AN EXPERIMENTAL ANALYSIS OF INTRAGUILD PREDATION AMONG THREE GENERA OF WEB-BUILDING SPIDERS: *HYPOCHILUS, CORAS* AND *ACHAEARANEA* (ARANEAE: HYPOCHILIDAE, AMAUROBIIDAE AND THERIDIIDAE)

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ABSTRACT. We investigated predatory interactions among three species of web-building spiders which co-occur on sandstone outcrops along the Cumberland Plateau in east Tennessee: *Hypochilus thorelli* (Hypochilidae), *Achaearanea tepidariorum* (Theridiidae) and *Coras montanus* (Amaurobiidae). Previous studies have shown that these spiders are essentially ecological equivalents with respect to activity, web-site characteristics and prey capture and that each species preys on the others. This type of predatory interaction between potential competitors is referred to as intraguild predation. We performed removal experiments to determine the significance of intraguild predation for each of the species as predators and as prey. Three types of treatment plots were established: from each plot two of the three study species were removed (weekly, July-October 1993) and the third remained. Control plots were established from which no spiders were removed. We predicted that if the treatments resulted in removal of an important source of prey then: 1) the number of individuals of the remaining species should decline over time as a result of web-relocation, and 2) body condition of spiders remaining should be lower in the treatments than in the controls. If treatments had the effect of removing predation then the number of individuals remaining in treatment plots should increase relative to the controls where intraguild predation could occur. There were no significant differences in the number of spiders of the remaining species on treatment versus control plots, indicating that the treatment did not result in spider relocation as a response to potential food removal. However, at the end of the experiment body condition of *H. thorelli* was significantly lower on plots from which the other two species were removed than on control plots. This suggests that removal of the other two species may have resulted in removal of a significant source of prey for *H. thorelli*. In addition, we present evidence that treatments may have removed a source of predation on dispersing *A. tepidariorum* spiderlings.

Competition and predation are the two types of interspecific interaction thought to have major influence on community structure (Sih et al. 1985). Predatory interactions among members of the same guild (sympatric taxa that use similar resources, and thus may compete with each other: Root 1967; Polis et al. 1989; Simberloff & Dayan 1991) are termed intraguild predation (hereafter designated IGP). This type of predation is distinguished from predation in the traditional sense in that by eating a guild member, an individual not only gains energy and nutrients, but reduces potential competition for food. Intraguild predation has recently been proposed as an important and previously unrecognized factor which may influence the distribution, abundance and evolution of many species (Polis et al. 1989; Polis & Holt 1992).

Because most spiders are generalist predators on arthropods, different species may interact as both competitors and predators, making them ideal model organisms for the investigation of IGP. Several studies of IGP have included spiders; however, these studies found that spiders were intraguild prey of other taxa (Pacala & Roughgarden 1984; Polis & McCormick 1986, 1987; Spiller & Schoener 1988, 1990; Hurd & Eisenburg 1990; Moran & Hurd 1994). Studies of competitive interactions among spider species must consider the possibility of IGP. Riechert & Cady (1983)

tested for competition among four genera of web-building spiders inhabiting rock outcrops on the Cumberland Plateau in eastern Tennessee. They established experimental plots from which three of four species were removed and one species remained, and control plots from which no spiders were removed. Comparing population densities and egg production of spiders on experimental plots with those on controls, they found no evidence for competitive release by spiders remaining in the removal plots. However, on some of the removal plots they observed a negative effect of removals on the species remaining. Because they observed that almost 50% of the diet of one of the species studied consisted of spiders, they hypothesized that the absence of competitive release may have been due to the fact that they may have been removing prey rather than competitors (Riechert & Cady 1983; Wise 1993).

Though there is ample evidence that spiders prey on each other, (Polis 1981; Polis et al. 1989; Jackson 1992) to date no experimental studies have explicitly tested for IGP between spider species. Our study examined this possibility. We tested the hypothesis that IGP influences the distribution and abundance of three of the four species examined by Riechert & Cady (1983). We selected the Tennessee sandstone outcrop community as we felt it offered an especially promising model system to test for IGP: 1) there was already evidence that IGP might play a role in mediating competitive interactions (Riechert & Cady 1983), 2) because the three species all spin their webs on a vertical rock face we did not need to consider interspecific differences in microhabitat selection, and 3) the spiders are individually easy to observe and manipulate (e.g., compared to cryptic species or those in a more three-dimensional habitats such as vegetation). Our predictions were as follows: if the experimental treatments (removals) resulted in the removal of an important source of *food* for the species remaining on treatment plots, then 1) the number of individuals of the remaining species should decline over time and 2) body condition of the spiders remaining should be significantly lower in the treatment plots than in the control plots. The first prediction follows from the fact that when web-building spiders are deprived of food, they will relocate (i.e. move to a new web site, thus potentially leaving the plot). The second prediction is based on the fact that food-deprived spiders will have lower fat stores and thus lower body condition than well-fed spiders. If the experimental manipulations had the effect of removing *predators*, then the prediction was that the number of individuals of the focal species remaining in the treatment plots should increase relative to the control plots. This would be the case if the removals reduced the density of predators on the focal species.

