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ANT COMMUNITY ASSEMBLY IN THE SISKIYOU-KLAMATH ECOREGION

A Dissertation Presented

by

Sarah E. Wittman

to

The Faculty of the Graduate College

of


The University of Vermont

In Partial Fulfillment of the Requirements  
for the Degree of Doctor of Philosophy  
Specializing in Biology


October 2007

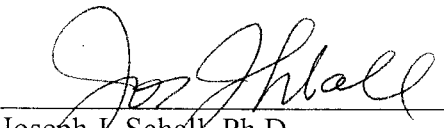
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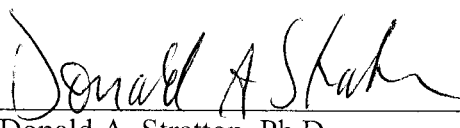
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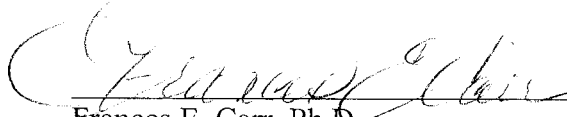
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## Abstract

Interference competition is widely considered to structure ant communities. Competition's effect, however, may be contingent upon disturbance or the abiotic environment. The interaction of temperature and competition is implicit in a wide body of ant community research; however, very few studies have experimentally manipulated these variables. To investigate the role of competition and temperature on ant communities, I (i) employed null models to investigate how species partition their spatial, temporal, and thermal environments in disturbed and undisturbed forests, (ii) used pairwise behavioral experiments to construct a Markov chain model to predict relative abundance patterns and correlated behavioral indices to species co-occurrence patterns, and (iii) conducted a shade, physiological thermal tolerance, and fully factorial shade and removal experiment to investigate the interaction of competition and temperature on ant community structure. The results of these studies are summarized below.

First, I took advantage of a natural experiment, the 2002 Biscuit Fire, to investigate how species partition their temporal, thermal, and spatial environments in disturbed and undisturbed forests with null models. I found that most sites displayed a high degree of temporal niche overlap and species aggregation along the thermal axis. Half of the sites, however, had regular spacing of the temperature at which species obtain maximum activity. Species co-occurrence patterns in space modulated with diurnal temperature variations. Unburned sites had more spatial segregation of species than burned sites. Overall, it appears as though species activity is regulated, at least in part, by the thermal niche axis, and ant communities may repeatedly assemble and disassemble throughout the day.

Second, I used data from pairwise behavioral experiment to generate transition probabilities for a Markov chain model. Assuming the landscape represents a large number of patches, the model predicted the relative abundance of an assemblage. I compared Markov chain predictions of relative abundance to relative abundance measurements on the local and regional scale. I used the same pairwise behavioral data to predict species co-occurrence values in three sites. Neither model accurately predicted community patterns. The only significant result was the Markov chain prediction of bait occurrence on the local scale; however, the relationship was opposite of the prediction.

Finally, I conducted a shade experiment to investigate how communities respond to an altered thermal environment and associated their response to results from physiological thermal tolerance experiments. I then conducted a fully-factorial shade and *Formica moki* removal experiment to investigate if thermal responses were mediated by competitive effects. The addition of shade tables greatly reduced temperatures in the field, and *Temnothorax nevadensis* abundance was consistently lower in shade treatments. Decreased abundance at shade stations did not appear to be an indirect effect of *F. moki* activity. Physiological thermal tolerance was strongly associated with changes in abundance in shade treatments: the lower a species thermal tolerance, the greater its positive change in abundance after shade additions. The only species with a strong foraging response to *F. moki* removal was *T. nevadensis*, a species who was often co-occurred with *F. moki* on baits. I did not find evidence for the interaction of competition and temperature, and it appears as though physiological differences strongly influence the foraging activity of Siskiyou ant communities.

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## **Introduction**

Competition has long served as the cornerstone around which the framework of community ecology has been built. Competition forms the basis of simple, foundational theories, such as the theory of limiting similarity (Grinnell 1922, Hutchinson 1959), the concept of niche partitioning (Grinnell 1917, MacArthur 1958), the competitive exclusion principle (Gause 1934), character displacement (Lack 1947, Brown and Wilson 1956), and co-occurrence patterns (Diamond 1975).

Competition's ubiquity was called into question because correlative data do not test that competition is the causal force of observed patterns (Connell 1975). Much debate also focused on whether patterns purportedly driven by competition differed from random (Connor and Simberloff 1979, Strong et al. 1979). As more field-based competition experiments were conducted and the methods (Stone and Roberts 1990, Winemiller and Pianka 1990, Gotelli 2000) and software (Gotelli and Entsminger 2006) of null models advanced, reviews of field experiments (Schoener 1983, Gurevitch et al. 1992) and co-occurrence studies (Gotelli and McCabe 2002) found significant support for competition's structuring role in communities.

Competition is considered the "hallmark of ant ecology" (Hölldobler and Wilson 1990). Noxious organisms generally have few predators (Schoener 1983) and are assumed to be controlled primarily by competition, unless food resources are abundant. Many ants bite and use chemical warfare, and conspicuous interference competition over similar resources indicates food resources are limited (Schoener 1982) or were in the evolutionary past (Connell 1980).

Further evidence of competition's role is seen in ant mosaics (Jackson 1984), intraspecific (Ryti and Case 1992) and interspecific (Savolainen and Vepsalainen 1989) nest spacing, dominance hierarchies (Cerda et al. 1997, Sanders and Gordon 2003), reduced reproductive output in the presence of dominant species (Pontin 1963, Savolainen and Vepsalainen 1989), dominance-diversity relationships (Andersen 1992, Parr et al. 2005), and disassembly of native communities (Sanders et al. 2003, Gotelli and Arnett 2000) by competitively superior invasive species (Holway 1999).

In this dissertation, I investigate the role of competition in disturbed and undisturbed habitats and under natural and manipulated thermal environments in the Siskiyou-Klamath ecoregion of southwestern Oregon. I employ null models to investigate how species partition their spatial, temporal, and thermal environments (Chapter 1), use pairwise behavioral experiments to construct a Markov chain model to predict relative abundance patterns and correlate behavioral indices to species co-occurrence patterns (Chapter 2), and conduct shade, physiological thermal tolerance, and factorial shade and removal experiments to investigate the interaction of competition and temperature on ant community structure (Chapter 3).

***Chapter 1 – Disturbance effects on spatial, temporal, and thermal partitioning of ant communities.***

In communities with strong competitive interactions, species may segregate along different niche axes. Schoener (1974) suggests the most differentiation occurs along the spatial and dietary axes. Species may also segregate through time (Case and Gilpin 1974,

Carothers and Jaksic 1984), although less research has focused on the ecological consequences of temporal partitioning (Kronfeld-Schor and Dayan 2003) and the role of temperature as a shared resource (Tracy and Christian 1986). Environmental variability is also a real component of communities (Chesson 1986), and different mechanisms may be important in communities at equilibrium than communities at disequilibrium (Wiens 1984).

I used data collected from bait stations sampled throughout the day in burned and unburned forests in the Siskiyou Mountains to quantify patterns of temporal niche overlap, species co-occurrence, and spacing of thermal activity. Observed indices were compared to the distribution of indices generated by repeated randomization of assemblages to determine if patterns were different than expected by chance. Species at the majority of sites displayed a high degree of temporal niche overlap and species aggregation along the thermal axis. Half of the sites, however, exhibited regular spacing of the temperature at which species obtain maximum activity. Species co-occurrence patterns in space modulated with diurnal temperature variations. Unburned sites had more spatial segregation of species than burned sites. Overall, it appears as though species activity is regulated, at least in part, by the thermal niche axis, and ant communities may repeatedly assemble and disassemble throughout the day.



*Chapter 2 – Behavioral dominance does not predict patterns of relative abundance or species co-occurrence in Siskiyou ant communities.*

Although interference competition is widely accepted to structure ant communities, it is still uncertain what community patterns would look like if they were exclusively driven by interference competition. I used data from pairwise behavioral experiments to generate transition probabilities of a Markov chain model. The matrix elements represent the probabilities that a species will persist in a patch after an encounter with other species. Assuming the landscape represents an infinitely large number of patches, the model predicts the equilibrium distribution of different species, i.e. the relative abundance of an assemblage. I compared Markov chain predictions to relative abundance measures on the local and regional scale. I used the same pairwise behavioral data to make predictions about species co-occurrence. I used a null model to determine co-occurrence values among all species pairs in three southwestern Oregon ant communities. I then correlated pairwise experimental indices of behavioral dominance to those values. Neither model accurately predicted community patterns on any scale. The only statistically significant result was the Markov chain prediction of bait occurrence on the local scale; however, the relationship was opposite of the prediction: behaviorally dominant species occupied relatively few baits.

### ***Chapter 3 – Disentangling competitive and thermal drivers of ant community structure.***

The interaction between competition and temperature is implicated in the maintenance of local diversity (Cerda et al. 1997) and dominance-diversity patterns on continental scales (Andersen 1992, Parr et al. 2005), classifications of ant functional groups (Andersen 1995, 1997), how ants communities respond to disturbance (Andersen 1991, York 2000, Farji-Brener et al. 2002), the success and spread of invasive species (Holway 1999, Holway et al. 2002, Krushelnycky et al. 2005), and management implications of agroforestry (Perfecto and Vandermeer 1996, Armbrrecht et al. 2005).

Surprisingly, very few studies have experimentally altered the thermal or competitive environment to investigate community response, and none, to my knowledge, have manipulated these factors simultaneously. Additionally, few studies have investigated how species physiological differences interact with their competitive environment to explain species distribution patterns in animal communities (Dunson and Travis 1991).

