contiguous. Four criteria served as the basis for their selection: size, structure, location, and presence of spiders. Each cliff was

minimally 4 m high, and had a protective overhang over at least half its length. Four of the five cliffs were designated as experimental cliffs; the fifth was maintained as a control. Two of the treatment cliffs had high structural complexity, and two low. The control cliff was selected because it had areas of high and low complexity. Preliminary visual inspection indicated that all outcrops initially had similar densities and ratios of A. tepidariorum and C. montanus.

Coelotes montanus were removed from two experimental cliffs. These were hereafter referred to as Achaearanea I (low structural complexity) and Achaearanea II (high structural complexity). On two other cliffs only A. tepidariorum were removed; these were designated Coelotes I (low complexity) or Coelotes II (high complexity). Control Achaearanea and Control Coelotes refer to the species on the control cliff (low-high complexity) from which no spiders were removed.

Each cliff was gridded by gluing small squares of surveyor's tape onto the rock surface at each corner of a square meter. Only the lower 3-3.5 m of each cliff was gridded since spiders were most abundant in the vicinity of the forest floor. The grid assisted in mapping the dispersion patterns of spiders on the cliff surfaces and in determination of cliff structure.

The control cliff's gridded surface was 8 x 3 m, and was protected by a large, high overhang which allowed most of its surface to remain dry even during heavy rains. Parts that became wet had growths of moss and lichens. The substrate was loose leaf litter with moist soil for half its length, and a rocky ledge with some vegetation for the

remainder. Parts of this cliff's structure were very complex, while other sections were simply vertical, bare rock. Thus, this cliff possessed a good representation of all structures found on the other four cliffs.

One experimental cliff, Achaearanea I, was gridded over 9 x 2.75 m. A very high, large overhang (5 m high x 3 m deep) extended over its entire length, protecting it from all rainfall. This kept the rock surfaces dry, and few mosses or lichens grew there. The substrate contiguous with this cliff base was dry, loose or packed sandy soil, with patches of vegetation and leaf litter. Rocks and sticks were scattered over the ground surface. A large group of ant lion larvae (Myrmeleontidae) occupied the loose soil, indicating dry soil.

The Achaearanea II experimental cliff was gridded over 10 x 3 m. Half its length was covered by an overhang smaller than that on Achaearanea I which still protected the cliff surface from rainfall. The other half of its length was partially protected from rainfall by the foliage of adjacent hemlock trees (Tsuga canadensis). However, this part of the cliff became wet in heavy rains, and it was covered with moss and lichens. The substrate under the overhang was thick leaf litter, and mull humus deposited by the hemlocks was found under the other half of the cliff.

Coelotes I was gridded over 7 x 3 m and had a large, low protective overhang over 20% of its length. The other half was partially protected by the deciduous leaf canopy (it became wet in moderate rains). Moss and lichens covered most of the surface of this cliff,

and the overall substrate was loose leaf litter which abutted the base of the cliff.

Coelotes II was measured over 9 x 2.5 m and was shielded from most rain by small, high overhangs over most of its length. Of the two Coelotes experimental cliffs, this one was more similar than Coelotes I (in terms of size and structure) to the control cliff. Moss and lichens were found on the surfaces where water dripped during and after rains. The substrate below the cliff varied from leaf litter to bare, moist soil.

The relative amount of space available to spiders on the cliffs was calculated using volume measurements of those microhabitat features that extended out from the cliff faces (large overhangs, ledges), and a two-dimensional measurement for flatter areas of structure (<2 cm protrusions). Very complex structures (i.e., patches of many cracks, crevices, and other complex features) were quantified by determining the two-dimensional surface area covered by these structures, then a third dimension of approximately 1-2 cm was used to complete the calculation. The volumes of these spaces were totaled on each cliff and expressed in cubic centimeters. This provided a relative measure of space that was comparable between the cliffs, and agreed with the observed structural complexities and sizes of the cliffs. Volume measurements were used due to the three-dimensional character of Achaearanea webs. Three-dimensional space was a more relevant measure of positions occupied by spiders on the cliffs than square surface area.

Four of the cliffs had available space indicies that were within 6.23% of each other (in terms of available space; Table 1[1]). The other cliff (Coelotes I) was smaller and less complex than the others.

I.5 General Methods--Marking, Weighing,and Surveying Spiders

Methods specific to each of the three experiments are described within their own chapters. The general methods detailed here were applied to both experimental and control cliffs.

Weekly inspections of the cliffs began in May 1980, in March 1981, and March 1982. March was found to be the time of year when significant spider activity began (e.g., Coelotes reproduction, Achaearanea maturation). Observations ceased in mid-December in 1980 and 1891; and all experiments were concluded in November 1982. All adult A. tepidariorum and C. montanus found were marked, weighed, and measured. Spiders were captured with as little damage to the webs as possible, with most captures resulting in no disturbance to web structure. To capture Achaearanea, vials were carefully placed under individuals, and they were induced to drop into them. (Dropping from the web is a typical defensive behavior of many web building spiders.) I plucked the signal threads at the outer edges of Coelotes webs in order to coax the spiders out of their webs and get them within capture range. A vial was then rapidly brought over the spider. Since Coelotes webs

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[1]This and all subsequent tables are in Appendix A.

were usually close to rock surfaces, snares were not damaged by this procedure. Spiders were weighed to the nearest 1 mg with a Roller Smith field balance, and their lengths were measured to the nearest 1 mm. Achaearanea were restrained from marking in a large modified plastic syringe. A pine needle dipped in nontoxic enamel paint was used in marking the lateral aspect of femurs three or four. The restraining device was not necessary for Coelotes, for they remained still at the bottom of a vial long enough to mark them. Coelotes were paint-marked with a pine needle on the mid-dorsal surface of the carapace. The carapace was the one visible surface of Coelotes where they could not remove the paint by grooming with the forelegs. Five colors were used, providing a sufficient number of color combinations to make each spider individually recognizable. The spiders were returned to their webs and observed following release to ensure they resettled at the site. Of 555 spiders treated in this manner over three years, only three were lost due to handling.

In addition to marking, spider positions within the grid were recorded (quadrat and position with a quadrat). From then on, until a spider disappeared, a detailed record of its presence and activity was kept at each survey. An Achaearanea was considered gone from a cliff when it could not be found over two consecutive days of surveys. Inactive Coelotes webs were merely classified as "no response" because they were sometimes inactive for long periods (ca. 3 wks, presumably during molting). Egg sacs were carefully removed from the webs, weighed, marked with small dots of paint, and returned. All five

cliffs were surveyed at least twice a day during 2 to 4 day field sessions. Field sessions were normally no more than 4 days apart. A survey consisted of locating every adult female spider on the particular cliff face, and then recording position, presence of egg sacs, possession of prey, or any other changes since the last survey. If the spider had changed position, its movement was noted and the new location mapped. As new adult females became adult or immigrated, they were marked as described and included in subsequent surveys.

All adult females were weighed at monthly intervals. All spider-spider interactions and prey captures were recorded when observed, and all prey observed in the webs of spiders of any age were also measured and recorded.

Prey availability was measured by setting out 30 cm diameter embroidery hoops stretched with Stickem special-impregnated cheesecloth (Riechert and Tracy, 1975). The hoops were placed for the duration of each field session under or on overhangs of cliffs similar in structure and exposure to the experimental cliffs. In this manner, available prey were sampled for the same time period that spider feeding was observed. Hoops were not placed near the experimental or control cliffs. Positions and orientations of the hoops were varied, and different substrate and moisture conditions were sampled. Many times hoops were placed in the same place and position as existing webs. Captured arthropods were removed and measured to the nearest 1 mm for a total of 4353 trap-days over the three years. Adequate sample size (number of traps) was determined by setting the standard error of the

mean to 10%, employing the variance of the number of insects caught per trap, and solving for N in the equation for standard error of the mean. The adequate number was found to be 72 traps; 128 were actually set. Temperatures above the cliffs (plateau surface), on the sides of cliffs, and under cliffs were recorded from 4 to 10 times daily throughout each field session.

CHAPTER II

REMOVAL EXPERIMENT

The purpose of this experiment was to gather information on the inter- and intraspecific interactions between and within A. tepidariorum and C. montanus. Population dynamics, patterns of dispersion, reproduction, use of cliff structures, and prey relationships were monitored to identify any changes affected by the removals. These data were then tested to discern any evidence indicating competitive release of one species in the absence of the other.

II.1 Methods

Starting in 1980, single-species removals were performed systematically for 3 consecutive field seasons (April-November) on each of the 4 experimental cliffs. Only C. montanus were removed from the Achaearanea experimental cliffs, and only A. tepidariorum were deleted from Coelotes experimental cliffs. No manipulation occurred on the control cliff. The following methods were used on each of the 4 treatment cliffs.

All removals were accomplished by carefully scrutinizing each cliff's surface and removing, by hand, individuals of the designated species. The webs of these spiders were also destroyed and removed. Most removals took place at night (with the aid of a headlamp), as this was when the highest proportion of spiders were most active on their

webs (Riechert and Cady, 1983; Fig. 1[2]). The removals were repeated every week during the field seasons.

A complete census and mapping of every immature Achaearanea or Coelotes on each of the 5 cliffs was conducted at predetermined intervals. These censuses provided information on population density, dynamics, and age structure. The size, microhabitat feature occupied, and coordinates within a quadrat were recorded for each spider. A total of 12,238 spiders were mapped during the 3 years.

Censusing in 1980 was done every 10 days, but only once every 30 days during the 1981 and 1982 field seasons. Seventeen censuses were made during the study. In addition to the censuses, all 5 of the cliffs were regularly surveyed as described above. Thus, parameters of prey capture (energy input), reproductive output, and microhabitat selection were monitored on all cliffs. Some limitations exist in this information on Coelotes. There are no data concerning their egg production for the 1980 field season because it took a season to learn where to look for their egg sacs. Also, Coelotes take their prey into their funnels soon after prey capture, so prey data on this species were collected only from actual sightings of prey capture. On the other hand, prey snared by Achaearanea were always easily visible for up to two or three days after capture, and their egg sacs were readily

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[2]This and all subsequent figures are in Appendix B.

visible. Consequently, data on reproduction and diets were more extensive for Achaearanea than for Coelotes.

Nonparametric methods were used for the statistical analyses of the data (Chi-square, Wilcoxon Matched-Pairs test (Conover, 1971), comparison of percentages (=T statistic, Sokal and Rohlf, 1969)), except where sample sizes and distributions met parametric assumptions (t-test). Microhabitat diversities were calculated using the Shannon-Wiener diversity index (Pielou, 1975; log base 10). Coefficients of similarity were derived using a modification of the index (Riechert and Cady, 1983) developed by Curtis (1959). Since most of the comparisons between cliffs and species were based on different sample sizes, the coefficient of similarity was calculated from relativized data (Riechert and Cady, 1983). The higher the index value, the greater the observed similarity. These coefficients may be expressed as percent similarities by multiplication by 100.

II.2 Results

If either species influences the other's population size, changes in numbers are expected after the treatments. No change would indicate no interspecies effect on population size.

II.2.1 Achaearanea tepidariorum

The number of Achaearanea immatures remained constant on the cliffs from which Coelotes had been removed (Table 2). Their numbers

on the control cliff increased just from 1980 to 1981, but remained otherwise constant during the study (Table 2). Numbers of Achaearanea adults on the experimental cliffs did not change significantly throughout the experiment except on Achaearanea I in 1981 (Table 3). The number of spiders decreased from 1980-1981, but 1982 showed an increase to a level near that of 1980 (Table 3). The slight numerical decrease of Achaearanea adults on the experimental cliffs may have been due to the loss of an important prey item (Coelotes), or expansion of territory size by the residents. The number of Achaearanea adults on the control cliff did not vary throughout the study. Thus, there is no strong evidence that the population densities of Achaearanea are influenced by Coelotes, except perhaps to enhance the existence of Achaearanea.

The mean weights of adult Achaearanea and the weights of their egg sacs were significantly greater on the experimental cliffs than on the control cliff (Table 4). Data from experimental cliffs were pooled because they were not found to be different (Box's M test; $F = 1.26$, $P > 0.35$). Since the number of egg sacs and the number of eggs per sac were not different on the experimental and control cliffs (Table 4), greater reproductive effort by Achaearanea was in the form of heavier eggs. This suggests that Achaearanea were obtaining more prey in the absence of Coelotes. The fact that the Achaearanea adults were heavier on these cliffs following the removals (Table 4) also supports this suggestion. Note, however, that benefits from heavier eggs did not

result in an increase in the population size of Achaearanea (Tables 2, 3), implying that factors other than interspecific competition with Coelotes were limiting the population expansion of Achaearanea.

II.2.2 Coelotes montanus

The number of immature Coelotes on Coelotes II significantly increased from 1980 to 1981, and they were also more numerous in 1982 than in 1980 (Table 5). No consistent trend was observed on the less structured experimental cliff (Coelotes I). Environmental pressures were possibly related to the decrease in spider densities on Coelotes I in 1982 since this cliff had fewer protective overhangs than Coelotes II. In contrast to the Coelotes I, the numbers of Coelotes immatures decreased on the control cliff after 1980 (Table 5).

Although adult Coelotes numbers showed no definite trend on Coelotes I, they were significantly more numerous after removal of Achaearanea on Coelotes II (Table 6). Of the two Coelotes experimental cliffs, Coelotes II was most similar to the control cliff in size and structure. It thus provided the most representative data of the two experimental Coelotes populations, and is considered the most important Coelotes experimental cliff in most analyses. Coelotes I was smaller, contained fewer websites preferred by Coelotes, and had no extensive protective overhangs. The number of adult Coelotes occupying the control cliff did not change significantly across the three years (Table 6). The Coelotes population levels appeared to increase on a

cliff from which Achaearanea had been removed, indicating that the agelenid's population levels were influenced by the presence of Achaearanea.

As in the case of Achaearanea, the adult Coelotes on the experimental cliffs were heavier compared to those on the control cliff (Table 7). Although egg sac weights were similar between the two treatments, more sacs were laid on Coelotes II in 1982 than 1981 (after the removals had been in effect) (Table 7). Thus, the Coelotes population increased in reproduction and (in general) population density in the absence of Achaearanea. In contrast to Achaearanea populations, the increased reproduction of Coelotes was manifested as increased numbers of individuals, at least on one of the cliffs (Coelotes II).

The adult densities of both species remained relatively static on the control cliff (Tables 3, 6), suggesting that any changes in adult numbers on the experimental cliffs with structure similar to the control cliff were not due to direct environmental effects. Note that an increase in Achaearanea immatures on the control cliff was concurrent with a decrease in Coelotes immatures (Tables 2, 5). From this evidence, it appears that the presence of Achaearanea had an influence on both immature and adult Coelotes populations.

II.3 Utilization of Microhabitat Space

Microhabitat associations of the spiders on the cliffs may reflect avoidance of interspecific competition for space, or it may simply represent the preferences of needs by each species for particular cliff

structures. When measured on a broad scale, it was found that these two species overlapped in their use of space (Riechert and Cady, 1983). Microhabitat use was considered on a finer scale herein.