METHODS

The study site was located along the sandstone outcrops of the Cumberland Plateau, in a canyon cut by Clear Creek where it is crossed by Lilly Bridge, in Morgan County, Tennessee. We studied the three most abundant species of web-building spiders: *Hypochilus thorelli* Marx 1888 (Hypochilidae), *Coras montanus* (Emerton 1889) (Amaurobiidae), and *Achaearanea tepidariorum* (C.L. Koch 1841) (Theridiidae). The lampshade spider, *Hypochilus thorelli*, is a cribellate spider whose distribution is restricted to rock outcrops in the Appalachian region (Forster et al. 1987). *Hypochilus* sits in the center of a tubular web which extends perpendicularly from the rock surface, pulled into a shape resembling a lampshade by support strands (Ferguson 1972). *Coras montanus* builds a funnel web, the base of which extends into crevices in the rock. *Achaearanea tepidariorum* builds a tangle web under ledges on the rock outcrop. Despite the differences in web structure, these three species are so similar in size, microhabitat, activity period, and prey captured that they have been termed "ecological equivalents" (Riechert & Cady 1983). The fourth species included in Riechert & Cady's study, *Araneus cavaticus* (Keyserling 1882) (Araneidae), was not included in this study because it was not common at our study site, and as an aerial web-builder shows less habitat overlap with the other three species (Riechert & Cady 1983).

Study plots were established along a continuous sandstone bluff running parallel to the east bank of Clear Creek approximately 1.2 km long and 18 m high. The specific section of rock used in the study was chosen for its relatively uniform structural features and be-

H1	DZ	C1	DZ	A 1	DZ	C2	DZ	CONTROL 1	DZ	A 2	DZ	H2	DZ	CONTROL 2
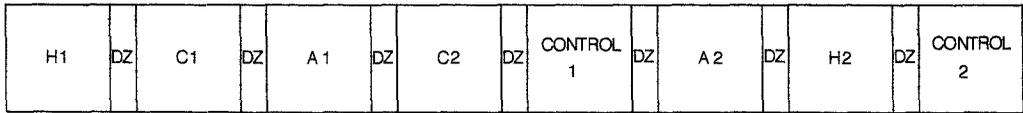
H = HYPOCHILUS REMOVAL PLOT
C = CORAS REMOVAL PLOT
A = ACHAEARANEA REMOVAL PLOT
CONTROL = NO REMOVALS
DZ = 'DEAD ZONE' BUFFER AREA FROM WHICH
        ALL SPIDERS WERE REMOVED

→ N

Figure 1.—Diagrammatic representation of study plots (not to scale). Treatment and control plots measured 20m long × 2m high. Plots labeled "H" are *H. thorelli* remaining plots (i.e., all other spider species were removed each week), plots labeled "C" are *C. montanus* remaining plots and plots labeled "A" are *A. tepidariorum* remaining plots. Plots labeled "DZ" are "dead zone" areas (measuring 1 m long × 2 m high) from which all spiders were removed on a weekly basis. Treatments were randomly assigned.

cause the entire length of this section faced the same compass direction (west).

Before beginning manipulations we quantified spider species present, the relative abundance of each, and the types of prey each captured. All spider species occupying our study cliffs were counted and assigned to one of three age categories: 1) spiderlings (recently emerged from egg sacs), 2) juveniles, and 3) penultimate to adults. Prey censuses were conducted weekly between 1 July–12 August 1993. The primary goal of the prey censuses was to quantify the extent of IGP by each of the three species. At each prey census all spiders on the study plots were visually examined in their webs and scored as to whether they were feeding or not. If they were eating we recorded the taxon of the prey (often prey was too badly macerated for identification). Prey censuses lasted approximately two hours, the length of time required to traverse the length of the study area and examine every web. To control for the effect of time of day on the taxa of prey captured, we scheduled censuses in a stratified fashion such that all two hour time intervals between 0600–2100 h were sampled once.