I conducted a shade experiment to investigate how species respond to an altered thermal environment and then associated their changes in abundance to results from physiological thermal tolerance experiments. I then conducted a fully-factorial shade and removal experiment of a widespread behaviorally dominant species, *Formica moki*, to investigate if species respond directly to changes in the thermal environment or if abundance is an indirect effect of behaviorally dominant species activity. The addition of shade tables greatly reduced temperatures in the field. One species, *Temnothorax*

*nevadensis*, consistently exhibited lower abundance in shade treatments. Decreased abundance of *T. nevadensis* in shade treatments was not an indirect effect of *F. moki*, or likely any other species activity in shade plots. Physiological thermal tolerance was strongly associated with changes in abundance in shade treatments: the lower a species thermal tolerance, the greater its positive change in abundance after shade additions. The only species with a strong foraging response to *F. moki* removal was *T. nevadensis*, a species who was often co-occurred with *F. moki* on baits. I did not find evidence for the interaction of competition and temperature, and it appears as though physiological differences strongly influence the foraging activity of Siskiyou ant communities.

### **Summary**

The major findings of this dissertation suggest that temperature is a major structuring force of Siskiyou ant communities. Null model analyses revealed species peak activity is regulated, at least indirectly, by the thermal niche axis, and that communities may assemble and disassemble with diurnal temperature variations. Markov chain models indicated behavioral dominance did not accurately predict ecological dominance. Species physiological thermal tolerance was strongly associated to species response to shade additions, and I did not find evidence for the interaction of competition and temperature. Thus, it appears as though physiological differences strongly influence the foraging activity of Siskiyou ant communities.

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## **Chapter 1**

### **Spatial, temporal, and thermal partitioning of Siskiyou ant communities.**

#### **Abstract**

In communities structured by competitive interactions, species may segregate along different niche axes, and disturbance may act to alter these competitive interactions and use of niche space. We investigated how ant assemblages partition their spatial, temporal, and thermal environments in disturbed and undisturbed forests in the Siskiyou Mountains of southwest Oregon. We used data collected from bait stations sampled throughout the widely variable diurnal temperature range to quantify patterns of temporal niche overlap, species co-occurrence, and spacing of thermal activity. We used null models to compare observed indices to the distribution of indices generated by repeated randomization of assemblages to determine if patterns were different than expected by chance. Species at the majority of sites displayed a high degree of temporal niche overlap, and species aggregation was common along the thermal axis. Half of the sites, however, had regular spacing of the temperature at which species obtain maximum foraging activity. Throughout the diurnal temperature range species co-occurrence patterns in space modulated between random and significant segregation. Unburned sites had more spatial segregation of species than burned sites. Overall, it appears as though species activity is regulated, at least indirectly, by the thermal niche axis, and ant communities may repeatedly assemble and disassemble throughout the day.

## **Introduction**

In communities with strong competitive interactions, species may segregate along different niche axes. Schoener (1974) suggests the most differentiation occurs along the spatial and dietary axes. Species may also segregate through time (Case and Gilpin 1974, Carothers and Jaksic 1984), although less research has focused on the ecological consequences of temporal partitioning (Kronfeld-Schor and Dayan 2003). Because the thermal environment incorporates both spatial and temporal niche components, it may also be an informative resource with which to investigate species partitioning (Tracy and Christian 1986).

Environmental variability is also a real component of communities (Chesson 1986), and different mechanisms may be important in communities at equilibrium than communities at disequilibrium (Wiens 1984). Disturbance may act to ‘reset’ the reassembly process through the removal or reduction of species. Recently disturbed ant (Badano et al. 2005, Sanders et al. 2007b) and vertebrate (Arrington et al. 2005, Sara et al. 2006) communities have random co-occurrence patterns while species show significant segregation in older and intact communities.

Ant communities are widely held to be structured by competition (Hölldobler and Wilson 1990), and evidence includes spatial mosaics (Jackson 1984, Savolainen and Vepsäläinen 1989, Ryti and Case 1992, Sanders et al. 2007a), aggressive behavioral interactions (Fellers 1987), dominance-diversity relationships (Andersen 1992, Parr et al. 2005), and

dominance hierarchies (Cerda et al. 1997, Sanders and Gordon 2003). However, ant mosaics may not necessarily be indicative of competition (Ribas and Schoereder 2002), and in areas where dominant species are naturally reduced (Cerda et al. 1998) or experimentally removed (Gibb and Hochuli 2004) other factors such as temperature may be more important in structuring communities. Temperature has been found to be important in determining foraging (Cerda et al. 1998, Albrecht and Gotelli 2001) and diversity (Andersen 1992, Retana and Cerda 2000) patterns, community response to disturbance (Andersen 1991, York 2000, Farji-Brener et al. 2002), and the success and spread of invasive species (Holway 1999, Krushelnycky et al. 2005). However, although temperature is often cited as an important determinant of community patterns, we do not know how ant species may partition temperature as a niche axis (Roughgarden et al. 1981) which requires knowledge of the duration and occupancy of the thermal environment (Tracy and Christian 1986).

We used null model analysis to investigate how ant assemblages partition their spatial, temporal, and thermal environments in the burned and unburned forests of the Siskiyou Mountains. Although the use of null models has a long and contentious history (Gotelli and Graves 1996, Weiher and Keddy 1999), methodological advancements (Stone and Roberts 1990, Winemiller and Pianka 1990, Gotelli 2000) and software development (Gotelli and Entsminger 2006) allow accurate detection of non-random patterns through the generation of ‘null’ communities in which the effect of competition is removed (Connor and Simberloff 1979).

We used data collected from bait stations sampled throughout the day to quantify how species utilize different niche axes in disturbed and intact habitats. To examine temporal niche overlap, we evaluated assemblage overlap in bait occupancy throughout the day. To evaluate how assemblages partition their thermal environment, we quantified species co-occurrence along the thermal gradient and the spacing of temperatures at which species reach maximum foraging abundance. Finally, we investigated how species partition their spatial environment, and if this partitioning varies depending on time of day, by evaluating species co-occurrence patterns at three times of day.

## **Methods**

### **Study sites**

We studied ants in burned and unburned forests in the Siskiyou Mountains near the Oregon-California border, USA, during June-August of 2003. The Siskiyou Mountains are known for their high plant diversity with many rare and endemic species and vegetation types (Whittaker 1954, Whittaker 1960). The climate of the study area is Mediterranean, with cool winters (mean January minimum temperature = 0 °C) and warm dry summers (mean July maximum temperature = 31.7 °C; mean annual precipitation = 154 cm, with only 4 cm falling between June and August). Forests are mostly open stands of *Pinus jeffreyi* with other sclerophyllous trees reduced to a shrub layer.

### **Sampling Design**

From July to September 2002, a major forest fire, the Biscuit Fire, burned approximately 202,000 ha of the Siskiyou Mountains (Figure 1). We sampled 16 forest plots, half burned and half unburned, during the summer of 2003 (Figure 2). In each plot, we placed

an  $8 \times 8$  m sampling grid and sampled ants at bait stations (arranged in a  $5 \times 5$  grid with 2-m spacing) nine times throughout the day. Each bait station consisted of two laminated  $7.6 \times 12.7$  cm index cards. We baited one card with approximately 5.5 g of tuna and the other with a cotton ball soaked in honey water. These baits represent protein and carbohydrate food resources. There is some evidence that ant species differ in their preference for protein baits or carbohydrate baits (Yanoviak and Kaspari 2000). Therefore, using different bait types should have sampled a potentially wider spectrum of species. We stocked the bait stations each morning at approximately 08:00 and replenished them with tuna and water as necessary throughout the day and evening.

At each of the 16 plots, we observed ants during three observation blocks throughout one day: one in the morning beginning at 08:30, one in the afternoon beginning at 13:00 and one in the evening beginning at 18:30. During each of the three observation blocks, we visited the bait stations three times, once every 30 minutes and observed each bait station for approximately 20 seconds during each visit. Thus, each bait station was visited a total of 9 times (3 observations in 3 blocks). Neither mean July maximum temperature nor precipitation in 2003 differed significantly from their long-term average values.

Baits tend to under-sample trophic specialists and subordinate or single-foraging species because baits are often dominated by mass-recruiting species. We used several baits in an area and made multiple observations throughout the day to minimize these problems (Bestelmeyer 2000). We supplemented the bait station data by hand searching the plots, but only one ant species, *Lasius flavus*, was found only by general collecting. Our

sampling strategy captured the potential changes in the activity of foraging ants over the course of the day.

For each observation at a bait station, we recorded the number and identity of each species, and we measured the soil surface temperature to the nearest 0.1 °C using a Raytek® Raynger ST20 XB hand-held infrared thermometer (Santa Cruz, CA USA). Individual workers were collected at the end of the observation period if they could not be readily identified in the field. Phil Ward at the University of California, Davis confirmed the species identifications. Voucher specimens are deposited at the University of Tennessee in Knoxville. Nomenclature follows Bolton (1994, 2003).

## **Analysis**

### Temporal Niche

We used null model analyses to examine the temporal overlap of ant assemblages occurring in each of the 16 plots. Matrices were constructed with species ( $n = 5$  to 12 species) as rows and time of day ( $n = 9$ ) as columns. Matrix entries were the number of baits (max = 25) occupied by each species at each time of day.