II.3.1 Mapping Results

When the positions of the spiders on the cliffs are plotted, it becomes evident that there are specific places on the rock surfaces that they occupy more often during the season than other spots (Figs. 2-5). There is a finite number of these sites, and the overall trend is for spider distributions to be clumped, except for adult Coelotes (Table 8). Their individuals seemed to be regularly distributed over the cliff faces, perhaps because they had not yet saturated the available websites. This was due to repeated occupation of the same websites, and possible intraspecific effects within adult Coelotes. These data, along with the findings of Riechert and Cady (1983), indicate that website availability is generally limited on these outcrops, and so a high probability exists that within and/or between species competition for microhabitat space is occurring.

Despite the apparent overlap in microhabitat use existing between these two species (Riechert and Cady, 1983), their preferred microhabitats do differ in a couple of important features. Achaearanea associates more with overhangs (OVH) and horizontal corners that form small overhangs (HCRO) (Figs. 6, 7), whereas Coelotes makes use of mostly vertical and horizontal crack (VC, HC; Figs. 8, 9). Achaearanea utilize the overhangs for suspending their relatively large vertical

space webs, while Coelotes require cracks for placement of their funnel and sheet webs. Because of these differences, one might not expect to find direct conflict for websites between the adults. However, similar areas on the cliffs protected from environmental extremes may be sought by both species. This may effectively exclude individuals of either species from constructing a nearby web, and also might interfere with their prey capture. Interspecific competition for available space is potentially greatest among the immatures since at this life stage both species were observed to utilize the same sized cracks and small overhangs. It was thus important to test for possible shifts in microhabitat associations as a result of the removal experiments.

II.3.2 Microhabitat Shifts

Whenever a spider was mapped during a census, its association with a particular microhabitat was also recorded. These data were used to detect any changes in the use of cliff structures following the removals. If two species are competing for space, some shift in microhabitat use may be expected after the treatment. A shift is evident when spiders utilize particular structures that were excluded from their use while they were coexisting with the other species. A shift may also reflect an expansion of microhabitat use associated with increased densities of given spider populations remaining after removals (intraspecific competitive effect).

A shift in microhabitat use between immature Achaearanea and Coelotes is suggested by an increase during the study in the similarity

of microhabitat occupation between the two species on their respective experimental cliffs (Table 9). The index increased 31.4% from 1980 to 1982 on the experimental cliffs versus an 18.9% rise on the control cliff during the same period. In order to account for any change in sampling efficiency over the course of the study, the increase in similarity on the control cliff is subtracted from the coincident gain on the experimental cliffs. The resulting 12.5% rise in similarity for the treatment was significant ($T = 9.364$, $P < 0.001$; T = test statistic for difference between two percentages). Thus, the two species shifted their occupation of cliff structures and used more similar microhabitat features on their respective experimental cliffs after the removals than before the treatment. This result may also indicate an intraspecific competitive effect.

After removal of Achaearanea, Coelotes immatures increased their use of small overhangs (HCRO; $T = 4.38$, $P < 0.001$) and vertical corners (VCR; $T = 5.73$, $P < 0.001$) while reducing their occupation of vertical cracks (VC; $T = 4.17$, $P < 0.001$) (Fig. 8 (A)). Coelotes immatures on the control cliff increased only their use of horizontal cracks (HC; $T = 5.85$, $P < 0.001$) (Fig. 8 (B)). No clear shifts were observed for immature Achaearanea in their use of cliff structures on the experimental cliffs (Fig. 6).

The diversity of microhabitat use by the immatures changed more for Coelotes than Achaearanea during the study, and is in agreement with the preceding analyses of microhabitat associations. The microhabitat diversities of Achaearanea immatures on the control and

experimental cliffs did not change to any great degree, and any notable changes were concurrent between the treatment and control cliffs (Fig. 10). A different result was observed for immature Coelotes. Their microhabitat diversities on both the experimental and control cliffs tended to increase in 1981 and 1982 from levels found at the initiation of the treatment. The increase in the diversity of microhabitat association on the major Coelotes experimental cliff (i.e., Coelotes II) was of greater magnitude than the corresponding increase on the control cliff (magnitude of increase: Coelotes II, 0.77285, control, 0.30489; Fig. 10). The spiders on Coelotes I did not increase the diversity of their microhabitat use in relation to the control cliff (Fig. 10). This was possibly due to the repeated use of the same websites by immature Coelotes over the sampling period. Also, sample sizes were smaller on Coelotes I than on Coelotes II. Therefore, the diversity of microhabitat features used by Achaearanea immatures did not change after removal of Coelotes, but the immatures on Coelotes II increased their diversity of microhabitat use in the absence of Achaearanea.

The results from these three analyses of the use of microhabitat space by immature Coelotes and Achaearanea indicate that Coelotes shifted their use of space in the absence of Achaearanea; no such shift was observed for immature Achaearanea on the treatment cliffs. This suggests that immature Coelotes moved into cliff structures on the experimental cliffs that were previously occupied by Achaearanea. The fact that the features into which Coelotes moved were two of the three

most prevalently used by Achaearanea further implies that the young Coelotes experienced a release from competition for microhabitat space upon the removal of Achaearanea. However, these shifts by Coelotes may also be interpreted as being a result of their increased density. Their larger populations may have tended to fill the preferred microhabitats first, with the remaining spiders spreading into the secondary microhabitats. This still awaits experimentation.

The adults of the two species did not demonstrate the shifts in microhabitat associations shown by the immatures. There were no significant changes in the similarity of microhabitat use by adults (magnitude of difference: experimental, 0.137; control, 0.099; T = 0.987, P = 0.162; Table 10), and no distinct changes were evident in the actual use of microhabitat structures by the adults during the experiment (Figs. 7, 9). The microhabitat association diversities showed no specific trends for the adults across the three years (Fig. 11). A large decrease in microhabitat use diversity was observed on Coelotes I in 1982, and is probably the result of a small number of spiders which occupied the same websites during the year. Therefore, it generally appears that utilization of space by immature Coelotes was affected more by coexistence than the other species/age groups of Achaearanea or Coelotes.

II.4 Prey Results

Any changes in the population levels of the spiders on the experimental cliffs may be related not only to changes in competition

for available space, but also to changes in the amount of food they received after the removals. Absence of one species may relieve competition for food, increasing availability of energy to the spiders remaining on the cliffs.

II.4.1 Diets

Competition between the two species may have been reduced through resource partitioning if the diets of the spiders were different. The overall diets of Achaearanea and Coelotes appeared to be similar. Prey sizes compared between the combined age classes of the two species were not different ($F = 1.426$, $P < 0.234$), and a discriminant analysis indicated no significant separation between the two species (Wilks Lambda = 0.993, $P < 0.234$), correctly classifying only 44.16% of them according to prey size. When the adults were separated from immatures for two-way comparisons, significant differences were found in prey size between the immatures of one species and the adults of the other (Table 11). However, no differences in prey size were found between Achaearanea and Coelotes when their immatures or adults are compared (Table 11). This indicates that adults and immatures were eating different-sized prey, while members of a given age class of either species were eating prey of similar sizes.

Coleoptera were the most common prey type eaten by the immatures of both Achaearanea and Coelotes, and Achaearanea ate relatively more Hymenoptera than did Coelotes ($\chi^2 = 55.85$, $P < 0.001$; Fig. 12). The diets of these two species were otherwise similar, as a large amount of

overlap existed between the types of prey eaten by immatures Achaearanea and Coelotes (Table 12). Therefore, there is potential for interference competition for food between the immatures of these two species.

The diets of adult Achaearanea and Coelotes were similar to those of the immatures. The most important prey item was also Coleoptera, however, Achaearanea appeared to take a broader, more even range of prey typed than did Coelotes (Fig. 13). The adults also shared a large percentage of their respective diets (Table 12).

II.4.2 Diets on Experimental vs. Control Cliffs

There is a possibility that the spiders on the experimental cliffs were receiving different amount of prey in the absence of the other species. The number of prey eaten by immature Achaearanea did not differ between the control and experimental cliff (Table 13). Unfortunately, no prey data were available for immature Coelotes found on the control cliff, so in order to detect any changes in prey for young Coelotes due to removals, data from the first year of removals are compared to those of the two subsequent years (after the treatment had time to take effect). An increase in the number of prey captured by immature Coelotes after the removals was evident (Table 13). More dipterans were eaten by immature Achaearanea after removals ($T = 4.36$, $P < 0.001$), while Coelotes immatures ate fewer Coleoptera ($T = 1.66$, $P = 0.048$) (Fig. 12). The types of prey captured by immature Achaearanea showed a high degree of overlap between the experimental

and control cliffs (Table 14), while the mix of prey items consumed by immature Coelotes differed from the first year of removals to the third year of treatment ($T = 2.10$, $P = 0.018$) (Table 14). Similar comparisons performed on Achaearanea showed (as above) no change in the proportions of prey typed eaten. These results indicate that the diets of immature Achaearanea did not shift in the absence of Coelotes, whereas the amounts of prey consumed by Coelotes immatures increased, and their diets changed where Achaearanea had been removed.

Adult Achaearanea and Coelotes each ate more prey on their respective experimental cliffs than on the control cliff (Table 15). There were no noticeable shifts in the type of prey captured by adult Achaearanea during the experiment, but Coelotes adults increased their consumption of Coleoptera in the absence of Achaearanea ($T = 1.613$, $P < 0.05$; Fig. 13). This may have been because Achaearanea webs are designed to capture large crawling insects (e.g., Coleoptera). There were no real differences in the overlaps of prey types for the adults of each species on the control and experimental cliffs (Table 16). Although the adult spiders did not experience a major change in their diets after the removal of the other species, each one received more prey in the absence of the other, indicating a probable interspecific exploitative competitive effect. Results from these analyses of the prey consumed by each age class of Achaearanea and Coelotes indicate that they may interspecifically compete for food.

II.4.3 Interpredation

Spiders are highly predaceous animals, and most will eat whatever they are able to overpower. Because the two species occupy similar habitats, there is a good chance that interspecific predation occurs. Interpredation (one of a pair of species eating the other) may be a mechanism contributing to the coexistence of these two spider species.

Feeding records show that Achaearanea were indeed eating Coelotes. Adult female Achaearanea were directly observed to eat 63 Coelotes, and 20.95% of all spiders eaten by adult Achaearanea were Coelotes. On the control cliff, 26.3% of all spiders eaten by Achaearanea were Coelotes, and 9.5% of all the adult Coelotes found on the control cliff were ultimately eaten by adult Achaearanea. Even though the removal of Coelotes from the experimental Achaearanea cliffs were frequent and thorough, Achaearanea living there still continued to capture immigrating Coelotes. In all the hours spent watching spiders on the cliffs, an Achaearanea was not observed being eaten by a Coelotes. Based on these results, it is quite probable that by Achaearanea consuming Coelotes, the former species may limit the growth of the latter populations.

CHAPTER III

ADDITION EXPERIMENT

The addition experiment was performed to determine the extent to which spider densities and distributions reflect intraspecific versus interspecific limiting effects. If Coelotes were occupying space otherwise available to Achaearanea, removal of the former and addition of the latter may cause these spaces to be filled and maintained by newly arriving (added) Achaearanea. The nearly complete initial occupation of available Achaearanea websites was ensured by first saturating a cliff with them. This enabled the detection of any spots first occupied by Coelotes which were also favorable to Achaearanea. If Achaearanea moved into and remained in the areas from which Coelotes had been removed, similar utilization of microhabitat space by the two species is evident. Both the ability of Coelotes to withstand invasions of Achaearanea, and the effects of intraspecific interactions among Achaearanea were observed during the experiment.

III.1 Methods

The cliff chosen for the experiment was relatively small (compared to the other cliffs) and separated from nearby cliffs by at least 4 m in all directions. The cliff was 6 x 4 x 3 m and was a very large, convex-topped boulder, with straight sides and a large (1 m wide) central crevasse situated under a protective overhang. Mosses and lichens covered the exposed surfaces, and a thick leaf litter blanketed the

substrate at the base of the boulder. The cliff was protected from the effects of direct precipitation by a canopy of broadleaf trees and conifers.

The experiment was initiated at the beginning of September 1982 and continued through mid-November of that year. This was the period when adults of both species were present. The cliff was gridded, and all resident adult female Achaearanea were marked, measured, and returned to their webs. Spiders used for the additions were captured from cliffs at least 70 m from the addition cliff. Adult female Achaearanea were marked to designate the day of release, and were introduced singly at 10 min intervals at the top of the cliff. All additions were performed at night to reduce potential directional effects with respect to solar radiation.

The initial release included 15 adult female Achaearanea, whereas each of the 5 releases made at later dates each numbered 10 spiders. (The timing of the releases are shown in Fig. 14). Spider activity was monitored for an hour following each release, and activity checks were made during the remainder of the night. Observations at this cliff were included in field surveys until the end of the experiment, with spider positions and release group identity noted at each survey.

After 31 days and the initial 4 releases of Achaearanea (45 spiders), all C. montanus and their webs were removed. The position, microhabitat association, and age of each spider were noted. The fifth release of 10 adult female Achaearanea took place immediately after the Coelotes removals, and the final addition of 10 spiders occurred the

next night. In total, 65 adult female Achaearanea were introduced to this small cliff, which was then regularly surveyed for 34 more days after the final release.

Due to time constraints, I did not perform the reciprocal addition experiment with Coelotes.

III.2 Results

III.2.1 Releases Before Coelotes Removals

The initial additions appeared to fill most of the available websites on the cliff. A lower percentage of the second two releases remained at day 31 compared to the first two releases (First two--72%, Last two--60%; T = 1.08, P = 0.13; Fig. 14). Although this difference was not statistically significant, it does suggest that there were fewer websites available to the second two additions. Furthermore, the relative numerical consistency of the first two additions from day 10 to 25 compared to the gradual decrease of the second two releases from day 18 to 31 reflects the occupation of available websites by the first two innoculations (Fig. 14). This decrease of the later additions was possible due to cannibalism and/or emigration of these spiders upon failure to secure a website. In addition, not all spiders added to the cliffs actually established webs. At any one time, approximately 15-20% of the first two release groups were observed not to possess established webs, while 30-35% of the second releases were not in a well-defined web. Note that the original residents were most numerically prominent on the cliff throughout this experiment.

Observations showed that roamers often settled between two spiders that already occupied space under overhangs. The residents then moved to increase the interspider distances by shifting 5-10 cm. This settling by roamers and subsequent web displacements of previous residents usually occurred only if the initial webowners did not have large and well-established webs. Thus, the spiders added to the cliffs sometimes moved into areas with little regard to the presence of other spiders, perhaps due to the importance of shelter offered by those microhabitats. There was no evidence of any spiders immigrating onto the addition cliff.