Removal experiments tested for the impact of IGP on each of the three species. Two replicates of each of three treatment (heterospecific removal) and control (no removal) plots were interspersed along a continuous 165.0 m length of rock outcrop according to a randomized design (Fig. 1). Each plot (treatment or control) was 20.0 m long × 2.0 m high, and was separated from adjacent plots

by a 1.0 m long × 2.0 m high "dead-zone" from which all spiders were removed weekly. In treatment plots spiders of all species except one were removed. We designated each treatment plot by the name of the taxa *not* removed (i.e., *Hypochilus* remaining plots had heterospecifics removed weekly to examine the effect of heterospecific removal on *Hypochilus*). There were two replicates of each treatment: *H. thorelli* remaining plots, *C. montanus* remaining plots, and *A. tepidariorum* remaining plots. No spiders were removed from either control plot.

Spiders to be removed were counted and collected from treatment plots every seven days. The webs of removed spiders were scraped from the rock. The removed spiders were relocated 0.8 km to the end of the cliff and released. Initially all removed spiders were marked on the abdomen with enamel paint (Testor™, Testors Corp., Rockford, Illinois, USA) to determine if they could return to the study plots. However, after four weeks no marked spiders were found and marking was discontinued. Individuals of the focal species (designated to remain) were censused weekly. All spiders on the control plots were censused weekly, none were removed.

Spiders were censused weekly and recorded as belonging to one of two age classes: spiderlings or juveniles/adults. Spiderlings were the smallest size class present and were easily recognized as they were observed dispersing from egg sacs. Unlike our initial censusing, we did not distinguish between juveniles and adults as separate categories. Distinguishing

between juveniles and adults accurately re-
quired removing spiders for closer examina-
tion. This disturbance might have induced re-
location which would have confounded our
results. However, since the effects of hetero-
specific removal may be different for spider-
lings than it is for other size classes we felt it
important to at least distinguish between these
two categories. For example, spiderlings dis-
persing from egg sacs may be more vulnerable
to predation by larger juvenile and adult con-
specifics and heterospecifics (Polis 1988).

Achaearanea tepidariorum is unique among
the three focal species in that females lay their
eggs in the web rather than elsewhere. During
weekly censuses, the number of egg sacs per
female A. tepidariorum was recorded. We also
noted the condition of these egg sacs: un-
hatched, hatched with spiderlings in the moth-
er's web, or empty. Using this information, we
were able to estimate dispersal success by
looking at the number of new spiderlings ap-
pearing on a plot each week as a function of
how many egg sacs were observed hatching
the previous week. Recently dispersed spider-
lings are very small and easy to distinguish
from individuals which have fed several
times. The ratio of new spiderlings with webs
to the number of recently hatched egg sacs the
previous week gives us an index which allows
us to estimate how successful dispersing spi-
derling are at establishing themselves in each
plot.

The experimental study was initiated on 7
July and terminated on 16 October 1993. At
the end of the experiment remaining spiders
were collected from the plots and brought into
the laboratory to be weighed and measured to
assess nutritional condition. There was wide
variation between plots in the number of H.

thorelli. To reduce variation induced by vary-
ing sample size, we randomly selected 24 in-
dividuals (the number of spiders on the plot
with the fewest individuals) from each of the
heterospecific removal and control plots for
weighing and measuring. Spiders were ran-
domly selected using a modification of the
wandering quadrat method (Catana 1955).
Horizontal and vertical coordinates were es-
tablished by laying a tape measure along the
length of the plot and holding a measuring
stick up against the plot. Sequential numbers
selected from a random number table deter-
mined a horizontal/vertical point on the plot,
and the H. thorelli nearest to this point was
removed for measurement. The length of pa-
tella-tibia of leg 1 was measured to the nearest
0.01 mm using dial calipers. Spiders were
weighed to the nearest 0.01 mg using an an-
alytical balance. We used the residual index
(Jakob et al. 1996) to compare the body con-
dition of spiders on removal versus control
plots. We regressed ln(body mass) on ln(length
patella-tibia leg 1) of all spiders pooled (for
each species) and used the residual distances
of individual spider points from this regres-
sion line to serve as estimators of body con-
dition (positive residuals indicate spiders fat-
ter than predicted by the least-squares
regression line, negative residuals indicate
thinner spiders). We compared the residuals
for spiders from the heterospecific removal
plots to the control plots using a t-test.

Voucher specimens will be deposited in the
collection of the Ohio Biological Survey, Mu-
seum of Biodiversity, Columbus, Ohio, USA.