We utilized the Czekanowski index (Feinsinger et al. 1981) which evaluates the overlapping histogram area of resource (=time of day) utilization. It is a symmetrical index that ranges from 0 (no overlap) to 1.0 (complete overlap) and is calculated for each unique species pair in the assemblage. For species 1 and 2, with resource utilizations  $p_{1i}$  and  $p_{2i}$ , the Czechanowski index is defined as:



$$O_{12} = O_{21} = 1.0 - 0.5 \bullet \sum_{i=1}^n |p_{1i} - p_{2i}|$$

The observed niche overlap indices were then compared to those obtained from randomized communities. Communities were randomized using Randomization Algorithm 2 (RA2) of the niche overlap model in EcoSim, version 7 (Gotelli and Entsminger 2006). RA2 retains zero states; if a species naturally never occurred during a specific time period, it would not in the randomized assemblage either. RA2 also relaxes niche breadths, substituting a random uniform number for bait occupancy throughout the day. This algorithm is recommended when certain resource states are unavailable for some species (e.g. when physiological constraints prevent activity during hot times of the day) but there are no other constraints on resource utilization (Gotelli and Entsminger 2006). Resource states were set as equiprobable, as time is equally available to all species.

If species are partitioning the time of day in which they are active, then the niche overlap index should be smaller than expected by chance (i.e. than the indices generated from the null community). If species are active during similar times, then the index may be larger than expected by chance.

### Thermal Niche

#### *Co-Occurrence*

We also investigated if species coexistence patterns were thermally-dependent. We tested if species segregate or aggregate their occurrences within temperature intervals.

The temperature range of community activity was sorted into ten intervals (average interval=5°C). If at least one forager was active during a given temperature range, that species was marked as ‘present.’ Thus, matrices were constructed with species as rows (n = 5 to 12) and temperature bins (n=10) as columns. We utilized the C-score of Stone and Roberts (1990) to evaluate species co-existence patterns. This score measures the average number of checkerboard units of all species pairs of an assemblage. Species pairs that occur in the following pattern:

	temp 1	temp 2
species a	0	1
species b	1	0

or

	temp 1	temp 2
species a	1	0
species b	0	1

are defined as one checkerboard unit.

Each checkerboard unit is calculated by  $(r_a - S)(r_b - S)$  where  $S$  is the total number of ‘sites’ (e.g. temperatures) shared by the species pair, and  $r_a$  and  $r_b$  are the row totals for species a and b, respectively. Species that always occur together will have a C-score of zero. The greater the segregation in species, the larger the C-score will be.

Assemblages were randomized using the fixed – user-defined model in EcoSim, version 7 (Gotelli and Entsminger 2006). In this model row totals (=total number of temperature intervals occupied by a species) are fixed. Thus, species occurred in the same frequency in the randomized as in the observed assemblage. Temperature bins were weighted based on their sampling frequency. The probability that a species was assigned to a temperature bin was weighted on how frequently baits were sampled within that temperature range.

#### *Temperature at Peak Activity*

We utilized the Body Size Module in EcoSim, version 7 (Gotelli and Entsminger 2006) to evaluate the spacing of the temperatures of peak activity. The variance of the spacing (i.e. difference between) each adjacent thermal activity peak within an assemblage was calculated for each site. Assemblages with equal spacing of thermal peaks will have small variance values; assemblages with unequal spacing will have large values. Observed variance values of temperatures at peak activity were compared to those from randomized assemblages.

Each site (n=16) was analyzed separately; thus, the input matrix had one column by 5 to 12 (=species) rows. For each species, the temperature at which each species reached maximum activity (=highest observed worker numbers throughout the day) was entered into the matrix.

Null communities were created three ways. First, temperature values were randomly selected from a uniform distribution ranging from user-defined endpoints: 15°- 55°C, the smallest and largest temperature values with ant activity shared by all sites. Second, temperatures were selected from a uniform distribution with data-defined endpoints: the minimum and maximum peak activity temperatures in the observed data set. Third, temperatures were selected from a normal distribution with site-defined characteristics, with the mean and standard deviation determined from 450 temperature readings throughout day. The consistency in *P* values was compared across models with Fisher's combined probability. The difference in SES values in burned vs. unburned habitats was compared with a t-test. The SES reports the number of standard deviations the observed index is above or below the mean of the randomized assemblage to allow comparison among multiple tests (Gurevitch et al. 1992).

#### Co-occurrence by Sampling Period

In all analyses, except thermal activity peak, the presence-absence matrix entries were pooled across nine sampling periods. Thus, species active at one, two, or all sampling periods were scored the same way. To further investigate how species co-occurrence may differ at different times of day, matrices were constructed separately for different sampling periods. Analyses were run on one sampling period in the morning, afternoon, and evening. Thus, presence-absence matrices were constructed with species (n=1 to 9) as rows and bait locations (n=25) as columns. A total of 48 (2 burn states x 3 times of day x 8 replicates) matrices were evaluated. Again, we utilized the C-score of Stone and Roberts (1990) to evaluate species co-existence patterns. Null assemblages were created in EcoSim using a fixed-equiprobable model (SIM2) which has a low type I error when

analyzing C-scores (Gotelli 2000). In this model, row totals (= number of baits a species occupies) are held constant and the 25 bait stations are treated as equally suitable for species occupation.

Differences in SES values were compared between burn types and among times of day with a two-way ANOVA. We also evaluated if sites' thermal characteristics affected the co-occurrence patterns of its constituent species throughout the day. We evaluated if hotter sites have more variable species co-occurrence patterns with the Standard Test module in EcoSim, a randomization test analogous to a conventional regression test relieved of its parametric assumptions (Edgington 1995). This test compares the observed slope to the distribution of slopes from repeatedly reshuffled data.

## **Results**

We observed a total of 34,048 individuals in 24 species in 11 genera (Table 1). More total workers were found in unburned forests (mean=2799 workers/site) than burned forests (mean=1588 workers/site;  $t=2.29$ , 14 d.f.,  $P=0.038$ ). Unburned plots (mean species richness=8.63, range=6-12) also tended to have higher species richness than burned plots (mean species richness=7.25, range=5-9 ;  $t=1.45$ , 14 d.f.,  $P=0.079$ ).

Temperature varied considerably throughout the day, and baits in unburned sites (mean temperature=33.9°C, range=10.4-79.6°C) were cooler than burned sites (mean temperature=36.4°C, range=8.8-81.2°C;  $t=7.81$ , 7198 d.f.,  $P < 0.0001$ ). A summary of site attributes is listed in Table 2. For additional site details and specific species response to fire, see Ratchford et al. (2005).

### Temporal Niche

In forests, 13 of 16 sites show higher overlap than expected by chance; the three non-significant forest plots occurred in burned sites (Figure 3). These results suggest ant assemblages are sharing the temporal resource more than would be expected if competition was important.

### Thermal Niche

#### *Co-occurrence*

Six of 16 sites (half burned, half unburned) show non-random species associations across the temperature intervals, suggesting in some sites species are aggregating during certain temperature intervals (Table 3).

#### *Temperature at Peak Activity*

When temperatures were selected from a uniform distribution with user-defined endpoints, half of the sites had variance values smaller than the mean variance of the 1000 null assemblages. One site had a variance value larger than the null assemblages. The model with temperatures selected from a uniform distribution with data-defined endpoints found two burned sites with smaller variance values and two unburned sites with larger variance values than the null assemblages. Nine sites had lower variance values than expected with the normally distributed, site-defined model. Eight sites had lower variance values and one site had a larger variance value when Fisher's combined probability was used to test for consistency across the three models (Figure 4).

The T-test comparing SES values between burned and unburned sites for the uniform user-defined, uniform data-defined, and normal site-defined models were not significant ( $P=0.2948, 0.0556, 0.0892$ , respectively).

#### Co-occurrence by Sampling Period

There was significant species segregation (SES values  $>2$ ) in 3 of the 16 sites in the morning, zero sites in the afternoon, and 7 of 16 sites in the evening (Figure 5). The remaining periods were not significant, indicating random species coexistence patterns.

Burned sites had lower SES values than unburned sites ( $F_{1,40}=4.134, P=0.0487$ ). Co-occurrence patterns were significantly different throughout the day ( $F_{2,40}=17.059, P=<0.001$ ). Tukey's HSD revealed differences among all time of day, with highest SES values in the evening, intermediate values in the morning, and lowest values in the afternoon. The interaction of burn by time was not significant ( $F_{2,40}=1.8667, P=0.1679$ ).

There was also a significant positive relationship between site average temperature and the variability of species coexistence patterns throughout the day. The observed slope was 0.09402 while the mean of the simulated slope was 0.00087 ( $P=0.0188$ ) which indicates a positive association between temperature and variability in SES values throughout the day.

## Discussion

Communities, to some degree, are always constrained by the physical environment (Wilson 1999) and, on a general diurnal scale, thermal constraints likely dictate ant community activity. In the majority of sites, species display greater temporal overlap than expected (Figure 3), and assemblages in many sites appear to aggregate along the thermal gradient (Table 3). Species appear to broadly synchronize their activity throughout diurnal time and temperature; moderate morning activity declines sharply during the afternoon heat and then rises throughout the evening (Figure 6). Temporal overlap, however, is not exclusively driven by inactivity patterns during the heat of middle of the day: we used a randomization algorithm which preserves species natural inactivity patterns (i.e. zero bait occupancy) in the randomized assemblages. Albrecht and Gotelli (2001) also found significant temporal niche overlap in ant communities during months when physiological constraints influence foraging activity.