III.2.2 Releases after Coelotes Removals

A positive association was found between former occupancy of a quadrat by any Coelotes and the subsequent occupation of the same area by added Achaearanea (Phi coefficient = 2.6189, $P < 0.005$). This relationship also exists when just former inhabitation by adult Coelotes is considered (Phi = 3.1414, $P < 0.001$). This association was supported by direct observations of Achaearanea occupying spots where Coelotes had been removed on both the addition and removal cliffs. The Achaearanea added after the removal of Coelotes initially persisted on the cliffs in greater numbers than did the previously added spiders (Added after--30%, Before--19.4%, $T = 0.97$, $P = 0.166$; Fig. 14). Although not statistically significant, this difference suggests that those Achaearanea introduced to the cliff after the deletion of Coelotes had moved into the sites formerly occupied by Coelotes. These

results indicate a high probability that adult Achaearanea and Coelotes prefer to occupy similar areas on the cliffs.

The Achaearanea from the second series of additions did not seem to persist in the newly available websites. This is indicated by the gradual drop in their numbers to a level near that of the previously added spiders (Day 38, Fig. 14). This decrease may have resulted from intraspecific interactions between the added Achaearanea and those already established on the cliff. The new spiders initially moved into the spaces left vacant by the removal of Coelotes; then, during attempts at web expansion, they started to interact with the other Achaearanea living nearby. These interactions probably caused the displacement or cannibalism of the newcomers. Both of these outcomes were observed as results of interactions between Achaearanea on other cliffs.

Note the decreased numbers of all spider groups as a result of frost (Day 40, Fig. 14). A larger proportion of Achaearanea added after Coelotes removals survived the frost than those added before the removals (Day 37 vs. Day 40: Added before--24% remaining, Added after--50% remaining, $T = 1.84$, $P = 0.032$; Fig. 14). Furthermore, there were proportionally fewer survivors among the spiders added before the Coelotes removal than among the combined original residents and Achaearanea added after the removal (spiders added before--13.33% remaining; residents and spiders added after--39.53% remaining, $T = 2.871$, $P = 0.002$; Fig. 14). Apparently the frost had less of an effect on the original residents and the post-Coelotes additions than on those

spiders introduced to the cliff before deletion of Coelotes. This highlights the value and importance of certain microhabitat features to the ability of spiders to survive meteorological extremes.

III.2.3 Achaearanea Intraspecific Interactions

One of the most striking observations on the addition cliff was the persistence of the original residents despite the large number of spiders added to the cliff. Most of these residents successfully defended their websites against the release of 65 other spiders. Seven of the thirteen interactions observed between the roamers and webowners were quite vigorous and ended in cannibalism. Five of the seven observed cannibalisms involved newly released spiders eating ones already on the cliff. In all cases, the victor was the larger spider, and often the loser did not have a large or well-established web.

Most of the original residents had well-developed webs in protected spots (i.e., overhangs) that not only afforded them a place away from precipitation and falling leaves, but also offered a refuge from meteorological extremes (such as frost). The benefits accrued from these preferred websites must have been worth the cost of their maintenance and defense, for these residents had to constantly repel intruders. Most of the spiders cannibalized did not have well-established webs (71.4%), suggesting that website structure may also be an important factor in the defense of the site. These results point to the operation of intraspecific competition for space among Achaearanea, and imply that many places where Coelotes live are also favorable to Achaearanea.

CHAPTER IV

ENCLOSURE EXPERIMENT

The enclosure experiment was designed to test the effects of hunger on nearest neighbor distances and the size/structure of Achaearanea webs. It provided data to help differentiate between the effects of prey levels and habitat structure on observed spider distributions. This experiment was not performed with Coelotes due to time constraints and problems with their enclosure and observation.

IV.1 Methods

An enclosure was constructed on a section of cliff with a 1 m high by 1 m deep overhang. The area under this overhang was well protected from rain and wind. The rock surface was relatively smooth, thereby controlling for any effects varied structure may have had in website selection. The substrate at the base of the cliff consisted of dry soil and loose, sparse leaf litter. Heavy gauge cheesecloth was permanently glued to the outer edge of the overhang across 3.5 m. The cloth draped to the ground where it was firmly pinned to the substrate; end panels and a central partition completed the enclosure. All arthropods and spider webs were removed from within the enclosure, and cracks and crevices were caulked so only the smallest of arthropods (e.g., small ants) could get in or out. The enclosure was observed for 10 days thereafter to detect any passageways for spiders or prey in or out of the enclosure.

The experiment was run twice by releasing 10 spiders on either side of the central partition. One of two different release methods was used each time in order to observe the effects of forced vs. free website choice by the spiders. The first run lasted for 45 days, while the other spanned 49 days. The spiders on one side of the central partition were fed to satiation with field-caught orthopterans, whereas the ones on the other side received 25% or less of what the sated spiders were given. Satiation was ensured by feeding spiders approximately twice the number of prey observed to be eaten by Achaearanea in natural settings on the cliffs (i.e., 4 prey items in excess of 200 mg/week).

Adult Achaearanea females scheduled for experimentation were captured one week before the releases and started on the satiation or deprivation feeding regimen. They were weighed and individually marked. After each spider established a web within the enclosure, web and website parameters were measured (web height, width at top, middle, and base, any capture strands extending to the substrate, interspider distances). These measurements were also recorded following web relocations or movements within the enclosure.

In one experimental run, the spiders were forced to establish websites at a regular interspider spacing, then allowed to interact (termed "Fixed Release"). The spacing was determined by the particular physiognomy of each side of the enclosure. The spiders were set as nearly equidistant from each other (and from the walls of the enclosure) as the overhang structure permitted (approximately 30 cm for the

sated spiders, 37 cm for the deprived spiders). Web establishment at a particular spot was accomplished by inducing adult female Achaearanea to initiate web construction in 7.5 cm long x 4.3 cm diam plastic vials. The open end of the vials were then placed tightly against the underside of the overhang within the enclosure, and were held there by supports from underneath. This allowed each spider access to the rock surface while it was still confined. The vials remained in this position until the spiders had attached their webs to the overhang surface (5 days), then the vials were carefully removed by cutting the silk lines attached to it. This left each spider hanging in a natural position in its new lair under the overhang.

In the other run of the experiment (the "Float Release"), the spiders were individually released at 15 min intervals at the center of either half of the enclosure. All spiders and webs from the previous experimental run were removed from the enclosure before initiating this second test. Furthermore, the rock surfaces were scrubbed with a dry rag to eliminate traces of silk before the releases took place to remove any cues influencing website selection silk may provide. Spiders in both runs of the experiment were monitored twice daily during field sessions to look for spider displacements and/or movements.

The experiments were terminated when the spiders were removed from the enclosure and weighed. The webs were dusted with corn starch to facilitate detection of all lines, and then measured (height, width, depth at three points, size of main tangle, accessory lines, and number of capture strands).

The data were analyzed using t-tests to compare mean web volumes, and Mann-Whitney tests compared spider weights and interspider densities. The Chi-square test was used to investigate the frequencies of spider movements.

IV.2 Results

The mean weights of food satiated and deprived spiders differed at the beginning and end of the fixed release experiment (Table 17). They differed in the float release experiment only at the initiation of the test (Table 17). The sated spiders were heavier at the start of the trials because the initial feedings began one week before the experiment. Since spider weight is known to be correlated with food consumption (Wise, 1975; Riechert, 1981), it was expected that they would also be heavier at the end of the experiment due to continued heavy feeding. The similarity of spider weights between the two feeding levels at the end of the float release appears to be related to the fact that this experiment was initiated later in the season. By the time the run was terminated in mid-November, Achaearanea had ceased foraging activity for about three weeks. Therefore, the last three weeks of the float experiment were not included in the analyses of movements or interspider distances. This made little difference, since any changes in interspider distances or movements occurred before the spiders stopped feeding.

IV.2.1 Interspider Spacing

It may be hypothesized that spiders receiving more food are more tolerant of other spiders than those not as well fed. This may be related to the size of the area that the spiders perceive as necessary to fulfill their energy requirements. A well-fed spider theoretically needs less area to capture maintenance amounts of prey. Therefore, sated spiders are expected to have smaller mean interspider distances than deprived ones.

Fixed release

The original interspider distances of the fixed release experiment found the sated spiders significantly closer to one another than the food deprived ones (Table 18). This was due to the logistics of forcing spiders to establish a web at the beginning of the experiment. However, at the completion of the run, the deprived spiders had significantly decreased their interspider distances to a value near that of the sated spiders (approximately 30 cm), while the sated spiders did not change (Table 18). Therefore, the spiders receiving less food decreased their nearest neighbor distances.

Float release

When the spiders were free to choose their websites, members of the food deprived group initially spaced themselves closer together than the sated spiders (Table 18). During this experiment, the sated spiders significantly reduced their spacing while the deprived ones

showed no significant change (Table 18). The mean interspider distance of these sated spiders gradually decreased (Table 19). Note that the final interspider spacing of each group was similar to that observed in the fixed release experiment. Thus, there is no evidence to support the hypothesis that hunger levels influence interspider distances for adult female Achaearanea. They appear to adjust their nearest neighbor distance to approximately 30 cm regardless of their hunger levels.

IV.2.2 Web Volume

The hypothesis relating prey levels to mean interspider distances may also be invoked in reference to the area occupied by their webs. Sated spiders are expected to require less web space to capture the necessary amounts of prey.

Although no statistically significant difference was found between the web volumes of sated and deprived spiders at the close of the fixed release experiment, the mean volumes differed by almost a factor of two (Table 20). The small sample size may have influenced this statistic. It does appear that sated spiders had generally smaller webs than food deprived spiders. In addition, web architecture was different. Of the food deprived spiders, 44% built webs with capture strands that extended to the substrate, while none of the sated spiders included these features in their webs. Since the spiders in the float release had stopped feeding near the end of the experiment, their webs did not reflect feeding status and were not useful for comparisons.

IV.2.3 Movement

The actions of spiders may be related to different hunger levels (Enders, 1975). Spiders not receiving prey may tend to increase their levels of movement (web abandonment) in order to search for a more productive website. These moving spiders may force others from their webs, in turn causing them to move (domino effect).

There was a significantly higher frequency of movement among the deprived spiders (11 movements) than among the sated spiders (2 movements) during the fixed release experiment ($\chi^2 = 6.3$, 1 df; $P < 0.025$). There was no significant difference in frequencies of movement between feeding levels among the float release spiders (sated = 12, deprived = 8; $\chi^2 = 0.8$, 1 df; $P = 0.37$). In the fixed release experiment, movement among the sated animals took place only on the first day, whereas the deprived spiders moved during the entire run (Table 21). It is possible that because the deprived spiders may have been initially placed at greater interspider distances than they normally occur, they may have moved more often. However, similar interspider distances found among the sated spiders at the start and finish of the fixed release experiment indicates little movement of the well-fed spiders. Thus, a direct relationship possibly exists between hunger level and spider movement on the cliffs.

Instances of cannibalism within the enclosures were observed only among the deprived spiders during the float release (2 observed). This probably reflected high frequencies of interaction affected by more movement motivated by hunger.

CHAPTER V

DISCUSSION

The results of this investigation suggests that three forces underly the coexistence of Achaearanea tepidariorum and Coelotes montanus in this spider community. One is interspecific competition between Achaearanea and Coelotes. Competitive release was exhibited only by Coelotes during the removal experiment, indicating that the presence of Achaearanea exerts a competitive influence upon Coelotes populations. At least part of this negative influence is by interspecific predation: Achaearanea were found to eat Coelotes, while the reciprocal predation was not evident. The third factor is intraspecific interactions within Achaearanea. Territorial contests (for websites) limit Achaearanea populations, and appear to possibly facilitate the coexistence of Achaearanea and Coelotes.

V.1 Achaearanea

Other field studies utilizing removal techniques indicate that intraspecific competition may limit a population's growth more than interspecific interactions (Wise, 1981b; Tinkle, 1982). The stability of Achaearanea populations after removal of Coelotes shows that any influence Coelotes exerts on Achaearanea does not limit the theridiid's population as strongly as restrictions imposed by either conspecifics or other factors (i.e., environment).

V.1.1 Immature Achaearanea Intraspecific Effects

Cannibalism has been shown to be an important factor limiting insect predator densities (see Price, 1975). Polis (1980) found cannibalism to probably be an effective agent of regulation for a scorpion population, and it has been demonstrated that cannibalism among immature spiders helps to govern their populations (Hagstrum, 1970; Hallander, 1970). Starvation is the most important cause of mortality for immature Achaearanea in the first month after their dispersal from the parent web (Valerio, 1974, 1977), so cannibalism may contribute to survivorship of those spiderlings by providing food to the stronger competitors. This, in turn, may help to limit future adult numbers, ensure the survival of superior competitors, and perhaps subsequently reduce the intensity of intraspecific competition among adults.

Nonexpansion of the experimental immature Achaearanea population may have been due to competition among conspecifics for limited living space on the cliffs. Achaearanea spiderlings require larger areas for web attachment with every molt (Valerio, 1977), so the amount of intraspecific competition for foraging space tends to increase as the juvenile population matures. Contests over limited space may initiate cannibalism, eliminate weaker individuals, and supply better competitors with a source of food. Cannibalism is a proximal effect ultimately arising from the limited availability of websites. Thus, the influences of habitat structure and interactions among conspecifics act

in concert to regulate the immature Achaearanea population. Emigration forced by interactions among conspecifics (as suggested in the addition experiment) may also restrict their number. Additional experiments are required to determine the importance of migration in regulating immature Achaearanea populations.

V.1.2 Interspecific Effects on Immature Achaearanea

The presence of immature Coelotes had little effect on population size, microhabitat use, or prey consumption of young Achaearanea. This suggests that interspecific competition with Coelotes is not an important limiting influence on immature Achaearanea.

V.1.3 Adult Achaearanea Intraspecific Effects

Cannibalism among adult Achaearanea was observed only three times on the removal and control cliffs during the three years of the study. All instances involved spiders situated next to each other, and one occurrence was the observed result of a web invasion. Considering the low incidence and contexts of these events, cannibalism among adult Achaearanea would not appear to significantly influence their population levels.

The limited existence of webspaces available to adult Achaearanea is indicated by (1) clumped distributions of the spiders on the cliffs, (2) an increased number of wandering Achaearanea females as the season progressed, (3) and the persistence of resident spiders on the cliffs in the face of web invasions.

1. Particular cliff structures were seen to be preferred by Achaearanea. Since the availability of these structures did not match the demand (Riechert and Cady, 1983), it is likely that websites are under contention by conspecifics.

2. Active interference is one way by which an intraspecific competitive effect may be achieved. Within-species interference effects among Achaearanea were studied by recording movement rates of the adults over time on control and experimental cliffs. The hypothesis was that as the season progresses and more Achaearanea females mature, the limited number of websites on the cliffs are filled. Thus, the spiders maturing later in the season are faced with a shortage of suitable places to establish a web. If these spiders were observed to move more often than those maturing earlier, then there is reason to believe that interspecific competition for websites is in operation.

An index of spider movement was calculated by first determining the month each individual adult Achaearanea first appeared, then counting the number of moves these spiders made over the time it was observed. The number of moves for all the spiders which first appeared in each month were totaled, and that total was divided by the number of spiders which matured in that same month. Comparisons of the indicies so obtained allows one to estimate if spiders maturing later in the season tend to move more or less often than those maturing earlier.