RESULTS

Prior to our manipulations C. montanus was
overall the most abundant species, represent-

Table 1.—Spider abundances on study plots before removals on 1 July 1993. Numbers in parentheses represent the percent of all spiders of a particular species on each plot (H1 and H2 = *Hypochilus* remaining plots, A1 and A2 = *Achaearanea* remaining plots, C1 and C2 = *Coras* remaining plots).

	Removal plots		
Species	H1	H2	A1
H. thorelli	30 (13.8)	45 (21.95)	29 (11.15)
A. tepidariorum	58 (26.6)	51 (24.9)	108 (41.54)
C. montanus	123 (56.4)	105 (51.2)	101 (38.85)
A. cavaticus	7 (3.2)	4 (1.9)	17 (6.54)
Pholcus sp.	0 (0)	0 (0)	5 (1.92)
Totals	218	205	260

ing almost 50% of spiders present (Table 1). *Achaearanea tepidariorum* ranked second in abundance, representing approximately 29% of spiders present, and *H. thorelli* was the third most abundant at approximately 14%. *Araneus cavaticus* and an unidentified pholcid were infrequent and variable in their occurrence on plots.

The percent of the total diet of each species represented by spider prey was substantial, ranging from 20–46% (Table 2). The diet of *C. montanus* was more difficult to quantify than the others as they often fed out of view (within their tubular retreat). This is reflected by the lower number of prey captures observed for this species (n = 17, Table 2). Including opiliones, over half of the diet of *H. thorelli* consisted of arachnids, with 46% represented by spiders alone. At least 10% of the diet of each species resulted from cannibalism or IGP. *Hypochilus thorelli* exhibited high predation on *C. montanus* (17% of total diet).

We were very effective at reducing heterospecific densities on the treatment plots. We suppressed the number of spiders targeted for removal by 65–90% (Table 3). We estimated our suppression of heterospecifics on the removal plots by taking the numbers seen on each plot prior to each weekly removal as a percent of the numbers of that species seen during the first census (Table 1). The weekly percents were averaged across the 12 week treatment period.

Despite the efficacy of removal of heterospecifics on removal plots, there was no significant response by the focal species. The number of the focal spider species left on each plot were not significantly different from the control plots. Because the initial number of focal spiders was variable, we examined the proportion of the initial number of the focal

Table 2.—Percent of total observed prey captured by *Hypochilus thorelli* (n = 47), *Coras montanus*, (n = 17), and *Achaearanea tepidariorum* (n = 172). July to October along Clear Creek, Morgan County, Tennessee, USA.

Prey	Predator		
	H. thorelli	*C. montanus*	*A. tepidariorum*
H. thorelli	2	6	2
C. montanus	17	0	6
A. tepidariorum	4	6	0
Other spiders	23	12	14
Opiliones	17	6	13
Myriapods	0	12	6
Insects	37	58	59

spider species at each census for statistical comparisons of treatments with controls. There were no significant differences between removal and control plots in the proportion of the initial number of juveniles and adults remaining for any of the three focal species (repeated-measures ANOVA on arcsin-square root transformed proportions: *H. thorelli* vs. controls: $P > 0.05$, $F = 0.178$, $df = 1$; *A. tepidariorum* vs. controls: $P > 0.05$, $F = 0.297$, $df = 1$; *C. montanus* vs. controls: $P > 0.05$, $F = 2.61$, $df = 1$). Visual inspection of the census data (Fig. 2) reveals no obvious trends. Thus the lack of significance is not likely due to a lack of power in these statistics resulting from the small sample size but rather a lack of an effect of heterospecific removal on focal species numbers.

There also appear to be no significant differences in the number of focal spiderlings establishing webs in heterospecific removal plots versus control plots as would have been predicted if removals reduced predation pres-

Table 1.—Extended.

Removal plots			Controls	
A2	C1	C2	Control 1	Control 2
23 (7.9)	24 (10.57)	35 (16.2)	18 (5.22)	47 (24.3)
88 (30.2)	58 (25.55)	82 (37.96)	96 (27.83)	43 (22.3)
179 (61.5)	133 (58.59)	86 (39.8)	230 (66.66)	92 (47.67)
1 (0.04)	8 (3.52)	12 (5.55)	1 (0.30)	11 (5.67)
0 (0)	4 (1.76)	1 (0.50)	0 (0)	0 (0)
291	227	216	345	193

Table 3.—Mean reduction in heterospecific density from weekly removals. Numbers represent the number of individuals of each species present on each plot each week (before removal), expressed as a percent of the results of the first census, averaged over the 12 weeks of the experiment (mean percent ± SD). Plot designations are the same as used in Fig. 1.