How can assemblages aggregate along the thermal axes, yet display even spacing of thermal activity peaks? The thermal co-occurrence model evaluates thermal activity in a relatively broad context: the matrix entries for the thermal co-occurrences model only represent species presence within a wide range of temperatures. Individuals may be active within a large temperature range, but the activity within that range may fluctuate widely (Figure 7). The more direct method of measuring the temperature at which species were most active revealed evenly spaced activity peaks (Figure 4), suggesting that species peak foraging activity may be shaped, at least indirectly, by the thermal niche axis. Regular spaced peak activities may emerge because of interactions with other



species during foraging bouts. To assuage the effects of dominant species, subordinate species may forage during different times when the thermal environment is not suitable for dominant species (Cerdeira et al. 1997, Bestelmeyer 2000). Thus, if the assemblage is generally active during the same period, subordinate species may only reach maximum densities on baits thermally distinct from those inhabited by dominant species. Thus, ecological interactions may interact with the thermal environment to determine when species attain maximum foraging densities. Alternatively, evolutionary processes may dictate species response to the thermal environment. Species may be responding directly to micro-thermal variations in the environment, and this fine-tuned response to the thermal environment may have evolved to escape competitive interactions in the past. That is, it may be evidence of the ‘ghost of competition past’ (Connell 1980). While invoking different mechanisms, even spacing of thermal activity peaks are likely a by-product of competitive effects either now or in the evolutionary past. Thus, overall community activity appears to be broadly synchronized by diurnal time and temperature, while individual activity peaks may be regulated by the interaction of temperature and behavior.

Because temporal niche and thermal coexistence and activity matrices were pooled across all baits, these models could not test for segregation in space. In previous studies with matrices constructed with pitfall data (Gotelli and Ellison 2002) or with bait data pooled across sampling periods (Sanders et al. 2007b), random local species coexistence patterns were found. However, when matrices were constructed with data within a single sampling period and run separately for each time of day, species segregation was

common, especially during the cooler hours (Figure 5). Additionally, SES values were significantly different during all three periods of the day, and assemblages in hotter sites had more variable SES values throughout the day. Initially, environmental filtering imposes restrictions on which species can tolerate the physical environment. Next, the process of biotic filtering occurs in which assembly rules may operate (Wilson 1999). In this system, environmental filtering occurs with high temperatures, and assembly rules (i.e. species segregation) occur during cooler temperatures, all within the diurnal timeframe. Thus, throughout the day communities are disassembled and reassembled as the thermal environment varies, indicating that assembly rules operate within constraints imposed by the physical environment (Belyea and Lancaster 1999).

Disturbance may alter ant communities by directly reducing or removing species and indirectly through habitat modification (Andersen 1991, York 2000, Andersen et al. 2006, Arnan et al. 2006). Species co-occurrence patterns were more random in burned habitats. Because burned habitats are occupied by fewer individuals and have a lower species density, competition may be reduced (Arrington et al. 2005). Burned sites were also hotter; this environmental filter may also prevent the operation of assembly rules.

The interaction of temperature and interspecific interactions is often cited as a structuring force in ant communities (Andersen 1995, Bestelmeyer 1997, Cerda et al. 1998), especially in dominance-diversity relationships (Andersen 1992, Parr et al. 2005). Temperature appears to mediate competitive effects in Siskiyou ant communities by imposing environmental filters which vary across habitats and throughout the day.

Future studies that experimentally disentangle the interaction of these putative interactive forces are needed to quantitatively determine their relative contribution to ant community structure.

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**Table 1. 1** A list of all ant species observed at bait stations. The presence (1) or absence (0) of each species is recorded for each of the 16 sampling plots.

Abbreviations used in subsequent Figures use the first initial of the genus and species (e.g. *Aphaenogaster occidentalis*=AO).

	O23	AIM	CDR	DCH	GRG	LEH	SHT	UDG	DGF	HPY	LM1	LM2	SCP	SSD	STF	WHY
<i>Aphaenogaster occidentalis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tapinoma sessile</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Camponotus vicinus</i>	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1
<i>Temnothorax nevadensis</i>	1	0	1	1	0	1	0	1	1	0	1	1	1	1	1	1
<i>Temnothorax nitens</i>	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1
<i>Formica subelongata</i>	0	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1
<i>Formica lasioides</i>	1	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0
<i>Prenolepis imparis</i>	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0
<i>Crematogaster coarctata</i>	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1
<i>Temnothorax rudis</i>	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0
<i>Brachymyrmex depilis</i>	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
<i>Formica moki</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
<i>Formica subpollita</i>	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Temnothorax rugatulus</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0
<i>Formica argentea</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
<i>Lasius pallitarsis</i>	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
<i>Camponotus essigi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Camponotus laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Formica accreta</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Formica neogagates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Liometopum occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Solenopsis molesta</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Temnothorax sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Temnothorax sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

**Table 1. 2** A summary of site attributes for each of the 16 plots. Latitude and longitude are given as decimal degrees, and temperature refers to the means soil surface temperature at each site.

Site	Burn Type	Elevation (m)	Latitude (dd)	Longitude (dd)	Aspect (°)	Temperature (°C)
AIM	Burn	467	42.07	124.11	230	37.6
CDR	Burn	797	42.19	123.98	149	35.7
DCH	Burn	513	42.10	124.06	170	35.1
DGF	Unburned	536	42.10	124.05	60	32.5
GRG	Burn	567	42.13	124.20	260	35.0
HPY	Unburned	477	42.20	123.79	45	22.8
LEH	Burn	478	42.01	124.08	150	36.4
LM1	Unburned	542	42.08	123.92	120	33.7
LM2	Unburned	447	42.15	123.85	60	33.0
023	Burn	565	42.45	123.90	20	32.2
SCP	Unburned	427	42.49	123.82	130	38.3
SHT	Burn	689	42.17	124.01	30	38.9
SSD	Unburned	432	42.49	123.78	292	37.4
STF	Unburned	375	42.48	123.88	200	35.1
UDG	Burn	510	42.23	123.71	140	40.3
WHY	Unburned	540	42.13	123.88	67	38.6

**Table 1. 3** Results of thermal co-occurrence analysis. Entries represent lower tail probability of detecting observed C-score values smaller than the average C-score generated in the randomized assemblage. Sites with significant species aggregation are in bold.

Burned		Unburned	
Site	<i>P</i> (obs<exp)	Site	<i>P</i> (obs<exp)
023	0.0894	DGF	0.1688
AIM	0.0780	HPY	0.3258
CDR	0.7836	LM1	0.2412
DCH	<b>0.0004</b>	LM2	<b>0.0028</b>
GRG	<b>0.0002</b>	WHY	0.0836
LEH	0.0556	SSD	<b>0.0016</b>
SHT	0.1006	STF	0.1980
UDG	<b>0.0046</b>	WHY	<b>0.0000</b>

## Figure Legends

**Figure 1.** Location of 16 forest plots. Circles represent sites burned by the Biscuit fire; triangles denote unburned sites. (From Sanders et al., 2007b)

**Figure 2.** Typical unburned (A) and burned (B) forest site.

**Figure 3.** Temporal overlap of ant communities in burned and unburned sites.

Connected circles represent expected Czekanowski Index niche overlap values; triangles represent observed values. Sites with asterisks indicate greater temporal overlap than expected by chance.

**Figure 4.** Results of thermal spacing of maximum foraging activity. The dashed line connects the observed variance values of the spacing of the temperatures at which species obtained maximum activity. Closed symbols represent the mean variance values of randomized assemblages constructed from a uniform distribution with user-defined endpoints (diamonds), from a uniform distribution with data-defined endpoints (triangles), and from a normal distribution with site-defined parameters (squares). Asterisks indicate sites with observed variance values with lower tail probabilities significantly smaller than expected across the three models. The cross indicates an observed variance value greater than expected across models.

**Figure 5.** Co-occurrence values for ant communities at three temporal snapshots. Light, medium, and dark gray symbols represent results for morning, afternoon, and evening, respectively. Burned sites are located left of the vertical double line, unburned sites to the right. Sites with SES values greater than 2.0 indicate significant species segregation (see text for details).

**Figure 6.** Relative activity of a sampled ant community across the diurnal thermal range. Species include *Aphaenogaster occidentalis* (Ao), *Camponotus vicinus* (Cv), *Formica lasiodes*, *Temnothorax nitens* (Tn), *Temnothorax nevadensis* (Tnv), and *Tapinoma sessile* (Ts).

**Figure 7.** Example of thermal activity peaks of species observed at one site. Species include *Aphaenogaster occidentalis* (Ao), *Formica subelongata* (Fsl), *Formica subpolita* (Fsp), *Prenolepis imparis* (Pi), *Temnothorax nevadensis* (Tn), and *Tapinoma sessile* (Ts).