The numbers of adult Achaearanea increased over the season, and those spiders that matured later moved more often than those which reached maturity earlier in the season (Table 22). Achaearanea adults

on the experimental cliffs moved more often than those on the control cliff (Table 22). Thus, intraspecific competition among Achaearanea for limited websites is indicated by the presence of more roaming spiders as websites are filled. No evidence was seen for interspecific competitive effects in spider movements.

3. Adult Achaearanea on the removal and addition cliffs responded similarly at first to the removals of Coelotes. An initial increase in adult Achaearanea numbers on the experimental cliffs, as well as their ability to immediately find websites on the addition cliff after removal of Coelotes, indicate that sites favorable to both Achaearanea and Coelotes were opened upon deletion of Coelotes. However, the numbers of these newly-arrived Achaearanea decreased as the experiments progressed, in response to either intraspecific interactions with the established webowners, or to the unsuitability of the websites.

Former Coelotes websites were suitable for supporting and protecting Achaearanea. This was shown by the ability of immigrating Achaearanea to withstand frosts in places originally occupied by Coelotes. Also, previous residence of a spot by Coelotes was correlated with subsequent inhabitation by added Achaearanea, and Coelotes immigrating onto the Achaearanea experimental cliffs were observed (approximately 15 times) to have shared the same sheltered areas very close to established Achaearanea webowners. Therefore, similar places were favorable to both Coelotes and Achaearanea, and the two species naturally coexisted in these sites. Immigrating Achaearanea probably did not remain and establish a web in former Coelotes sites due to the

immigrant's interactions with established Achaearanea, not the unsuitability of former Coelotes websites. Intraspecific competition for limited space, or more specifically, territoriality, seems to be operating to limit and structure the Achaearanea population. Similar results have been found by Schaefer (1978) for a linyphiid spider that also required particular structures to place their webs. Other workers have demonstrated that availability of websites is a limiting factor to web-building spiders, either by the presence of suitable structures (Cherrett, 1964; Coleburn, 1974) or through the availability of locations supplying the proper thermal/structural characteristics and prey availability (Riechert, 1976, 1981; Riechert and Tracy, 1975; Biere and Uetz, 1981).

Riechert (1978b) identified three criteria which delineate and energy-based territorial system (see Stimson, 1973; Gill and Wolf, 1975; Simon, 1975; Hawes, 1977). They are: (1) territory size varies with age and size of the individual; (2) territory size should vary with habitat and the prey found there; (3) the territory should provide enough energy to give a competitive advantage to its owner. In the case of Achaearanea: (1) The size of the space they command around their lairs increases with age as the spiders become larger (Valerio, 1977). (2) Riechert (1981) indicated that territory size for an energy-based territorial spider appeared to be under genetic influence, and so may be fixed. The web size may vary, but the defended area was inflexible. It was found that Achaearanea may have altered the volumes of their webs in relation to the amount of prey received, but nearest

neighbor distances were constant regardless of hunger levels. Thus, Achaearanea may also exhibit a fixed territory size with a flexible web size. (3) The ability of earlier-maturing Achaearanea (and the original residents on the addition cliff) to persist at a website indicates they were receiving adequate energy to maintain the web and actively defend it from intruders, and so, they were not induced to move (Turnbull, 1964). It appears that Achaearanea tepidariorum demonstrates characteristics suggesting that their territoriality may be energy-based. Further experimentation could define the flexibility of territory size and indicate specific benefits accrued by territory owners.

V.1.4 Territoriality and Coexistence

There is evidence from this study supporting the hypothesis that intraspecific territoriality may facilitate the coexistence of another species (Riechert, 1978b, 1981). Territoriality among Achaearanea serves to limit their numbers through interactions among conspecifics. In doing so, some Achaearanea are prohibited from occupying spaces which are potentially suitable for inhabitation by Coelotes. If intraspecific interactions had not existed between previously established Achaearanea and immigrating conspecifics, then the immigrants might have been able to remain in those spots to the exclusion of Coelotes. Therefore, it is possible that through the operation of territorial behavior among Achaearanea, spaces on the cliffs are kept free of conspecifics. These sites may then be used and maintained by Coelotes.

V.1.5 Interspecific Effects on Adult Achaearanea

The presence of female Coelotes had little effect on population size or microhabitat use by adult Achaearanea. Although more prey were captured by Achaearanea in the absence of Coelotes, this was not accompanied by a shift in their diet. Thus there is evidence for only a limited competitive effect of adult Coelotes on adult Achaearanea in relation to prey consumption. Spider weight is known to be correlated with food consumption (Wise, 1975; Riechert, 1981), so the increased volume of prey received by Achaearanea probably affected the observed rise in their body and egg weight. This did not produce an increase in their population numbers, but may have supplied the spiderlings with more yolk in the eggs, aiding in their development and survival, and leading to a subsequent increase of individual fitness.

V.2 Coelotes

While the Achaearanea population is limited by intraspecific interactions, it seems that the Coelotes population was influenced by the presence of Achaearanea. Both the adult and immature densities of Coelotes increased after the removal of Achaearanea, and adult weight and reproduction also increased in the absence of the theridiid. Moreover, immature Coelotes numbers decreased on the control cliff while the coexisting immature Achaearanea population increased concurrently.

V.2.1 Immature Coelotes Intraspecific Effects

Although the existence of intraspecific competitive effects in immature Coelotes was not tested for directly, some evidence exists indicating its operation. The shifts of prey and microhabitat use by immature Coelotes may be a reflection of intraspecific competitive interactions inducing the young Coelotes to move into other microhabitats as their densities increased. This would require further experimentation.

V.2.2 Immature Coelotes Interspecific Effects

The removal of Achaearanea left cliff spaces unoccupied, some of which appeared to provide adequate websites for immature Coelotes (shown by a shift in their use of microhabitat features (Werner and Hall, 1976)). The expanding population of immature Coelotes moved into websites which were once occupied by Achaearanea. Perhaps intraspecific competition among Coelotes induced this movement into other microhabitats. However, this needs to be tested experimentally. Here is evidence of interspecific competitive effects between Achaearanea and Coelotes.

Immature Coelotes ate more prey and their diet changed in the absence of Achaearanea. The size and weight at maturity of most spiders is related to rates of prey ingestion during maturation (Humphreys, 1975; Wise, 1975, 1976; Workman, 1979; Riechert, 1981). In addition, size at maturity and fecundity are correlated for some web-building spiders (Turnbull, 1962, 1965; Wise, 1974). Therefore, any

increase in energy inputs to the young Coelotes during their maturation may subsequently produce heavier, more fecund adults. Thus, interspecific interactions between Coelotes and Achaearanea immatures over microhabitats and food probably have compound effects upon the Coelotes populations, influencing future adult reproductive success while they are still juveniles.

V.2.3 Adult Coelotes Interspecific Effects

No changes were detected in the use of microhabitats by adult Coelotes during the treatments. Therefore, their competitive release on the treatment cliff may have been affected by two mechanisms; relaxation of predation pressure by Achaearanea, and/or reduction of exploitative competition for food. A decrease in predation only results in an expanded population, but a release from competition for food also produces an increase in body weight and reproduction.

Relaxation of predatory activities by Achaearanea on Coelotes after removal of the former species probably allowed expansion of the Coelotes population, suggesting a two-fold effect involving interpredation that contributes to their coexistence. First, a reduced number of Coelotes (due to predation) lessens interspecific competition between Achaearanea and Coelotes, and simultaneously reduces any intraspecific competition among Coelotes. Secondly, by obtaining part of its required food in the form of Coelotes, Achaearanea may not exploitatively deplete other prey from the pool available to other spider community members. This leaves more food for the Coelotes which are

able to escape predation and coexist with Achaearanea. A similar suggestion was made by Schaefer (1974, 1975) concerning three Pardosa species. Slobodkin (1961) predicted that more species may exist in an area than what is allowed by competition as a result of interpredation among competitors. Fox (1975) indicated that predation among individuals of competing species tends to "regulate" the total biomass of those species. Paine (1966, 1971) confirmed this, and indicated that it is more evident in sedentary or sessile animals. These web-building spiders are not highly vagile. Predation of Achaearanea on Coelotes may be viewed as an extreme form of interference competition that reduces the Coelotes population size, although Coelotes does not constitute a major portion of the diet of Achaearanea (Benke, 1978). The observed coexistence of Achaearanea and Coelotes may be an example of one predator facilitating the existence of another, and contribute to molding the structure of this spider community.

Other studies using field manipulations have found changes in food consumption after removal of one of two potentially competing populations (Menge, 1972; Werner and Hall, 1976; Dunham, 1980). These results have been interpreted as indicative of interspecific competition. Adult Coelotes consumed more prey and increased their use of coleopterans as a food source on the cliffs where Achaearanea had been removed. Although the shift in prey utilization was not complete, (no coincidental decreased use of any other prey type) Coelotes did receive more of their preferred prey in the absence of Achaearanea. Adult Coelotes also were heavier and laid heavier egg sacs where Achaearanea

were not present. Thus, another interspecific effect (contests over prey) may act to limit the Coelotes populations and further influence community structure.

This investigation of coexistence between Achaearanea tepidariorum and Coelotes montanus provides evidence that interspecific interactions (in the form of predation and competition) help to shape the interrelationships between two spider species, and as a result, influence community structure (MacArthur, 1972; Price, 1975; Pianka, 1983). Other field studies investigating spiders have attempted to show evidence of interspecific effects between species (see Wise, 1983). A few workers have suggested that vertical stratification of orb-weavers is evidence of interspecific contests (Enders, 1974, Taub, 1977; Uetz et al., 1978), while a recent field experiment presented evidence for interspecific competitive effects between two species of orb weavers (Spiller, 1984), and a more extensive study (Riechert and Cady, 1983) produced some evidence that interspecific competition exists between syntopic spiders. The present, more detailed investigation points out that subtle interspecific interactions between the immatures of Achaearanea and Coelotes were important to the establishment of structure within this spider community, probably by ultimately influencing adult fitness. The importance of examining interactions between immature members of a community in conjuction with the investigation of relationships between the adults is illustrated here. All age groups must be studied in order to get a complete picture of community structure. Intraspecific contests among Achaearanea for cliff space also

influences the structure of this community by limiting the number and shaping the distributions of Achaearanea. This in turn facilitates their coexistence with Coelotes by opening spaces on the cliffs where the agelenid may live.

V.3 Other Community Members, Achaearanea, and Coelotes

The effect of predation by other animals on Achaearanea and Coelotes was not quantified. However, during 5 years of observing the spider community on the cliffs, it was obvious that predation did occur. Coelotes were seen (3 times) being captured by spider wasps (Pompilidae). Hypochilus thorellii were seen to eat Achaearanea five times and Coelotes seven times. Other potential predators which were observed on the cliffs include birds (Dendroica sp.), salamanders (Aneides aneneus, Plethodon glutinosis, Eurycea lucifuga, E. longicauda), and a frog (Rana palustris). Although they were suspected of eating spiders, they were never seen to do so. The relatively constant number of both spider species on the control cliff, and the static number of Achaearanea on the experimental cliffs (as well as the increase of Coelotes on the experimental cliff), suggest that if outside predation occurred, it did so at a steady rate during the study. Given the low number of predatory events observed during the entire investigation, it appears that it is not a significant pressure on Achaearanea or Coelotes populations.

Predation by other spider community members (i.e., Hypochilus, Araneus, salticids) on the two experimental species highlights a

problem inherent with these types of studies. Indirect effects of other coexisting species on those in question are often impossible to monitor simultaneously (with the experiments) without disturbing the integrity of the treatments. Riechert and Cady (1983) found that Hypochilus increased reproduction in the absence of Coelotes. This finding, and the observed predatory actions by other spider species exemplify such effects. Thus, once experiments such as these begin to elucidate mechanisms of coexistence between two community members, more experimental work with other community inhabitants becomes warranted. Herein lies an advantage of studying a community with relatively few major species.

V.4 Conclusion

There exist inter- and intraspecific interactions among the adults and immatures of Achaearanea tepidariorum and Coelotes montanus which contribute to their ability to coexist and which also serve to structure their community. Interspecific competition between the immatures for space and food appears to influence the energy inputs available to Coelotes, and in turn ultimately affects their population's growth and reproduction. Predation of Coelotes by Achaearanea is another interspecific interaction which influences the structure of the spider community. Intraspecific territoriality among Achaearanea limits their population, and functions to provide spaces where Coelotes are able to place their webs and coexist with Achaearanea. Interactions between

and within these species have occurred under the overriding physical constraints of the cliff habitat, guiding the evolution and shaping the structure of this spider community.

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APPENDICES

APPENDIX A

Table 1--Estimated available microhabitat space on control and experimental cliffs.

	Available Microhabitat Space (Cubic centimeters)	Cliff Surface Area (Square centimeters)
Achaearanea II	3,791,059	250,000
Coelotes II	3,458,395	215,000
Control	3,118,156	185,000
Achaearanea I	2,959,445	255,000
Coelotes I	1,376,881	170,000

Table 2--Density/square meter estimates of immature Achaearanea on control and experimental cliffs during the study. Corresponding Wilcoxon Matched-Pairs test statistic (Z) with significance levels (P) for paired within-cliff comparisons of densities. N = number of quadrat pairs.

	MEAN NUMBER							PAIRED YEAR COMPARISONS					
	1980		1981		1982			1980-1981		1980-1982		1981-1982	
Cliff	Mean	±SE	Mean	±SE	Mean	±SE	N	Z	P	Z	P	Z	P
Achaearanea I	3.96	0.75	3.93	0.84	3.41	0.58	33	0.794	0.43	1.383	0.07	0.681	0.49
Achaearanea II	4.55	0.64	5.13	0.58	4.65	0.68	28	0.614	0.54	1.237	0.22	1.257	0.21
Control	6.70	0.98	8.63	1.10	8.08	1.28	21	3.380	0.05	0.355	0.72	0.093	0.93

Table 3--Total number of adult Achaearanea observed on control and respective experimental cliffs. Connecting lines indicate Chi-square significance of $P < 0.05$ or less.

	Number of Adult Achaearanea		
	1980	1981	1982
Achaearanea I	69 ----------	26 ----------	54
Achaearanea II	63	46	46
Control	41	43	44

Table 4--Adult female Achaearanea body weight and reproduction in the presence (control) and absence (experimental) of Coelotes. All weights in milligrams.

				Control versus Experimental		
	Mean	±SE	N	t	P	Degrees of Freedom
		Experimental				
Body wt.	52.06	1.23	505	2.34	<0.01	718
Egg sac wt.	32.89	0.67	397	2.31	<0.01	557
Number of egg sacs	1.98	0.12	310	0.72	=0.24	433
Eggs per sac	273.61	10.51	91	0.09	=0.47	120
		Control				
Body wt.	46.84	1.81	215			
Egg sac wt.	29.93	1.55	162			
Number of egg sacs	1.86	0.19	125			
Eggs per egg sac	278.63	20.26	31			

Table 5--Density/square meter estimates of immature Coelotes on control and experimental cliffs during the study. Corresponding Wilcoxon Matched-Pairs test statistic (Z) with significance levels (P) for paired within-cliff comparisons of densities. N = number of quadrat pairs.