Plot	Species removed from plot		
	H. thorelli	*C. montanus*	*A. tepidariorum*
H1	—	66 ± 13	65 ± 10
H2	—	65 ± 22	76 ± 11
C1	92 ± 8	—	84 ± 10
C2	83 ± 20	—	90 ± 5
A1	76 ± 25	72 ± 11	—
A2	81 ± 29	78 ± 11	—

sure on young spiders (repeated measures ANOVA on arcsin square-root transformed proportions; *H. thorelli* vs. controls: $P > 0.05$, $F = 0.671$, $df = 1$; *A. tepidariorum* vs. controls: $P > 0.05$, $F = 1.59$, $df = 1$; *C. montanus* vs. controls: $P > 0.05$, $F = 5.78$, $df = 1$; Fig. 3). However, comparing the index of spiderling dispersal (number of new spiderling webs in given week/number of hatching egg sacs in previous week) for *Achaearanea* plots versus control plots, we found that there were more new spiderlings settling in heterospecific removal plots than in control plots (repeated measures ANOVA on weekly index values; $P = 0.056$, $F = 16.29$, $df = 1$; Fig. 4).

There were no significant differences in the body condition of juvenile and adult *C. montanus* in heterospecific removal versus control plots at the end of the experiment (regression: $r^2 = 0.91$, $P < 0.001$; *t*-test on residuals: $t = -1.533$, $df = 33$, $P > 0.05$). There was a significant difference for *H. thorelli*, with individuals on control plots having higher residual values than individuals on heterospecific removal plots (regression: $r^2 = 0.76$, $P < 0.001$; *t*-test on residuals: $t = 2.9$, $df = 94$, $P < 0.05$; Fig. 5). This indicates that *H. thorelli* on control plots were better fed than *H. thorelli* on heterospecific removal plots. There were not enough juvenile or adult *A. tepidariorum* remaining at the end of the experiment to include in this analysis.

DISCUSSION

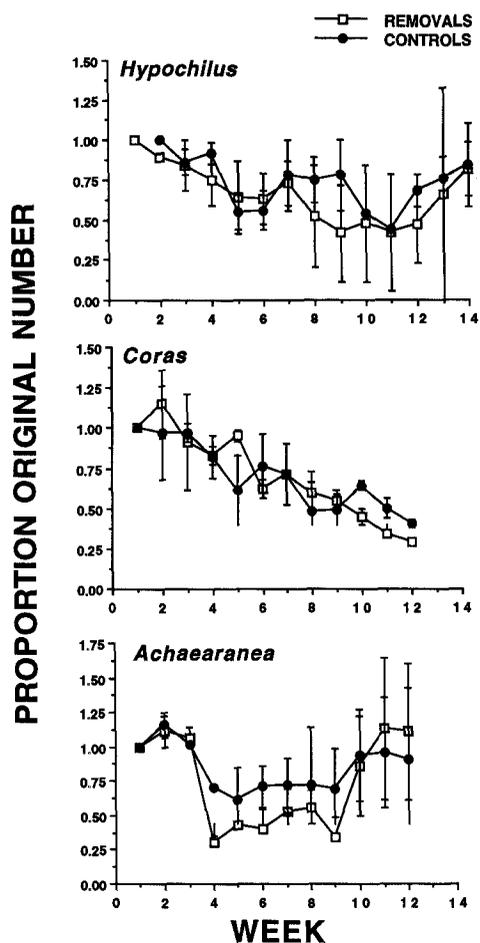The removal of heterospecific guild members had no effect on the densities of focal

Figure 2.—Summary of the effect of heterospecific removal on focal spider species numbers. The proportions are the number of juvenile and adult spiders remaining on heterospecific removal (□) and control (●) plots during each weekly sampling interval divided by the numbers at the start of removals. Each point represents the mean of the two replicates, ± 1 SE.