Figure 1.1

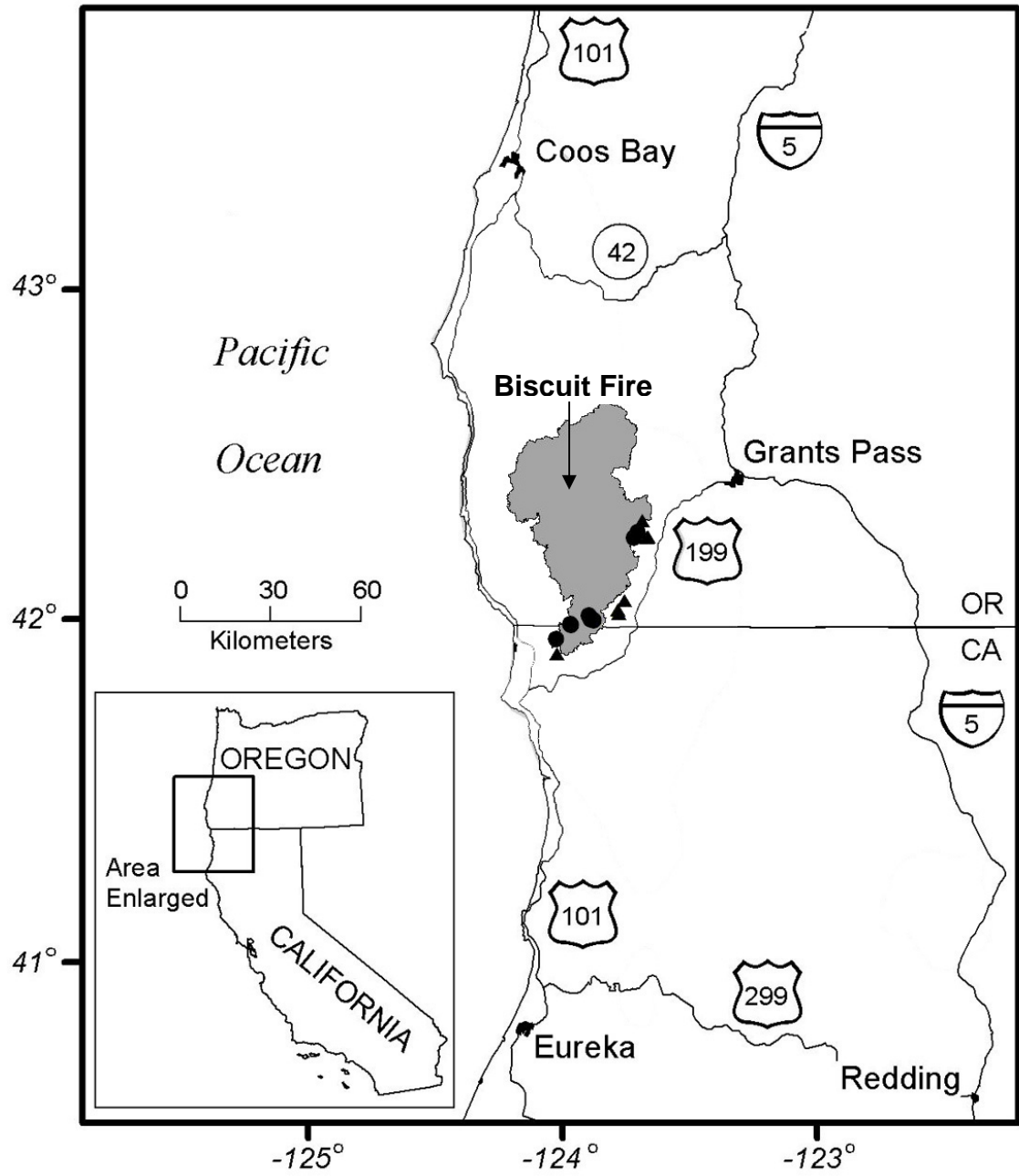


Figure 1. 2



Figure 1. 3

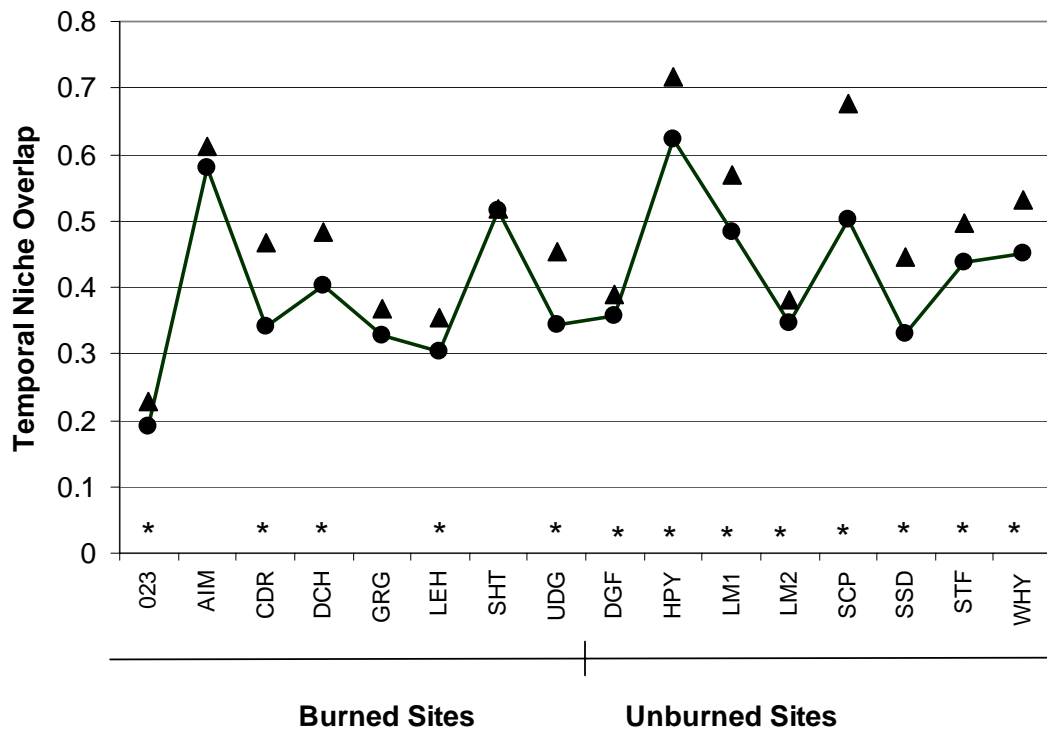




Figure 1. 4

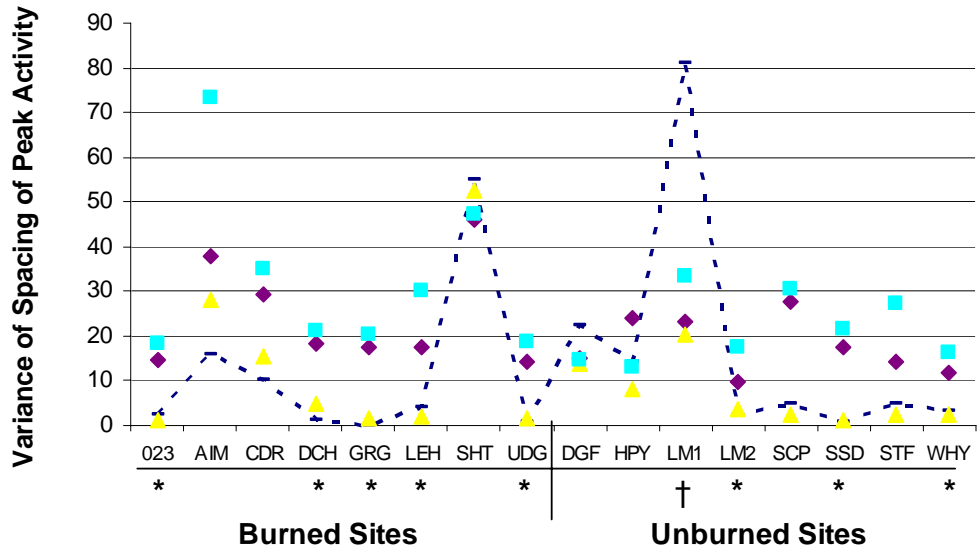


Figure 1. 5

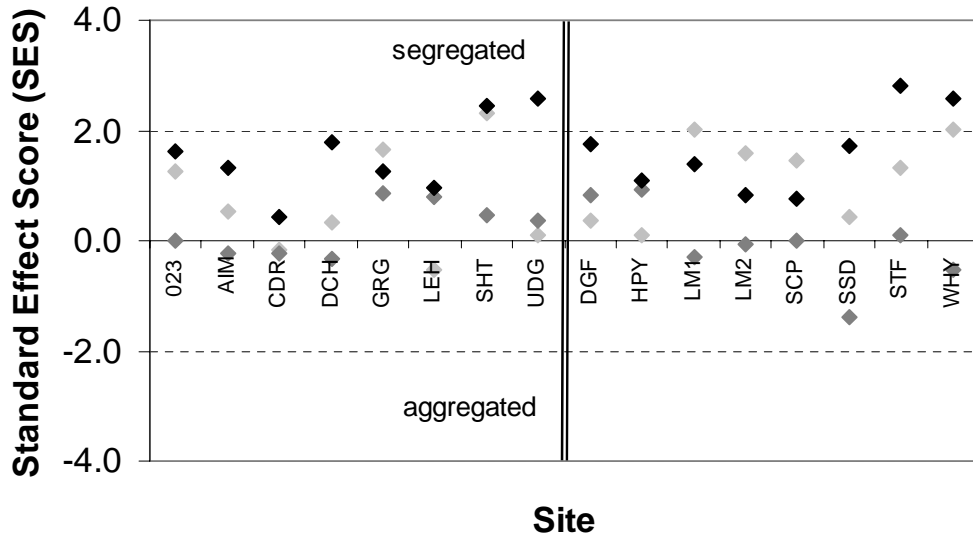


Figure 1. 6

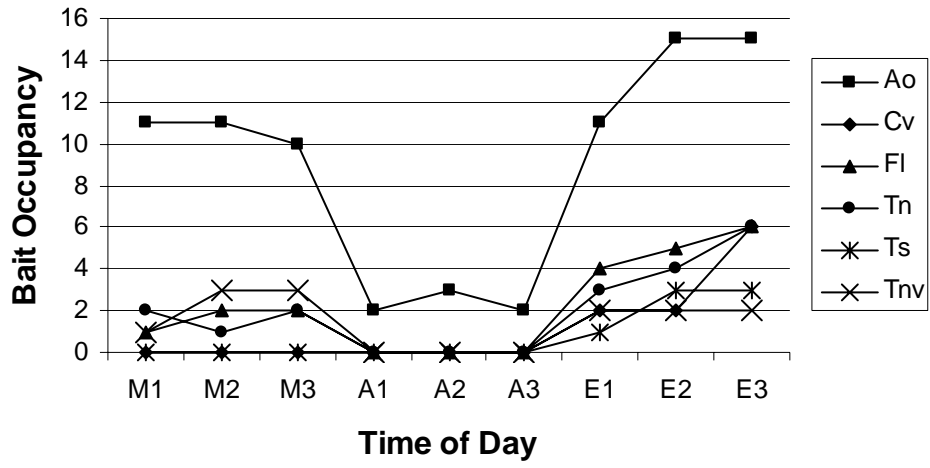
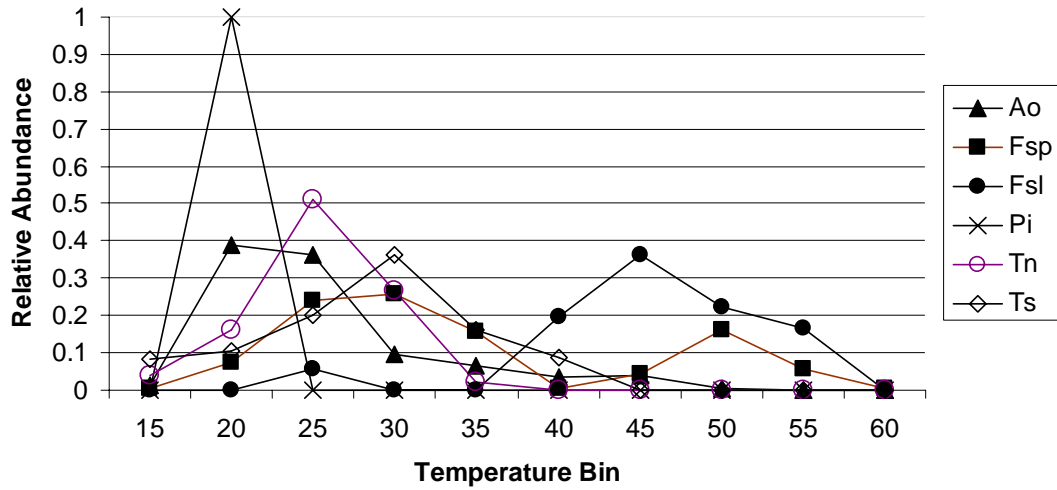


Figure 1. 7



## **Chapter 2**

### **Behavioral dominance does not predict patterns of relative abundance or species co-occurrence in Siskiyou ant communities.**

#### **Abstract**

Although interference competition is widely accepted to strongly structure ant communities, it is still uncertain what community patterns would look like if they were exclusively driven by interference competition. I used data from pairwise behavioral experiments to generate transition probabilities of a Markov chain model. The matrix elements represent the probabilities that a species will persist in a patch after an encounter with another species. Assuming the landscape represents a large number of patches, the model predicts the equilibrium distribution of different species, i.e. the relative abundance of an assemblage. I compared Markov chain predictions to relative abundance measurements on the local and regional scale. I used the same pairwise behavioral data to predict species co-occurrence patterns. I used a null model to determine co-occurrence values among all species pairs in three southwestern Oregon ant communities. I then correlated pairwise experimental indices of behavioral dominance to those co-occurrence values. Neither model accurately predicted community patterns on any scale. The only statistically significant result was the Markov chain prediction of bait occurrence on the local scale; however, the relationship was opposite of the prediction: behaviorally dominant species occupied relatively few baits.

## **Introduction**

Competition is considered the “hallmark of ant ecology” (Hölldobler and Wilson 1990), and ant species are often categorized in terms of their behavioral and ecological dominance. Behavioral dominance is defined by primary access to resources due to successful fighting abilities supplants other species (Cerda et al. 1997) whereas ecological dominance ranks species in terms of their effect on the entire community (Andersen 1992). An ant species is behaviorally dominant if its presence elicits avoidance or retreating behavior during its encounters with other species; however, it must also occur at a large proportion of food resources and monopolize those resources for it to be considered ecologically dominant (Andersen 1992).

Many studies have investigated how assemblages are organized by evaluating how species are arranged in term of behavioral and ecological dominance (Fellers 1987, Savolainen and Vepsalainen 1988, 1989, Cerda et al. 1997, Bestelmeyer 2000, Palmer et al. 2000, LeBrun 2005). Studies often investigate why behaviorally dominant species do not exert complete ecological dominance in a community. Explanations include differences in discovery times (Fellers 1987, Adler et al. 2007), competition-colonization trade-offs (Stanton et al. 2002), parasitoids (LeBrun 2005), resource size (Cerda et al. 1998) and resource type (Sanders and Gordon 2003).

Most studies that investigate ant behavioral dominance, however, use values determined by observations at food baits in the field (Fellers 1987, Savolainen and Vepsalainen 1988, Cerda et al. 1997, LeBrun 2005). Although bait observations are representative of natural

behaviors, they are limited to species which naturally come together, and data are not obtained about all species combinations in the assemblage. Even with unlimited sampling effort, some species may simply never interact during foraging bouts, perhaps due to competitive effects or due to habitat segregation. Either way, determination of behavioral dominance based solely upon natural observations may be lacking data on potentially important species combinations.

Additionally, although behaviorally dominant reduce the abundance of subordinate species at baits (Fellers 1987, Savolainen and Vepsalainen 1988, Andersen 1992), often subordinate species are the only ones observed to co-occur with behavioral dominants on baits (Fellers 1987, Savolainen and Vepsalainen 1989) or in nesting areas (Savolainen and Vepsalainen 1988, Bluthgen et al. 2004). Thus, it is uncertain how well behavioral dominance predicts ecological dominance and co-occurrence patterns at the level of the entire assemblage.

In this study, I test two hypotheses. First, I hypothesize that dominant behavior determines species turnover in a patch and will predict the relative abundance in a community. Second, I hypothesize that aggressive species will segregate on baits more often than subordinate species.

To test these hypotheses, I first experimentally quantified behavioral dominance between all species pairs in a local assemblage to determine how often each species attacks and retreats when encountering other species. I then used these behavioral data to construct a transition matrix whose entries represent the probability distribution that a species will