	MEAN NUMBER							PAIRED YEAR COMPARISONS					
	1980		1981		1982			1980-1981		1980-1982		1981-1982	
Cliff	Mean	±SE	Mean	±SE	Mean	±SE	N	Z	P	Z	P	Z	P
Coelotes I	2.44	0.60	2.80	0.28	2.16	0.32	21	1.213	0.23	1.429	0.15	2.035	0.04
Coelotes II	4.71	0.77	6.39	0.82	4.92	0.62	27	3.619	<0.001	2.299	0.02	1.714	0.09
Control	7.96	1.14	4.89	0.68	4.45	0.67	21	2.294	0.02	2.450	0.01	0.261	0.79

Table 6--Total number of adult Coelotes observed on control and respective experimental cliffs. Connecting lines indicate Chi-square significance of $P < 0.05$ or less.

	Number of Adult Coelotes		
	1980	1981	1982
Coelotes I	5	11	4
Coelotes II	10	35	25
Control	11	12	19

Table 7--Adult female Coelotes body weight and reproduction in the presence (control) and absence (experimental) of Achaearanea. All weights in milligrams.

				Control versus Experimental		
	Mean	±SE	N	t	P	Degrees of Freedom
		Experimental				
Body wt.	119.37	7.17	122	4.14	<0.001	206
Egg sac wt.	63.11	10.31	9	9	<0.10	(Mann-Whitney)
Number of egg sacs	0.295	0.06	98	1.75	<0.04	137
		Control				
Body wt.	70.22	9.82	86			
Egg sac wt.	55.33	6.01	3			
Number of egg sacs	0.106	0.14	44			

Table 8--Coefficient of Dispersion (variance-to-mean ratio = CD: >1 = clumped, =1 = random, <1 = regular spacing) of immature and adult Achaearanea and Coelotes on the control and experimental cliffs during 1980-1982. Significance levels of t-test (P) shown.

	1980		1981		1982	
	CD	P	CD	P	CD	P
			IMMATURE			
Achaearanea						
Experimental I	4.35	0.001	8.76	0.001	4.17	0.001
Experimental II	2.94	0.001	1.09	0.376	1.24	0.196
Control	2.19	0.001	3.87	0.001	2.48	0.001
Coelotes						
Experimental I	3.08	0.001	1.03	0.531	1.65	0.040
Experimental II	3.47	0.001	2.89	0.001	4.94	0.001
Control	3.06	0.001	2.25	0.001	1.99	0.004
			ADULT			
Achaearanea						
Experimental I	2.86	0.001	1.99	0.001	3.77	0.001
Experimental II	2.98	0.001	1.55	0.030	2.57	0.001
Control	4.23	0.001	3.68	0.001	6.08	0.001
Coelotes						
Experimental I	0.88	0.371	0.93	0.420	0.88	0.367
Experimental II	1.06	0.426	1.24	0.213	1.50	0.050
Control	1.08	0.405	1.35	1.51	3.09	0.001

Table 9--Estimate of microhabitat overlap between immature Achaearanea and Coelotes on the control and experimental cliffs during 1980-1982 (Coefficient of similarity after Riechert and Cady, 1983; see Methods, Chapter II).

	1980	1981	1982
Experimental	0.155	0.324	0.469
Control	0.083	0.201	0.272

Table 10--Estimate of microhabitat overlap between adult Achaearanea and Coelotes on control and experimental cliffs during 1980-1982 (Coefficient of similarity after Riechert and Cady, 1983).

	1980	1981	1982
Experimental	0.209	0.279	0.346
Control	0.191	0.222	0.290

Table 11--Overall Pairwise F-test of prey sizes between adults and immatures of Achaearanea and Coelotes. Degrees of freedom for all tests = 1,2127.

	Immature Achaearanea	Immature Coelotes	Adult Achaearanea
Immature Coelotes	0.0380 P = 0.84		
Adult Achaearanea	164.98 P < 0.001	21.234 P < 0.001	
Adult Coelotes	27.068 P < 0.001	12.243 P < 0.001	0.1915 P = 0.66

Table 12--Coefficients of similarity between Achaearanea and Coelotes immatures or adults computed on prey types during 1980-1982 (Coefficient of similarity after Riechert and Cady, 1983).

	1980	1981	1982
Immatures	0.677	0.821	0.748
Adults	0.791	0.809	0.837

Table 13--Number of prey captured by immature Achaearanea and Coelotes on control and experimental cliffs. Connecting lines indicate Chi-square significance of $P < 0.05$ or less.

Achaearanea		Coelotes					
		1980		1981		1982	
Number of Prey	Number of Spiders	Prey Number	Spider Number	Prey Number	Spider Number	Prey Number	Spider Number
Experimental 448	4079	19	1207	35	1387	29	715
Control 296	2585						

Table 14--Coefficients of similarity computed on prey types eaten by Achaearanea immatures between experimental and control cliffs and coefficients of similarity computed on prey types eaten by immature Coelotes between 1980 vs. 1981 and 1980 vs. 1982 (Coefficients of similarity after Riechert and Cady, 1983).

Immature Achaearanea			Immature Coelotes	
1980	1981	1982	1980 vs. 1981	1980 vs. 1982
0.7798	0.8979	0.9098	0.8553	0.6725

Table 15--Number of prey captured by adult Achaearanea and Coelotes on control and experimental cliffs. Connecting lines indicate Chi-square significance of $P < 0.05$ or less.

	Number of prey	Number of spiders	Chi-square
		Achaearanea	
Experimental	1162	304	
			24.42
			$P < 0.001$
Control	364	128	
		Coelotes	
Experimental	61	105	
			5.57
			$P = 0.018$
Control	3	19	

Table 16--Coefficients of similarity computed on prey types eaten by Achaearanea adults between experimental and control cliffs and coefficients of similarity computed on prey types eaten by adult Coelotes between 1980 vs. 1981 and 1980 vs. 1982 (Coefficients of similarity after Riechert and Cady, 1983).

Adult Achaearanea			Adult Coelotes	
1980	1981	1982	1980 vs. 1981	1980 vs. 1982
0.8568	0.9134	0.8686	0.6243	0.6682

Table 17--Mean weights of food sated and deprived Achaearanea at the beginning and end of the Fixed and Float release enclosure experiments. Means accompanied by standard error (in parentheses). Feeding regimes were begun 1 week before weighing and the start of the experiment.

	Deprived		N	Sated		N	Mann-Whitney	
				Fixed Release Mean Spider Weights (mg)				
Start	63.5	(6.07)	10	109.12	(7.91)	10	T = 6.5	P < 0.001
End	53.1	(8.53)	9	73.81	(6.97)	10	T = 15.0	P < 0.02
				Float Release Mean Spider Weights (mg)				
Start	46.1	(5.53)	10	63.8	(7.55)	10	T = 27.0	P < 0.05
End	54.0	(9.12)	7	58.5	(7.91)	9	T = 6.50	P > 0.05

Table 18--Mean interspider distances of food sated and deprived Achaearanea in the Fixed and Float release enclosure experiments. Means accompanied by standard error (in parentheses).

	Deprived		N	Sated		N	Mann-Whitney	
				Fixed Release Mean Spider Distances (cm)				
Start	37.25	(1.68)	10	30.29	(1.18)	10	T = 7.5	P < 0.001
End	33.44	(3.09)	9	30.66	(0.83)	10	T = 64	P > 0.10
Mann-Whitney	T = 36.6	P > 0.10		T = 50.5	P > 0.10			
				Float Release Mean Spider Weights (mg)				
Start	27.66	(5.45)	8	39.95	(4.85)	10	T = 10	P < 0.025
End	31.27	(2.57)	7	25.08	(4.58)	8	T = 20	P > 0.10
Mann-Whitney	T = 21	P > 0.10		T = 15	P < 0.05			

Table 19--Mean interspider distances of food-sated Achaearanea during the float release enclosure experiment.

Date	Mean Interspider Distance (cm) Distance	N
27 August	39.94	10
1 October	35.06	8
17 October	29.16	8
23 October	25.08	8

Table 20--Mean web volumes of food sated and deprived Achaearanea in the fixed release enclosure experiment. Means accompanied by standard errors in (parentheses).

	Web Volume (cubic cm)		N
Sated	23975.8	(5869.4)	10
Deprived	29406.7	(10414.3)	9
t-test	1.32	17 df P = 0.101	

Table 21--Number of movements made by food sated and deprived Achaearanea during the fixed release of the enclosure experiment.

Date	Numbers of Moving Spiders	
	Sated	Deprived
12 August	2	0
13 August	0	3
18 August	0	3
25 August	0	2
8 October	0	3

Table 22--Index of movement for adult Achaearanea in different months on control and experimental cliffs. (Method of calculation outlined in text.) Index represents amount of movement by spiders maturing in each month. T = statistic for differences between two percentages (Sokal and Rohlf, 1969); indicates significance level of difference between control and experimental cliffs.

Month	Control	Experimental	T	P
June	0.583 N = 12	0.571 N = 28	0.069	0.47
July	0.350 N = 60	0.693 N = 163	4.65	< 0.001
August	0.618 N = 34	0.769 N = 78	1.61	0.05
September	0.167 N = 12	0.952 N = 21	5.14	< 0.001

APPENDIX B

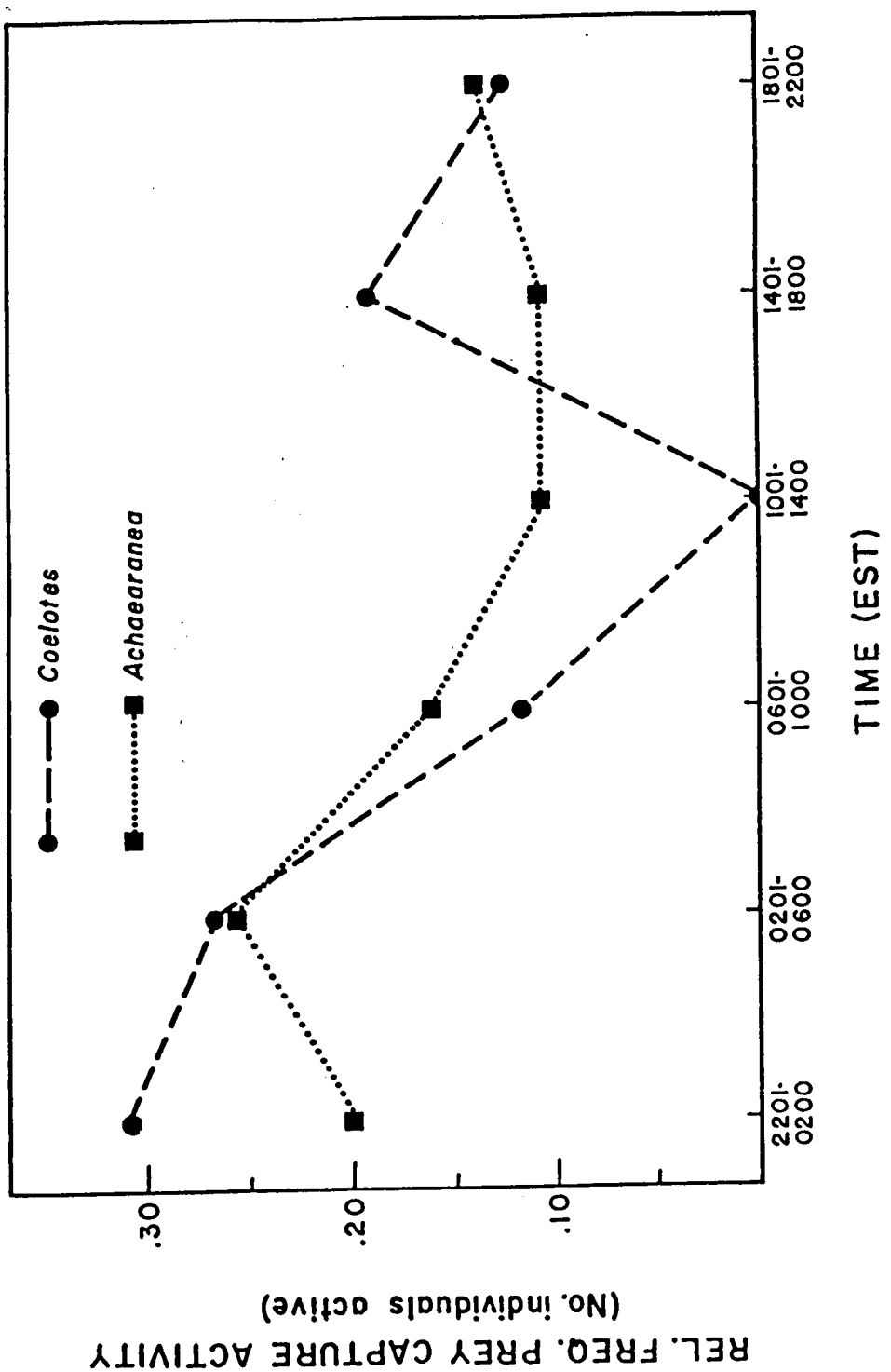

FIGURE 1--Diel activities of Achaearanea and Coelotes. Data represent number of individuals engaged in prey capture activities standardized between species (From Riechert and Cady, 1983).

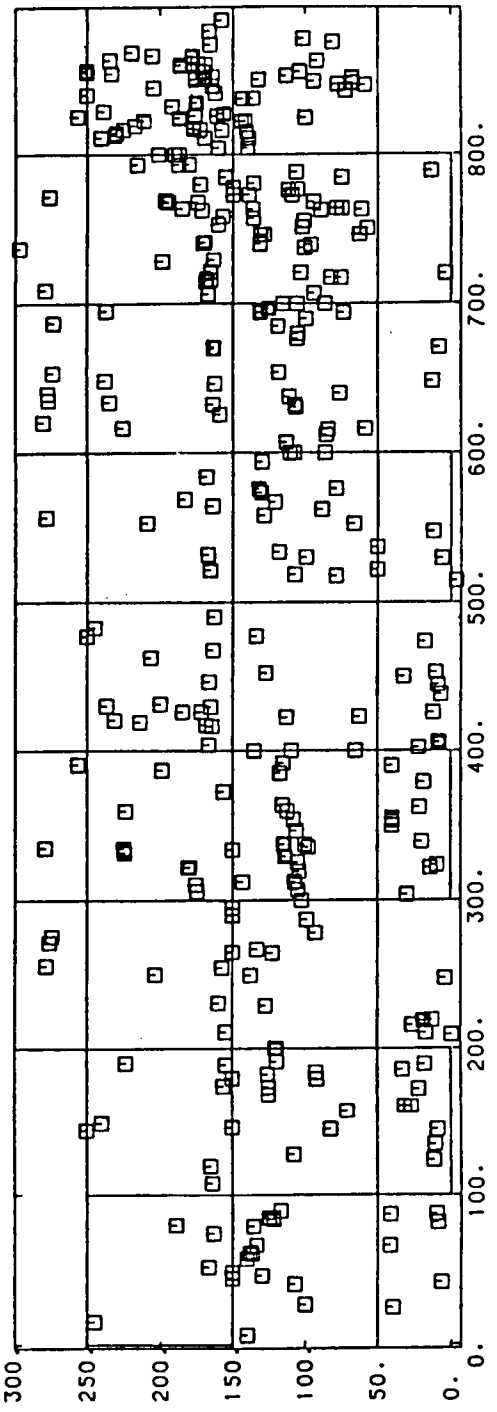

FIGURE 2--Plot of immature Achaearanea on experimental cliff Achaearanea II during 1982. Darker squares indicate multiple occupancy of that spot during the year. Distances in cm.