web spider species in a cliff face web spider community. There was evidence, however, for improved settlement success for hatchling *A. tepidariorum* as a result of the removal of heterospecifics. We also present evidence for reduced foraging success of the species with the greatest predilection for araneophagy: *H. thorelli*. Thus, while elements of our study support the conclusions of Riechert & Cady (1983) that IGP interactions may have confounded the results of their competition experiment, we did not find strong support for IGP effects in this system.
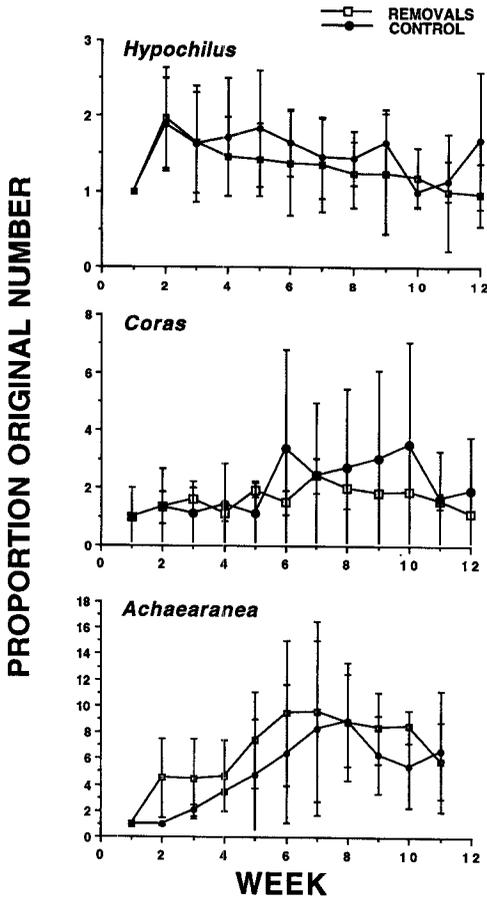
Figure 3.—The proportion of the initial number of spiderlings remaining on removal (□) and control (●) plots during each weekly sampling interval. Points represent the mean of the two replicates, ± 1 SE.
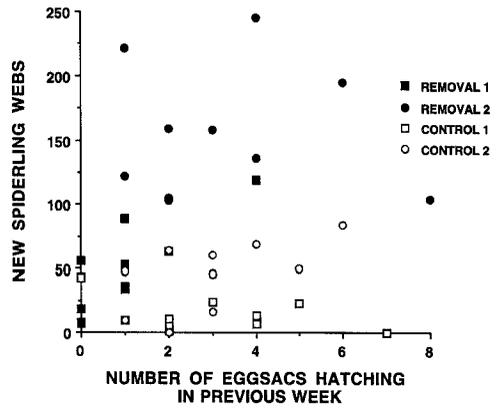

Figure 4.—The number of new *Achaearanea tepidariorum* spiderlings with independent webs on plots as a function of the number of hatching eggsacs on the plot in the previous week. Note that for any given number of eggsacs hatching, the number of new spiderling webs is generally lower in the control plots (open symbols) than in the removal plots (closed symbols).

less than weekly immigration back into plots. One of the problems encountered by Riechert & Cady (1983) was that high rates of immigration actually resulted in an increase in spider density in some plots, despite efforts to continually remove spiders (Wise 1993). In our study we were able to achieve a much greater level of success, with between 65–
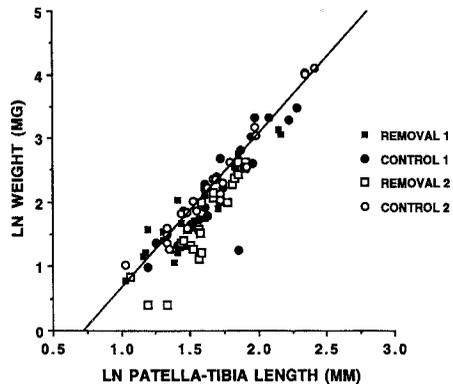
Our prey census data are remarkably similar to those of Riechert & Cady (1983), especially the high proportion of the diet of *H. thorelli* composed of spiders (Table 2; Riechert & Cady: 47%; this study: 46%). Of the spiders included in the diet of *H. thorelli*, *C. montanus* makes up a large proportion (17%). This is perhaps not surprising given our finding that *C. montanus* is also the most common spider on the cliff face (almost 50%, Table 1). Therefore, if heterospecific removals result in a reduction in prey, we might predict to find the greatest impact of heterospecific removals on *H. thorelli* numbers remaining.

In order for removal experiments to effectively test for competition or predation, removals must reduce densities to a level that is

Figure 5.—Regression of ln(body mass) on ln(length of patella-tibia, leg 1) for *Hypochilus thorelli* collected from removal and control plots and the end of the study. Open symbols represent removal plots, closed symbols represent control plots. Note that most (71%) of the data points from removal plots fall below the regression line, in contrast to less than half (46%) of data points from control plots.

90% mean reduction in the original densities of spiders. Therefore, we believe that we were removing a significant portion of potential heterospecific competitors.