persist in a patch. I used a Markov chain model to compute the equilibrium distribution of species, i.e. the relative abundance, assuming agonistic behavior determines patch turnover. Thus, I used short-term behavioral data to model a long-term, dynamic process – turnover in species composition. I compared the Markov chain prediction of relative abundance patterns to relative abundance patterns observed at the local and regional scale. Second, I used the pairwise behavioral data to make predictions about species co-occurrence patterns. I used a null model to determine co-occurrence values among all species pairs in three southwestern Oregon ant communities. I then correlated pairwise experimental indices of behavioral dominance to co-occurrence patterns observed in the field.

## **Methods**

### **Study area**

I sampled ant communities in the Siskiyou-Klamath eco-region near the Oregon-California border during June-August of 2003 and 2004. The area has a Mediterranean climate, with cool winters (mean January minimum temperature = 0 °C) and warm dry summers (mean July maximum temperature = 31.7 °C; mean annual precipitation = 154 cm, with only 4 cm falling between June and August). Forests are mostly open stands of *Pinus jeffreyi* with other sclerophyllous trees reduced to a shrub layer.

In 2003, I sampled 16 sites, half of which were burned by the 2002 Biscuit fire. In each site 25 bait stations were arranged in 5 x 5 array, separated by 2 meters, and baited with approximately 5.5 g of tuna and a cotton ball soaked in honey water. Baits were sampled nine times over a 12 hour period (08:00 – 20:00) to measure activity over a wide range of

time and temperature. Ratchford et al. (2005) provides detailed sampling and site details. Data summed over the 16 sites constitute the regional abundance of species. Data from two individual sites (SSD and WHY) were also used in the local co-occurrence analyses. In 2004 I sampled a new site (SE), approximately 200m from the SSD site. At SE, I used 15 tuna bait stations, separated by 5 to 20 meters, randomly located throughout the site. Baits were observed seven times over the 12 hour period and sampled over 5 weeks. All species found at the SE site were used for the local relative abundance and co-occurrence analyses.

### **Quantifying behavior**

Though most studies use encounters at baits to determine species behavioral dominance, all combinations of species interactions are often not observed. Thus, I experimentally forced all species at SE to interact during pairwise behavioral contests (Table 1). All pairwise behavioral data were not able to be obtained on all regional species (24 species = 276 unique combinations); thus regional analyses only include the six species within distinct genera that occurred at the most sites (Table 1). *Prenolepis imparis* was not used because it was not easily found at sites during 2004.

I conducted the pairwise behavior experiment by introducing one worker of each species pair into opposite ends of a piece of 8 cm by 64 mm clear Tygon tubing and sealed the ends. Scoring began at first contact, and all interactions were recorded for a total of 2 minutes. I recorded each individual's behavior at every contact, and all dominant, neutral, and subordinate behaviors were recorded. Dominant behaviors include any type of attack, which may include biting, chasing, lunging, or chemical warfare. Neutral behavior is no visible change in behavior after contact. Subordinate behavior represents

any type of retreat, which most often is running away, but may include spasming or death. A total of ten trials were conducted per species pair, and new individuals were used for each trial. The summary results of the all behavioral experiments are available in Appendix A.

I used a new piece of Tygon tubing and washed, dry hands for each trial. Ants were used within 3 hours of field collection with tuna baits and aspirators. Whenever possible, I used individuals collected from different colonies of the same species in consecutive trials.

With sufficient replication, one-on-one behavioral contests have been found to produce very similar data to bioassays using higher numbers of interacting ants (Roulston et al. 2003). To test if individual ants encountering heterospecifics in unbaited tubes was similar to behavior observed in natural field settings (i.e. at baits often with multiple interacting individuals), I compared species experimental and field Dominance Index (DI) values. Because behavioral dominance is defined as successful fighting ability which supplants other species (Cerda et al. 1997), I used Feller's (1987) DI measurement to quantify dominant behavior. This index reports the proportion of time that a species presence elicited expulsion behavior in another individual. Thus, a species dominance index derived from the behavioral experiment is the proportion of contacts in which it elicited retreating behavior in the other individual. I compared field and experimental DI values from both the local (SE) site and the regional data set with the Standard Regression Test module in EcoSim (Gotelli and Entsminger 2006), a randomization test



analogous to a conventional regression test relieved of its parametric assumptions (Edgington 1995). EcoSim's Standard Regression compares the observed slope to the distribution of slopes from repeatedly reshuffled data.