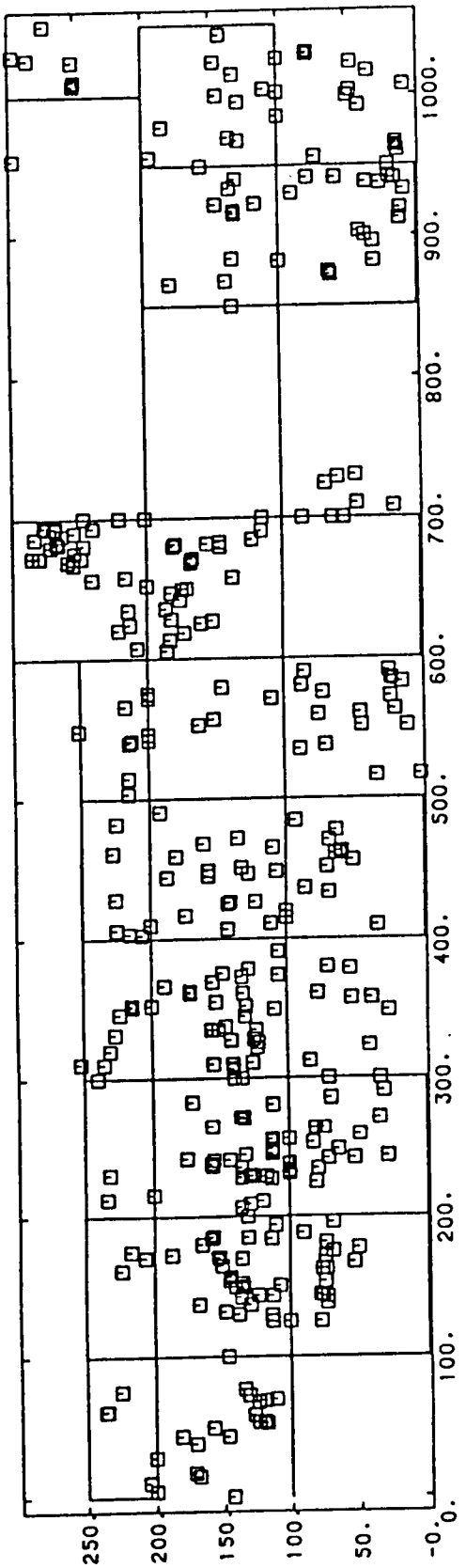

FIGURE 3--Plot of immature Coelotes on experimental cliff Coelotes II during 1982. Darker squares indicate multiple occupancy of that spot over the season. Distances in cm.

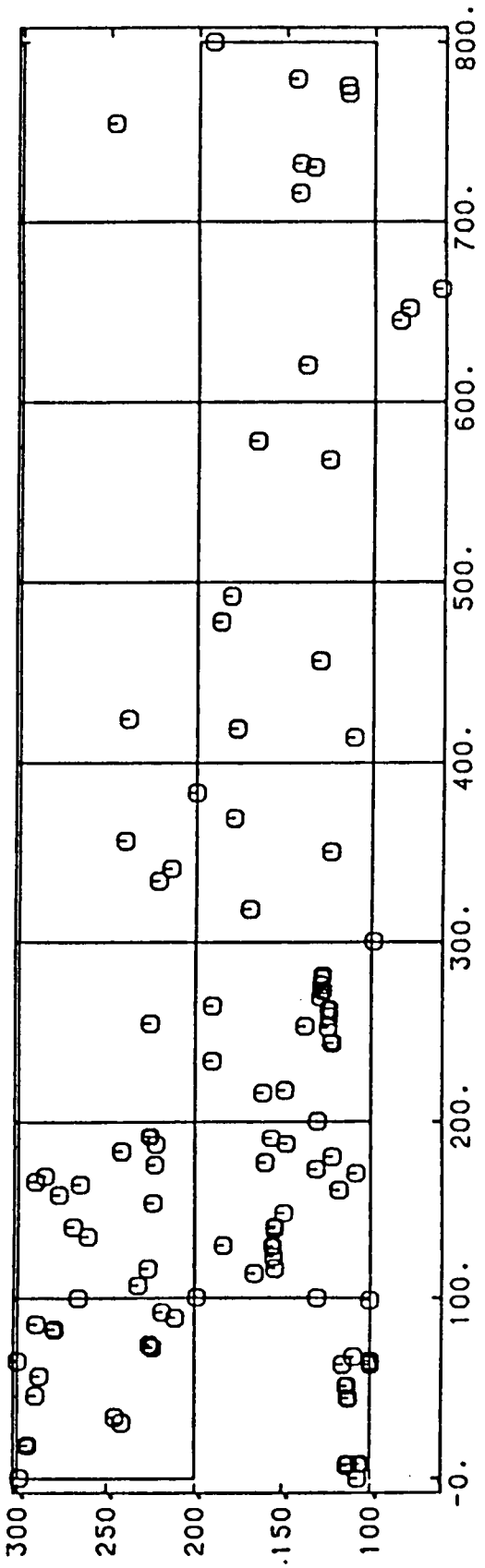

FIGURE 4--Plots of adult Achaearanea on control cliff during 1982. Darker circles indicate multiple occupancy of that spot during the year. Distances in cm.

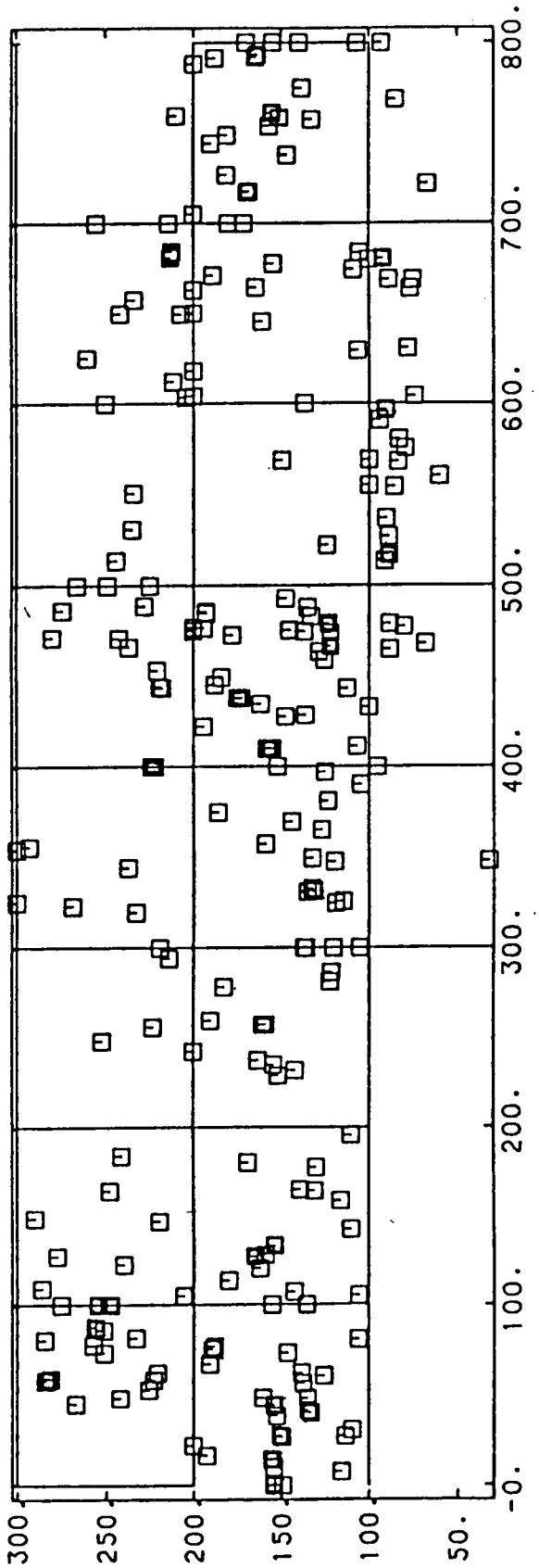

FIGURE 5--Plot of immature Coelotes on control cliff during 1982. Darker squares indicate multiple occupancy of that spot over the season. Distances in cm.

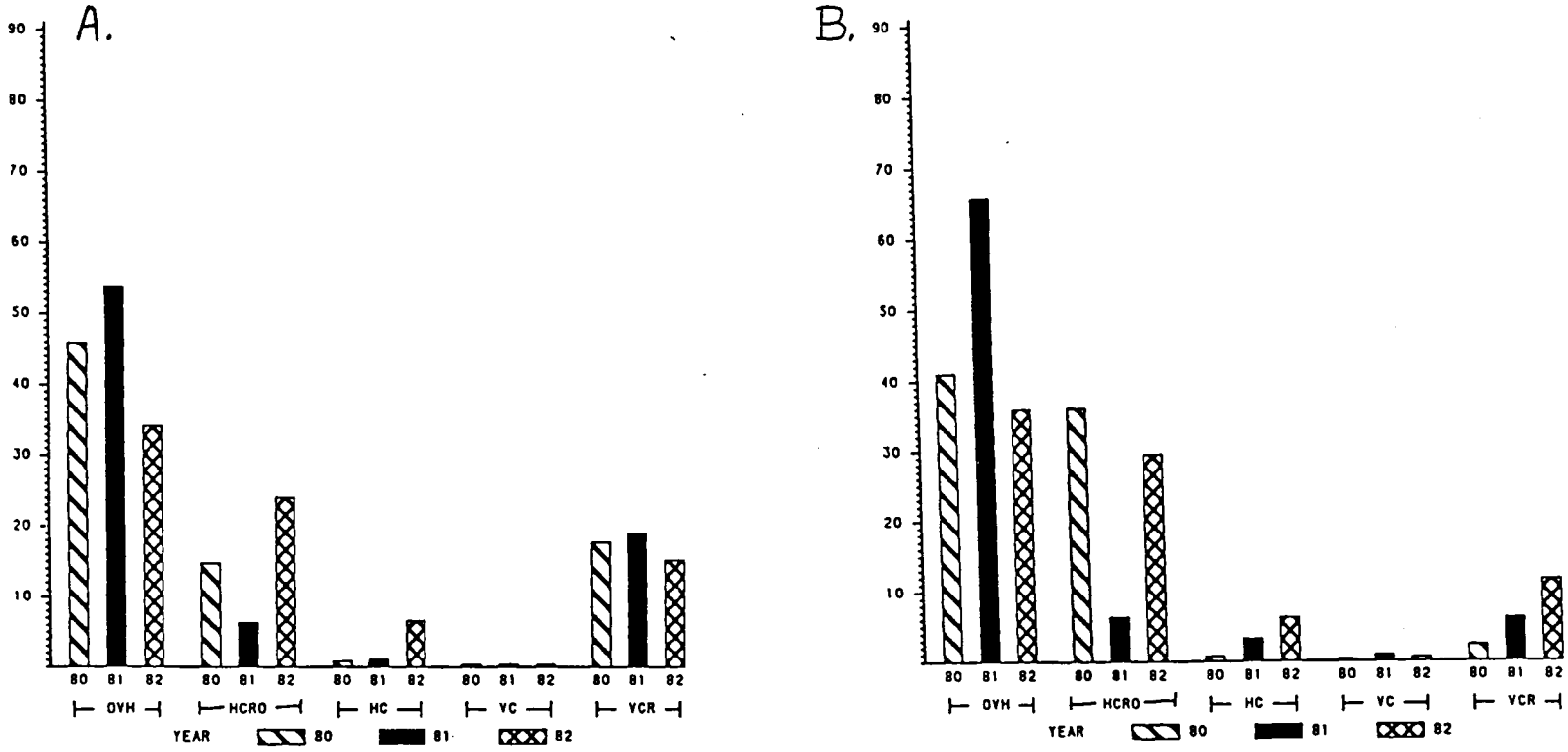

FIGURE 6--Relative percent of microhabitat occupancy (ordinate) by immature Achaearanea on the experimental (A) and control cliffs (B) during 1980-1982. Features shown represent the five most important microhabitats shared by Achaearanea and Coelotes. OVH = Overhang, HCRO = Horizontal corner forming a small Overhang, HC = Horizontal crack, VC = Vertical crack, VCR = Vertical corner.