In our study we assumed that exploitative competition for prey was not an important interspecific interaction, after the results of Riechert & Cady (1983). However, since their experiment was not replicated this assumption may not have been valid (Wise 1993). If our removals resulted in a release from exploitative competition, we should have seen a higher residual condition index for spiders from heterospecific removal plots (i.e., evidence for better feeding history). However, there were no detectable differences in body condition of *C. montanus* on treatment versus control plots, and the body condition of *H. thorelli* was lower on the removal plots. While this supports our original hypothesis on the effects of removing intraguild prey from *H. thorelli*, it also allows us to infer that we were not reducing exploitative competition for non-intraguild prey (i.e., insects), supporting the conclusions of Riechert & Cady (1983).

There was some evidence to support the hypothesis that the removal of heterospecifics resulted in lower levels of predation on spiderlings on heterospecific removal plots versus control plots. While there were no differences in the numbers of spiderlings establishing webs in heterospecific removal and control plots during the course of the experiment, there may have been some differential success of *A. tepidariorum* spiderlings in the removal plots. Although there was an equal, or often greater number of hatching egg sacs in the control plots, our analysis indicates that there were relatively fewer spiderlings establishing webs in these plots a week after hatching (Fig.5). There are at least three potential explanations for this observation: 1) egg sacs hatching on control plots had fewer spiderlings as a result of lower fecundity or higher egg mortality, 2) less space was available for spiderlings to establish webs on control plots due to a greater overall density of webs, or 3) as spiderlings dispersed from their egg sacs they were intercepted and eaten by heterospecifics in the control plots. It would be difficult to observe such acts of predation in the prey censuses because *A. tepidariorum* spiderlings are so small as to become completely surrounded by the chelicerae of even a small

heterospecific when being fed upon. Another possibility is that spiderlings avoid settling in areas with high densities of other web-builders. Such behavior could be adaptive in avoiding both predation and competition. Further experiments will be required to determine the mechanism to explain these results.

If removing heterospecifics from treatment plots resulted in removal of food, we predicted that the number of juvenile and adult spiders should decline in removal plots relative to control plots due to web relocation. No evidence was found to support this prediction for *C. montanus* or *A. tepidariorum*. We also predicted that a measure of body condition would show an effect of food limitation by the end of the experiment. No evidence was found to support this prediction for *C. montanus*. This would suggest that spiders make up a relatively insignificant proportion of the total prey biomass captured by *C. montanus*. This is supported by the results of our prey census (Table 2) in which we found that spiders make up 24% of prey observed by frequency. However, there was a significant difference in the body condition of *H. thorelli* in the direction predicted by the prey removal hypothesis. This result is consistent with the high proportion of spider prey in *H. thorelli*'s diet, and with the results of Riechert & Cady's (1983) study. Despite this evidence for removal of a significant amount of prey, we found no difference in the proportion of *H. thorelli* remaining on removal versus control plots, indicating that removal of food did not result in relocation by spiders. This may be due to the short time frame of the study. However, Vollrath (1985) similarly found that *Nephila clavipes* (Linne 1767) would leave prey-poor sites only under conditions of extreme prey deprivation. He suggests that high mortality while searching for new sites, or a low probability of finding a better site, might select for "acceptance" of prey poor conditions up to some threshold (Vollrath 1985).

While our study shows that other spider species form a significant part of the diet of *H. thorelli*, it is as yet unclear what benefits may be derived from the indirect component of intraguild predation, that is, removing potential competition for prey. All available evidence indicates that exploitative competition is not a factor in this spider community. Most experimental studies of web-building spiders

have found no evidence for exploitative competition (Schaefer 1978; Wise 1981; Horton & Wise 1983; Riechert & Cady 1983; this study), perhaps due to the fact that webs generally sample prey in a filtering fashion that rarely depletes local prey populations (Wise 1993). Though we did find evidence for significant predatory interactions in this rock-outcrop community, it may be that web-building spiders in general are poor candidates for investigating intraguild predation. Due to their sedentary nature, web-building spiders are unlikely to interact frequently unless they occur at very high densities (Wise 1993). Situations in which web-building spiders occur at high densities are usually restricted to conditions of abundant prey, which reduces the tendency for cannibalism or interspecific predation (Rypstra 1983, 1989; Dong & Polis 1992; Hodge & Uetz 1995). Interactions that result in predation may be rare for most species, restricted to chance interception of relocating individuals or aggressive, territorial encounters (Riechert 1982; Hoffmaster 1986).