### **Using behavior to predict relative abundance**

I utilized data from the behavioral experiment to construct a Markov chain model to predict relative abundance on the local and regional scale. Using one local site allowed for complete data on a single assemblage, and I was able to cross all (=8) species combinations (n=28). To gain a more robust estimate of relative abundance, I also used abundance values summed over the regional scale (=16 sites; see above), but only on the six most common species (Table 1).

I used two different measurements of relative abundance: bait occurrence and average number of foragers per bait. Bait occurrence was determined by species presence on a bait. If a species had at least one worker on a bait during a sampling period, it was counted as one bait occurrence (maximum value = number of baits per site). The second measurement was the average number of workers on a bait on which it occurred. This measurement does not take into account the total number of baits occupied; rather, it describes the ability of a species to successfully recruit to a visited bait.

### *Markov Chain Model*

Markov chains were first introduced to community ecology studies to model succession processes (Waggoner and Stephens 1970) and remain a useful yet underutilized tool in community ecology (Hill et al. 2004). Markov chains treat the landscape as a large set of patches which may take on different states; in succession models these states represent

different species. How a community changes through time is defined by the probability of one state (or species) at time  $t$  transitioning to another at time  $t+1$ .

I used behavioral data to predict both local and regional relative abundance. Because not all species were observed in all sites, I constructed matrices of two different dimensions. This local model includes 8 different states (=species), and thus its dimensions are 8x8. The regional model consists of a 6x6 matrix. The entries of the matrix are the transition probabilities that one species will persist or turnover in a patch from one time step to another. I used the dominance behavior observed in the experiment to create the transition probabilities. Two types of transition probabilities were calculated. The first, the diagonal values, represent the likelihood that a species replaces itself in the next time step. These values represent a species ability to persist in a patch. I used the proportion of times a species did not retreat during its encounters with all other species in the behavioral experiment as the diagonal values. The second type of transition probability is represented in the off-diagonal values. These values represent the probability that a species will turnover in a patch after an encounter with another species. I used the proportion of retreats of one species from another as the off-diagonal values. For example, in Table 4A, there is a 36.4% chance that *Aphaenogaster occidentalis* will replace itself (persist) in a patch, and a 4.4% percent chance that it will turnover to (be expelled by) *Crematogaster coarctata*.

I modified the original transition matrix (=“original” model), substituting zero values for each diagonal value in the transition probability matrix (=“zero” model). The

substitution of zeros on the diagonal means now there is a zero probability that a species can replace itself in the next time step. After each time step a species will not occupy the same patch, and the probability it will appear in the next time step is based solely upon its ability to expel another species. Species turnover is now determined exclusively by the off-diagonal values which represent the probability that one species will expel another.

These matrices are column-stochastic, i.e. each column sums to 1.0. Each column sums to one because entries are probability of transition from the “state” of occupancy by one species to another. The input vector, representing initial species abundance, was set at 1,000 individuals for each species. The model was run for 1,000 time steps until an asymptotic state distribution was reached. Because states represent species in this model, the asymptotic state distribution represents the equilibrium relative abundance of species.

I evaluated how well the original and zero Markov chain models predicted the relative abundance of species on the local and regional scale with simple linear regression. Local bait occurrence values were square-root transformed to satisfy assumptions of normality.

### **Using behavior to predict species co-occurrence**

I tested if agonistic behavior predicts species co-occurrence in three local ant assemblages (SE, SSD, WHY) in southwestern Oregon.

To evaluate species co-existence patterns, I utilized the C-score (Stone and Roberts 1990) which calculates the number of ‘checkerboard units’ of each species pair. Each checkerboard unit is calculated by  $(r_a - S)(r_b - S)$  where S is the total number of sites

(=baits) shared by the species pair, and  $r_a$  and  $r_b$  are the row totals for species a and b, respectively. Species that always occur together will have a C-score of zero. The greater the segregation in species, the larger the C-score will be. Results are reported in terms of the Standard Effect Size (SES) which scales the results in terms of standard deviations (Gurevitch et al. 1992). Large (greater than 2.0) SES values indicate significant species segregation. Species aggregation is indicated by small (less than -2.0) SES values.

Assemblages were randomized using the fixed-equiprobable model in EcoSim, version 7 (Gotelli and Entsminger 2006). In this model, columns (=baits;  $n=15$  for SE,  $n=25$  for SSD and WHY) are equally suitable for species, but row totals (=total baits occupied by a species) are fixed. Thus, species occurred in the same frequency in the randomized as in the observed assemblage. Presence-absence matrices were generated for a single evening sampling period, as this when non-random species co-occurrence values are most likely to occur (S. Wittman, unpublished data). The model was run separately for each unique species pair observed during this time ( $n=15$  for SE,  $n=10$  for SSD and WHY).

To test if behavioral dominance predicts co-occurrence patterns, I used simple linear regression using the DI values from the behavioral experiment (described above) as the predictor variable and the SES values as the response value. Because each point represents a unique species pair, each DI value is the average of the number of times each species caused the other to retreat. Thus, the DI value ranges from 0 (both species never retreated in the presence of the other) to 1 (both species expelled each other at every contact). Species with a strong ability to expel others are predicted to have high SES

values, while species which tolerate each others presence are predicted to have low SES values. Regression analyses were run in JMP version 4.0.2 (SAS Institute, Cary, North Carolina, USA).

## **Results**

### **Field and Experimental Dominance Rankings**

The local behavioral experiment utilized all species found at the SE site and repeatedly tested all species combinations, resulting in a complete behavioral data set based on hundreds of interactions. This is in contrast to observations based in the field, in which approximately a third of all possible species combinations were observed. Unique species combinations were observed an average of 7 times in the field (range=1-18) while each unique species pair was observed hundreds of times in the behavioral experiment (average=572). Because field observations also incorporate differences in recruitment abilities, more individuals were present during a field encounter (average=21) than during an experimental encounter (always 2). See Table 2 for the summary of differences between field observations and the behavioral experiment.

Although the behavioral experiment used one-on-one interactions in unbaited tubes, experimental dominance indices (DIs) were similar in those observed on baits in the field which include both single and multiple individual interactions. This is true for field DI values observed at one local site (mean of simulated slopes = -0.002, observed slope= 0.187,  $P= 0.024$ ) and moderately significant for behaviors summed across multiple sites (mean of simulated slopes = -0.039, observed slope= 1.80,  $P= 0.092$ ; Figure 1).

Dominance indices based on field observations were always larger than those based on experimental data (Figure 1).

### **Behavioral Prediction of Relative Abundance**

I used the data generated from the behavior experiments to generate four transition probabilities matrices (Tables 3 and 4) which were used in the original and zero Markov chain model to predict relative abundance at the local and regional scale. The original and zero models produced relatively similar relative abundance patterns (Figure 2). The largest difference in model predictions occurred with *Crematogaster coarctata*; the zero model predicted lower abundance for *C. coarctata* than the original model (Figure 2).

Overall, the Markov models did not accurately predict the relative abundance of species on either the regional or local scale (Figures 3 and 4). In only one of eight analyses was there a significant relationship between the Markov chain model predicted relative abundance and observed relative abundance. On the local scale, the zero Markov model predicted bait occurrence, but opposite of the hypothesis: dominant species occurred at fewer baits than subordinate species ( $F_{1,6}=11.77$ ,  $P=0.014$ ; Figure 5).

### **Behavioral Prediction of Species Co-occurrence**

Several species pairs exhibited non-random co-occurrence patterns across the three sites (Table 5). *Temnothorax nevadensis* was the only species which showed significant segregation, and it was usually with mass recruiting species (e.g. *C. coarctata*, *L.*

*luctuosum*, *T. sessile*). The only significant aggregation occurred between *T. nevadensis* and *F. moki*.

Behavioral dominance based on pairwise experiments did not predict co-occurrence patterns observed at SE ( $F_{1,13}=0.082$ ,  $P=0.779$ ; Figure 6), SSD ( $F_{1,8}=0.060$ ,  $P=0.813$ ) or WHY ( $F_{1,8}=0.203$ ,  $P=0.665$ ).

## **Discussion**

The one-on-one behavioral experiment served as an accurate tool to quantify species behavioral dominance. Using field data, only 9 of 28 unique species pairs were observed, and many pairwise interactions were observed only once or twice. In contrast, the behavioral experiment provided data on all species combinations, and species behavioral dominance values were based on replicated data sets (Table 2).

Because the behavioral experiment recorded hundreds of encounters, it is not surprising that the experimental DIs were lower than field DIs (Figure 1). For example, *L. luctuosum* only interacted with one other individual at SE during 525 total bait observations. Because in its single interaction it successfully expelled the other species, its field DI was 1.0. When forced to repeatedly interact with all other species in the behavioral experiment, its DI dropped to 0.40.

Even though the behavioral experiments were conducted with only one individual in an unbaited setting, species who dominated baits in the field were also the species dominant in the behavioral experiment (Figure 1). Thus, the behavior experiment provided a good

estimate of dominance observed in the field while providing a replicated data set about each species encounter.

When this behavioral data was transformed into a transition probability matrix for the Markov chain model, two types of models were created. The first, the “original” model, had all non-zero entries in its transition matrix. The original model incorporated both the ability of a species to persist (diagonal values) and to expel other species from their patch (off-diagonal values). The second model, the “zero” model, removed the ability of a species to persist in a patch from one time step to another, i.e. its transition matrix had zero entries along the diagonal. Nonetheless, the original and zero Markov models generated similar relative abundance patterns, with one exception, *C. coarctata* (Figure 2). Species with high persistence values (i.e. diagonal values) in the original model should be most affected, and *C. coarctata* does in fact have the highest persistence values of all the species (Tables 3 and 4).