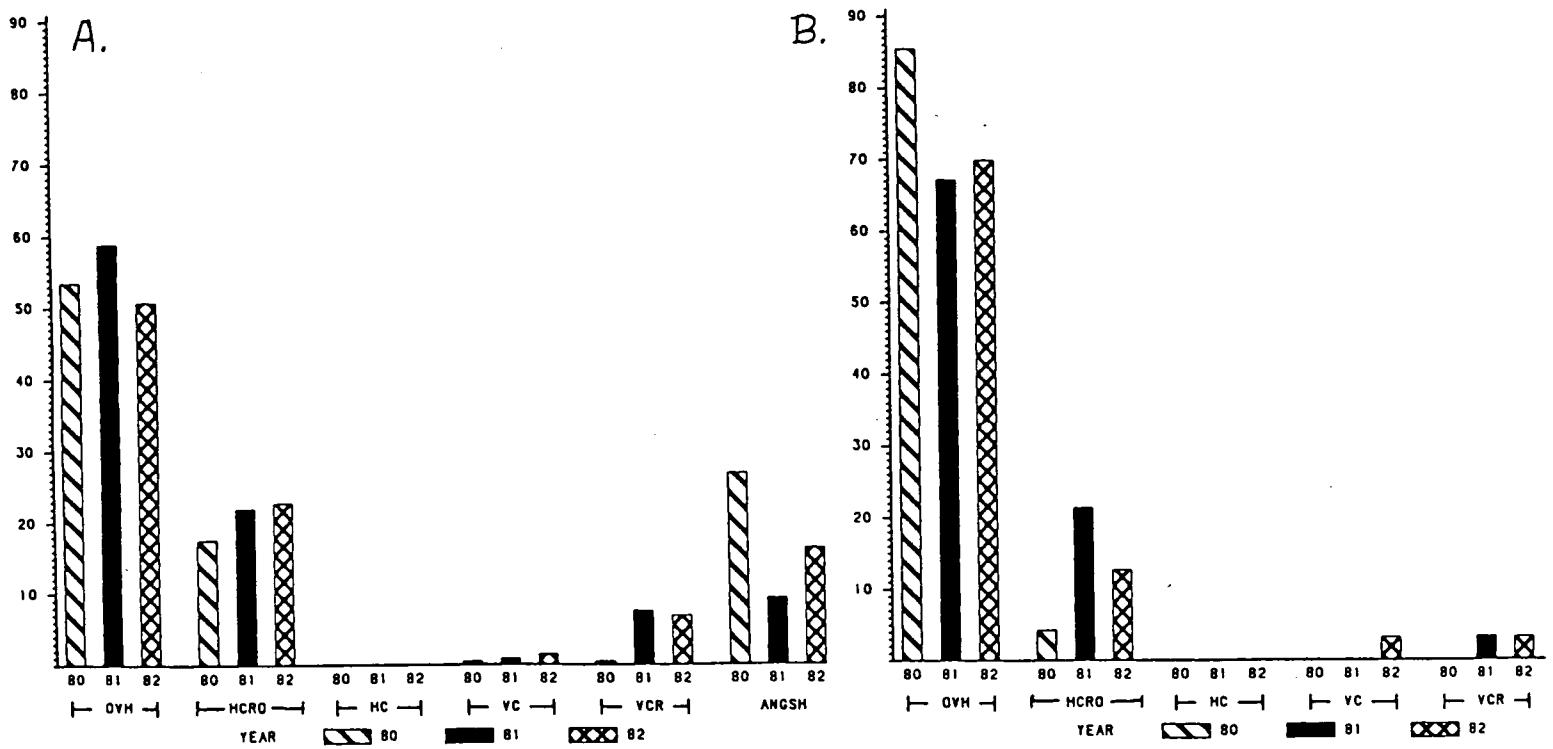

FIGURE 7--Relative percent of microhabitat occupancy (ordinate) by adult Achaearanea on the experimental (A) and control cliffs (B) during 1980-1982. Features shown represent the five most important microhabitats shared by Achaearanea and Coelotes. OVH = Overhang, HCRO = Horizontal corner forming a small Overhang, HC = Horizontal crack, VC = Vertical crack, VCR = Vertical corner.

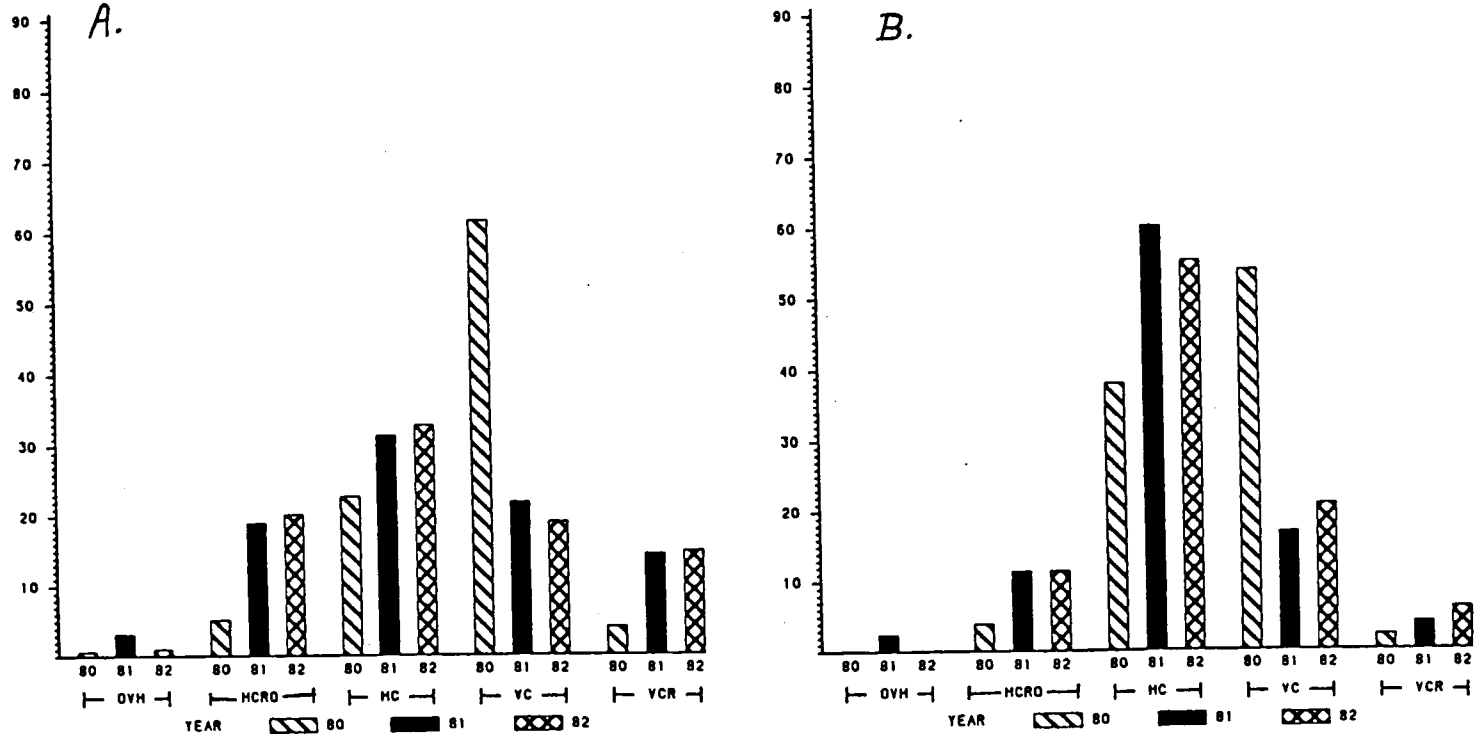

FIGURE 8--Relative percent of microhabitat occupancy (ordinate) by immature Coelotes on the experimental (A) and control cliffs (B) during 1980-1982. Features shown represent the five most important microhabitats shared by Achaearanea and Coelotes. OVH = Overhang, HCRO = Horizontal corner forming a small Overhang, HC = Horizontal crack, VC = Vertical crack, VCR = Vertical corner.

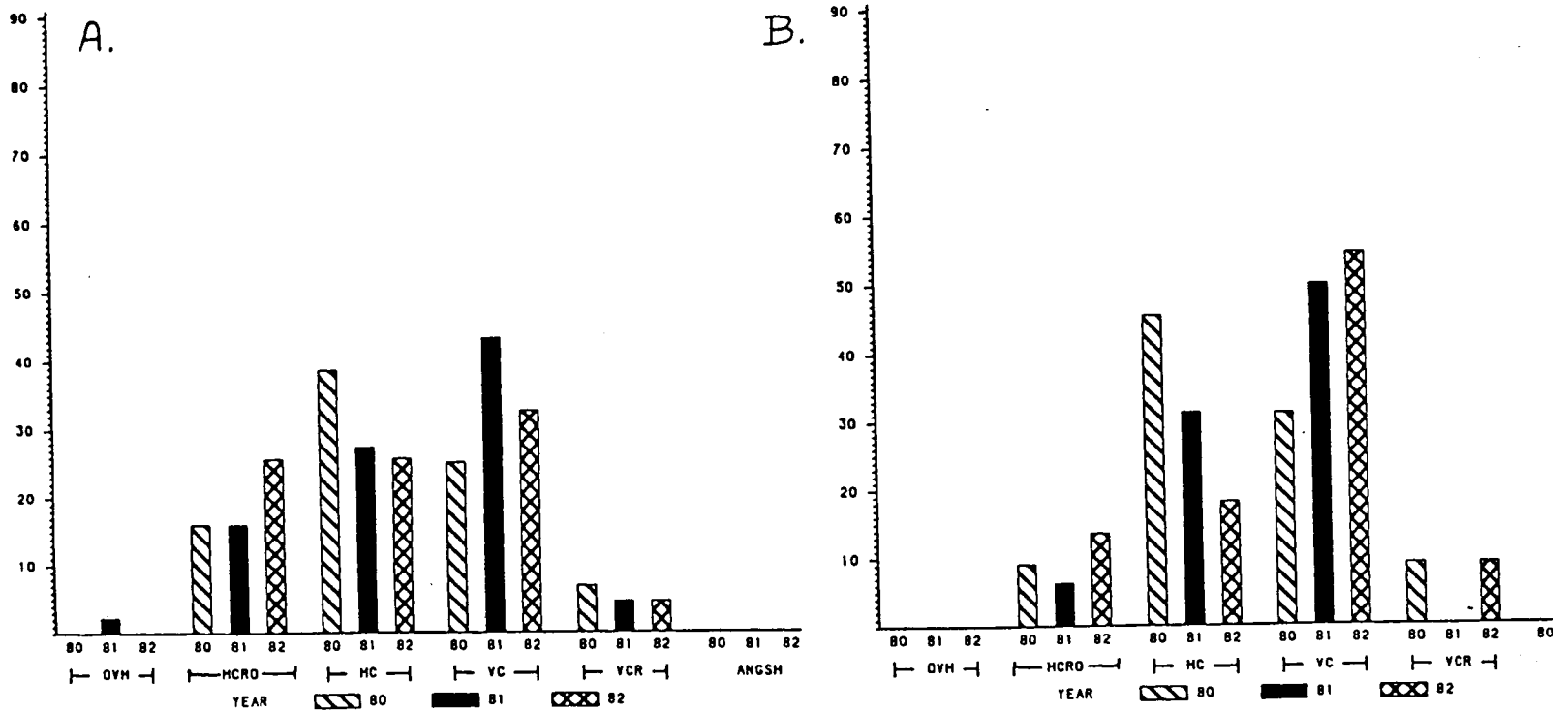

FIGURE 9--Relative percent of microhabitat occupancy (ordinate) by adult Coelotes on the experimental (A) and control cliffs (B) during 1980-1982. Features shown represent the five most important microhabitats shared by Achaearanea and Coelotes. OVH = Overhang, HCRO = Horizontal corner forming a small Overhang, HC = Horizontal crack, VC = Vertical crack, VCR = Vertical corner.

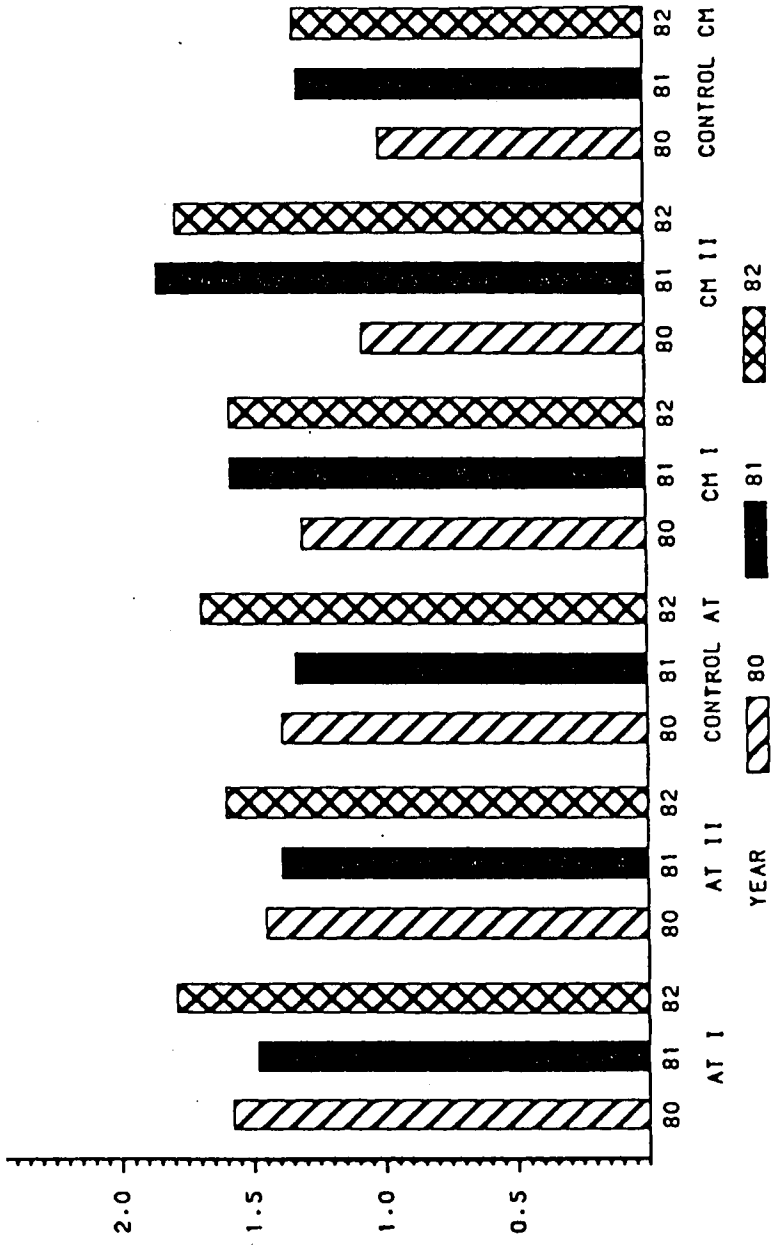

FIGURE 10--Shannon-Wiener diversity index (ordinate) of microhabitat use by immature Achaearanea and Coelotes on experimental and control cliffs during 1980-1982.