ACKNOWLEDGMENTS

LITERATURE CITED

Catana, A.J. 1955. The wandering quadrant: a new ecological method using interspace measurements. Bull. Ecol. Soc., 36:88.

Dong, Q. & G.A. Polis. 1992. The dynamics of cannibalistic populations: a foraging perspective. Pp. 13–37. In: Cannibalism: Ecology and Evolution Among Diverse Taxa. (Elgar, M.A. & B.J. Crespi, eds.). Oxford University Press, Oxford, England.

Ferguson, I.C. 1972. Natural history of the spider Hypochilus thorelli Marx (Hypochilidae). Psyche, 79:179–199.

Forster, R.R., N.I. Platnick, & M.R. Gray. 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae: Araneomorphae). Bull. American Mus. Nat. Hist., Vol. 185.

Hodge, M.A. & G.W. Uetz. 1995. A comparison of agonistic behaviour of colonial web-building spiders from desert and tropical habitats. Anim. Behav., 50:963–972.

Hoffmaster, D.K. 1986. Aggression in tropical orb-weaving spiders: a quest for food? Ethology, 72: 265–276.

Horton, C.C. & D.H. Wise. 1983. The experimental analysis of competition between two syntopic species of orb-web spiders (Araneae: Araneidae). Ecology, 64:929–944.

Hurd, L.E. & R.M. Eisenburg. 1990. Arthropod community responses to manipulation of a biotrophic predator guild. Ecology, 71:2107–2114.

Jackson, R.R. 1992. Eight-legged tricksters: spiders that specialize at catching other spiders. Bioscience, 42:590–598.

Jakob, E.M., S.D. Marshall & G.W. Uetz. In press. Estimating fitness: a comparison of body condition indices. Oikos.

Moran, M.D. & L.E. Hurd. 1994. Short-term responses to elevated predator densities: noncompetitive intraguild interactions and behavior. Oecologia, 98:269–273.

Pacala, S. & J. Roughgarden. 1984. Control of arthropod abundance by Anolis lizards on St. Eustatius (Neth. Antilles). Oecologia, 64:160–162.

Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. Ann. Rev. Ecol. Syst., 12: 225–251.

Polis, G.A. 1988. Exploitation competition and the evolution of interference, cannibalism and intraguild predation in structured populations. Pp. 185–202. In: Size structured populations: Ecology and Evolution. (L. Pierson & B. Ebenmann, eds.). Springer-Verlag, New York.

Polis, G.A. & R.D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol. Evol., 7: 151–154.

Polis, G.A. & S. J. McCormick. 1986. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. Oecologia, 71:111–116.

Polis, G.A. & S.J. McCormick. 1987. Intraguild predation and competition among desert scorpions. Ecology, 68:332–343.

Polis, G.A., C.A. Myers & R.D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev. Ecol. Syst., 20:297–330.

Riechert, S.E. 1982. Spider interaction strategies: communication vs. coercion. Pp. 281–315. In: Spider Communication: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton Univ. Press, Princeton, New Jersey.

Riechert, S.E. & A.B. Cady. 1983. Patterns of re-

source use and tests for competitive release in a spider community. Ecology, 64:899–913.

Root, R. 1967. The niche exploitation pattern of the blue-grey gnat catcher. Ecol. Monogr., 37: 317–350.

Rypstra, A.L. 1983. The importance of food and space in limiting web-spider densities: a test using field enclosures. Oecologia, 59:312–316.

Rypstra, A.L. 1989. Foraging success of web spiders: insights into flock formation. Anim. Behav., 37:274–281.

Schaefer, M. 1978. Some experiments on the regulation of population density in the spider *Floronia bucculenta* (Araneida: Linyphiidae). Symp. Zool. Soc. London., 42:203–210.

Sih, A., P. Crowley, M. McPeek, J. Petranka & K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Ann. Rev. Ecol. Syst., 16:269–311.

Simberloff, D. & T. Dayan. 1991. The guild concept and the structure of ecological communities. Ann. Rev. Ecol. Syst., 22:115–143.

Spiller, D.A. & T.W. Schoener. 1988. An experimental study of the effects of lizards on web-spider communities. Ecol. Monogr., 58:57–77.

Spiller, D.A. & T.W. Schoener. 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. Oecologia, 83:150–161.

Vollrath, F. 1985. Web spider's dilemma: a risky move or site dependent growth. Oecologia, 68: 69–72.

Wise, D.H. 1981. Inter- and intraspecific effects of density manipulations upon females of two orb-weaving spiders (Araneae: Araneidae). Oecologia, 48:252–256.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge Univ. Press, Cambridge.