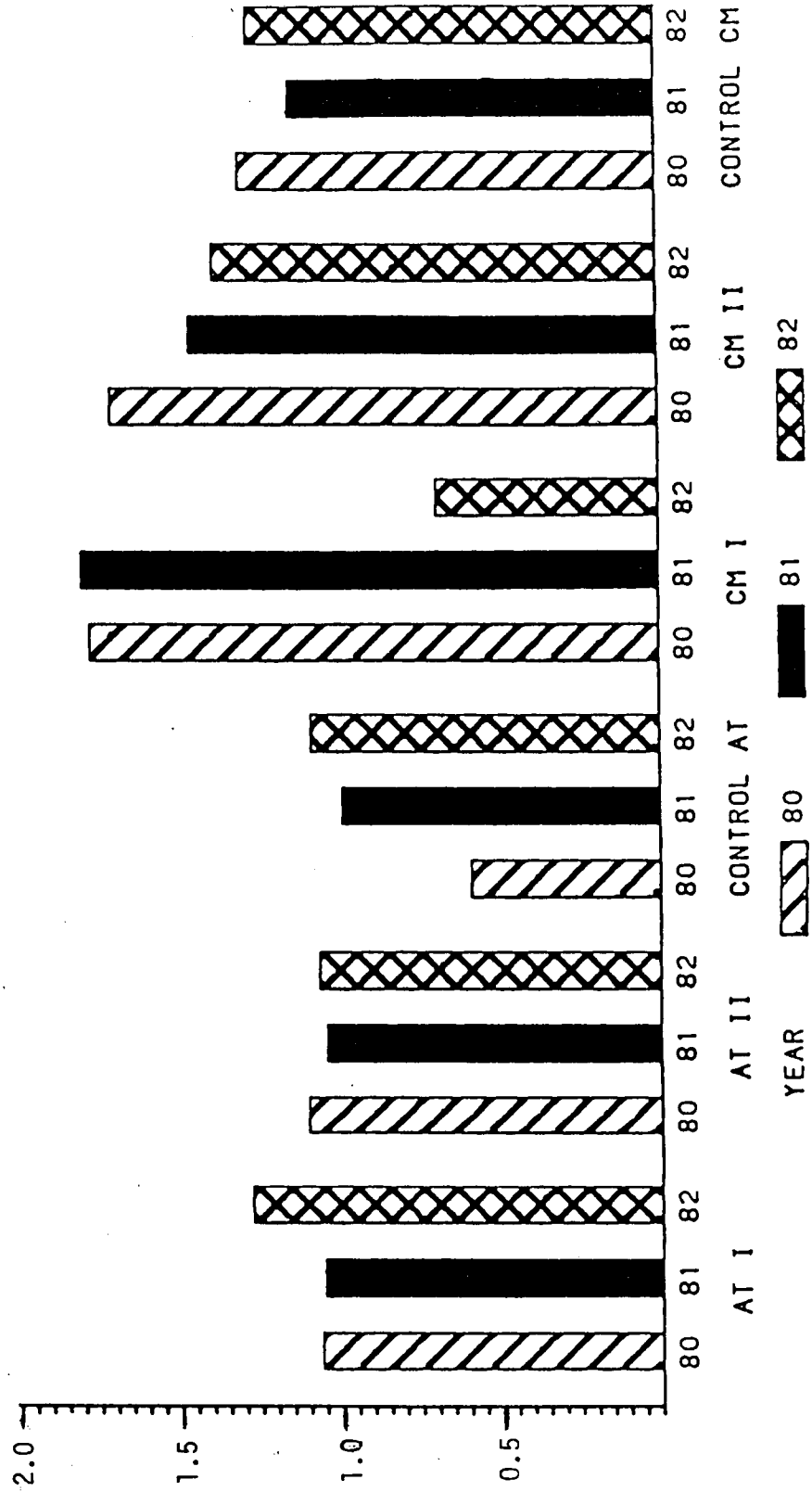

FIGURE 11--Shannon-Wiener diversity index (ordinate) of microhabitat use by adult Achaearanea and Coelotes on experimental and control cliffs during 1980-1982.

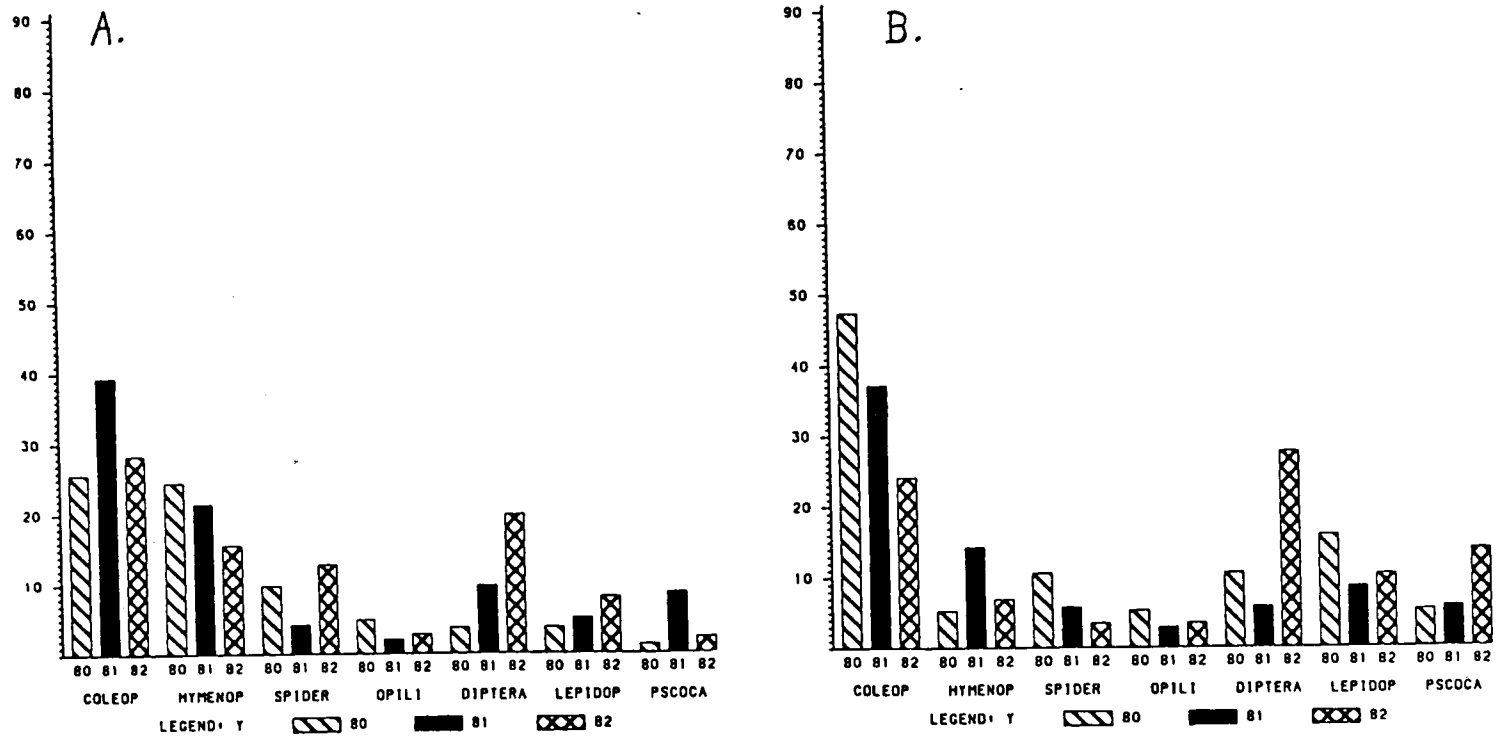

FIGURE 12--Relative percent of prey types captured (ordinate) by immature Achaearanea (A) and Coelotes (B) during 1980-1982. Prey types shown represent at least 80% of each spider species total diet.

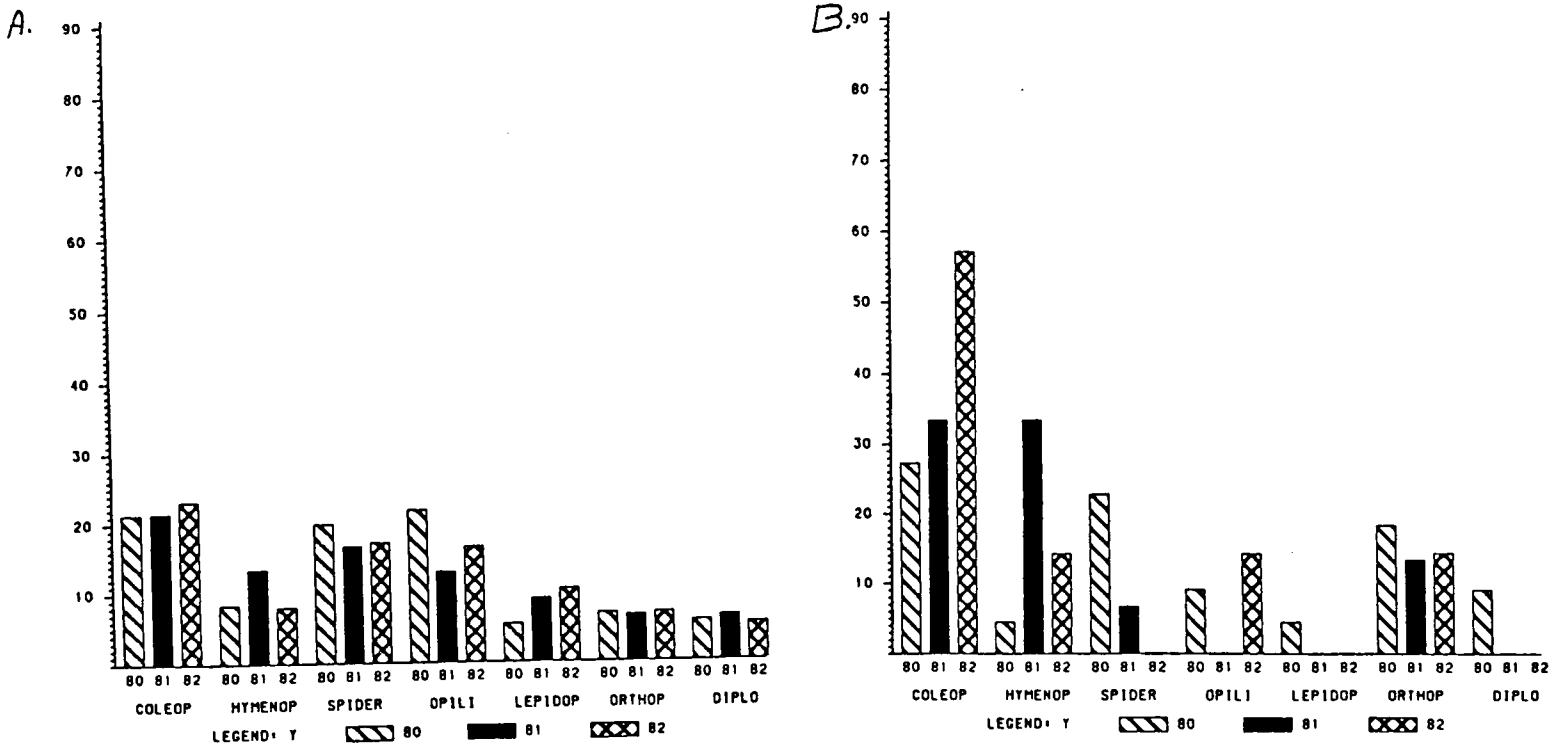

FIGURE 13--Relative percent of prey types captured (ordinate) by adult Achaearanea (A) and Coelotes (B) during 1980-1982. Prey types shown represent at least 80% of the total diet of each spider species.

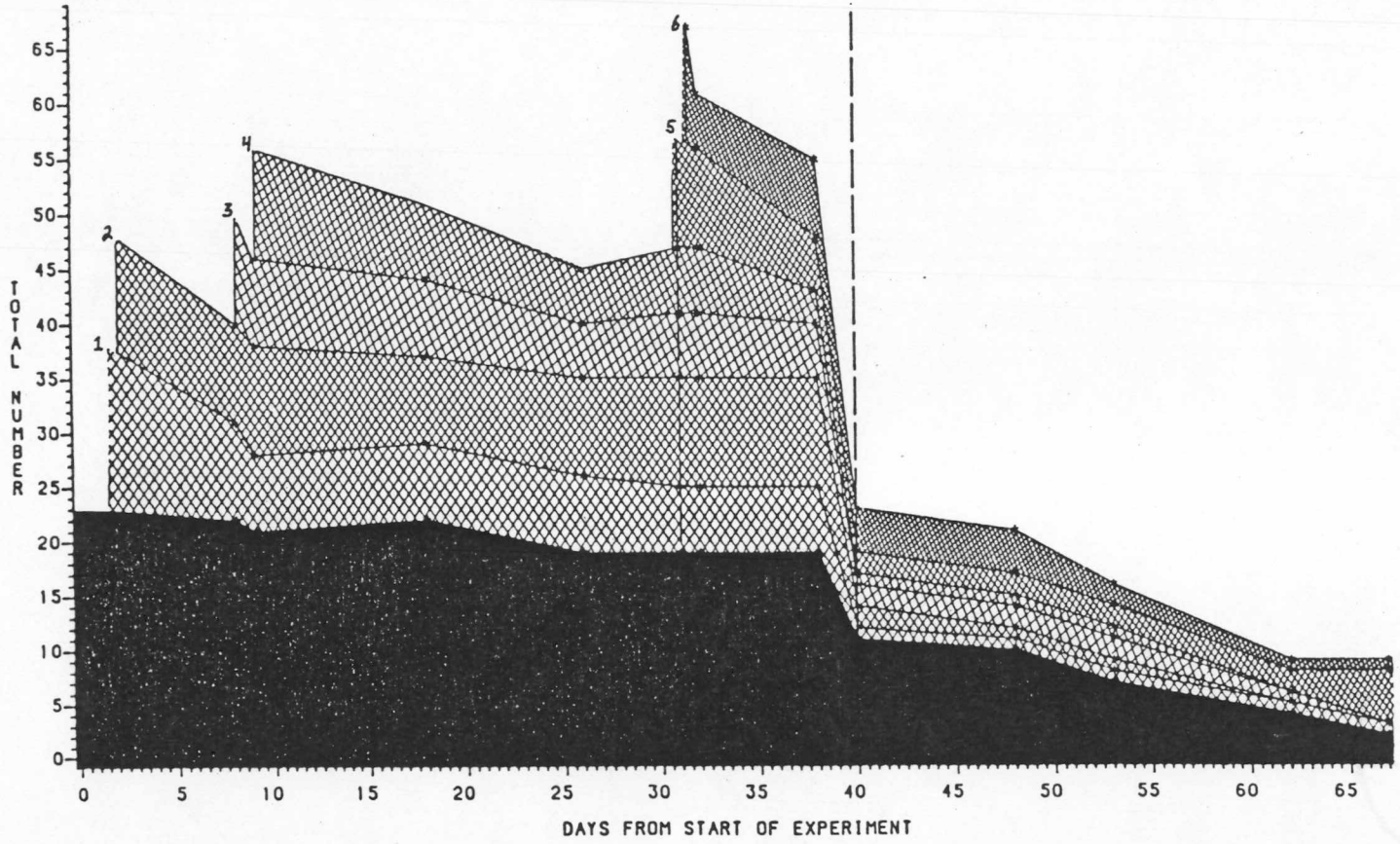

FIGURE 14--Cumulative frequencies of adult female Achaearanea on the addition cliff during the experimental period. Solid area represents numbers of original residents throughout the experiment. Crosshatched areas show numbers of added spiders remaining of each release group. Times of release are indicated by the numbers marking the release groups. The first (left most) vertical line indicates the day which Coelotes were removed from the cliff; the second marks the first hard frost.

VITA

Alan Bruce Cady was born in Syracuse, New York on August 10, 1954. During his primary education he was active in organized sports and music and was a member of the Boy Scouts of America. Upon graduation from West Genesee Senior High School in 1972, he attended Onondaga Community College for two years, earning an Associates of Arts degree in Math and Science in 1974. He then transferred with advanced standing to S.U.N.Y. College of Environmental Science and Forestry, and completed a Bachelors of Science degree in Forest Biology in 1976.

Alan then enrolled in a Masters of Science degree program at Ohio University in Athens, Ohio, and upon earning that degree in 1978, he attended The University of Tennessee to pursue a doctorate degree in zoology. He became a Ph.D. candidate in 1981, and received that degree, majoring in zoology in 1984.

The author is a member of the American Arachnological Society and has published on his research interest of spider behavioral ecology in different professional journals. He is presently an assistant professor of biology at Lindenwood College in St. Charles, Missouri, and is married to Anne K. Nestor of Oak Ridge, Tennessee.