Because the Markov models were constructed with data from species interactions which did not occur at baits, they incorporated species “inherent” aggression and dominance towards each other. This inherent response also manifests itself in a predictable way at food resources, i.e at bait observations in the field (Figure 1). Surprisingly, though, dominant species did not achieve high abundance in the field. Dominant species did not recruit more workers per bait, and dominant species did not occupy larger numbers of baits (Figures 3 and 4). In fact, the only significant relationship is opposite of the prediction: dominant species were less likely to occupy baits at the local site (Figure 5).



Dominant species have been defined as those species that are the numerical dominants, i.e. the species which show up in the greatest numbers at the greatest number of baits (Gibb and Hochuli 2004); this definition of dominance is employed in the dominance-discovery relationship (Andersen 1992, Parr et al. 2005). In the Siskiyou, those species that are behaviorally dominant are not the ones who achieve the high numbers of workers on baits (Figures 3B, 3D, 4B, 4D). A criticism of the analysis is that bait control can be achieved by subordinate species when they reach high densities, and when individuals of subordinate species outnumber dominants, their probability of attacking increases (Fellers 1987). One-on-one behavioral experiments did not predict dominance in the field in the invasive argentine ant (*Linepithema humile*) because its individual and colony level behavioral dominance differ (Holway 1999). Alternatively, species may be able to obtain numerical abundance without displaying high levels of interspecific aggression (Davidson 1998). Because in this study experimental (one-on-one) dominance is strongly correlated with field (large size range of interacting individuals) dominance, and abundance predictions based on dominance alone are highly unproductive of observed relative abundance of worker numbers (Figures 3B, 3D, 4B, 4D), I believe the behaviorally dominant ant species are not those who obtain numerical dominance in the Siskiyou Mountains.

Why might dominant species occupy fewer baits? An alternative way to approach the question is to address why dominant species may occupy fewer nests than subordinate species. Because at the local site baits were placed 5 - 20 meters apart, and few species

forage greater than five meters away from their nest (S. Wittman, unpublished data), bait occurrence data is also a good estimate for nest density. A potential mechanism may be that dominant species are poorer colonizers than subordinate species. Environmental conditions during colonization may favor subordinate species, i.e. the “niche hypothesis” (Pacala and Rees 1998). Alternatively, subordinate species may be stronger dispersers (dispersal limitation hypothesis). In acacia ant communities, species with more dominant workers have less dominant founding queens (Stanton et al. 2002). Although ants likely do not fight as intensely for nest sites in the Siskiyou, a similar pattern may be operating.

Although there was much variation in the co-occurrence patterns of species pairs across sites (Table 5; Figure 6), behavioral metrics did not provide any predictive power.

Behavioral predictions of co-occurrence patterns have been most often visited with ant mosaic theory (Leston 1973), in which dominants do not overlap and subordinates coexist with dominants. Much support for ant mosaic theory has been documented in simple tropical communities (see reviews in Majer 1993, Blüthgen and Stork 2007).

Segregation of dominants and coexistence of subordinates with dominants have also been documented in ground-nesting boreal communities (Savolainen and Vepsäläinen 1988).

In tropical ant communities, much research has focused on how associations with honeydew-producing hemipterans may fuel dominant ants’ territorial behavior (Davidson 1997, Blüthgen et al. 2000, Davidson et al. 2004). In boreal communities, dominant ants are territorial wood ants, which also are known to tend hemipterans (Styrsky and Eubanks 2007). It is rewarding for ants to be territorial with resources that are predictable in space and time (Davidson 1997) while strict territorial defense doesn’t behoove opportunistic

scavengers, as they would be guarding space with a variable rate of resource appearance (Styrsky and Eubanks 2007). In the Siskiyou Mountains ant communities are comprised of non-territorial opportunistic scavengers, and behavior is not predictive of co-occurrence patterns. Thus, behavior may only be predictive of co-occurrence patterns when stable resources are utilized by dominant, territorial species.

Community-level patterns of co-occurrence were not dictated by behavioral dominance, but the individual behavior of one species may explain its association with another. The only species that regularly displayed non-random associations with other species was *T. nevadensis*, which often segregated with mass-recruiting species. *Temnothorax nevadensis* may aggregate with *F. moki*. due to its ‘insinator’ (Wilson 1971) behavior. Savolainen and Vepsäläinen (1989) found *Leptothorax* sp. positively associating with *Formica* spp., and Fellers (1987) found it to coexist more often on baits with several species. (Note, Bolton (2003) reclassified *Leptothorax* spp. into three genera, and many became *Temnothorax* spp.). I observed *T. nevadensis* displaying the same behavior as reported in these studies. When this small ant encounters another species it freezes and brings its antennae close to its head, sometimes even lying on its side. Other larger species often ignore it while they are feeding on the bait, and after a few minutes it will retry its foraging attempt. If successful it often removes small pieces of food created by the larger species manipulating the large food item. This may also explain why *T. nevadensis* was unable to co-exist with species that recruit many, small workers who stay on the bait for a long time.

This study is the first to model relative abundance patterns and species co-occurrence of ant assemblages assuming community patterns are exclusively driven by dominance behavior. Although ant communities are generally thought to be strongly structured by interference competition, behavioral dominance models did not accurately predict relative abundance or co-occurrence patterns. Factors during colonization may play a larger role than interference competition in determining species bait occurrence, and dominance behavior may not be a good predictor of co-occurrence patterns in communities of opportunistic scavengers. In ant communities affected by parasitoids, models which incorporate dominance-discovery trade-offs, resource size, and the effects of parasitoids may help to understand co-occurrence patterns at small scales (Adler et al. 2007). Future work which incorporates differences in colonization ability and recruitment to resources of different size, in addition to differences in behavioral dominance, may provide a more complete understanding of the drivers of ant community structure.

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**Table 2. 1** Species used in the regional and local behavioral experiment. The six most common species in distinct genera found throughout the region (highlighted) were used in the regional analysis. All species found at SE (bold) were used in the local analysis. Entries indicate presence (1) or absence (0) at sites throughout the Siskiyou Mountains. Abbreviations used in subsequent Tables and Figures use the first initial of the genus and species (e.g. *Aphaenogaster occidentalis*=AO).

	O23	AIM	CDR	DCH	GRG	LEH	SHT	UDG	DGF	HPY	LM1	LM2	SCP	SSD	STF	WHY	SE
<b><i>Aphaenogaster occidentalis</i></b>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<b><i>Tapinoma sessile</i></b>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<b><i>Camponotus vicinus</i></b>	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1
<b><i>Temnothorax nevadensis</i></b>	1	0	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1
<i>Temnothorax nitens</i>	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0
<b><i>Formica subelongata</i></b>	0	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	0
<i>Formica lasiodes</i>	1	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0	0
<i>Prenolepis imparis</i>	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0
<b><i>CreMATogaster coarctata</i></b>	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1
<i>Temnothorax rudis</i>	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0
<i>Brachymyrmex depilis</i>	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0
<b><i>Formica moki</i></b>	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1
<i>Formica subpollita</i>	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
<i>Temnothorax rugatulus</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0
<i>Formica argentea</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
<i>Lasius pallitarsis</i>	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
<i>Camponotus essigi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Camponotus laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Formica accreta</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Formica neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Liometopum occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<b><i>Solenopsis molesta</i></b>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Temnothorax sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Temnothorax sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<b><i>Liometopum luctuosum</i></b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

**Table 2. 2** Summary of field observations and behavioral experiment in determining local species behavioral dominance.

	<b>Field</b>	<b>Experiment</b>
Conditions	Baits	Unbaited tubes
Total number of species observed	8	8
Observed number of unique species pairs	9/28	28/28
Average number of interactions observed per species	6.75	572
Average number of individuals present during encounter	21	Always 2

**Table 2.3** Transition probability matrix in the Markov chain model to predict the relative abundance of the six most common regional species. Entries, based on pairwise behavioral experiments, represent the probability of persistence (diagonal) or probability of expulsion of species x by species y (off-diagonal) (A). Matrix (B) assumes only expulsion behavior drives patch turnover; therefore, all diagonal entries are zero.

		Regional Species					
		t + 1					
		species y					
species x		AO	CC	CV	FS	TN	TS
t	AO	0.499	0.041	0.141	0.203	0.173	0.142
	CC	0.104	0.641	0.113	0.180	0.191	0.241
	CV	0.153	0.163	0.408	0.051	0.121	0.099
	FS	0.111	0.154	0.314	0.244	0.162	0.226
	TN	0.018	0.000	0.010	0.072	0.225	0.011
	TS	0.115	0.000	0.013	0.250	0.127	0.282

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		t + 1					
		species y					
species x		AO	CC	CV	FS	TN	TS
t	AO	0.000	0.115	0.239	0.268	0.224	0.198
	CC	0.207	0.000	0.192	0.238	0.246	0.335
	CV	0.305	0.455	0.000	0.068	0.156	0.138
	FS	0.222	0.430	0.531	0.000	0.210	0.314
	TN	0.037	0.000	0.016	0.096	0.000	0.015
	TS	0.229	0.000	0.022	0.330	0.164	0.000

**Table 2. 4** Transition probability matrix in the Markov chain model to predict the relative abundance of all local species. Entries (A) are the transition probability of persistence (diagonal) or probability of expulsion (off-diagonal). Matrix (B), with diagonal values of zero, assumes only expulsion behavior drives patch turnover.

		Local Species							
		t + 1							
		species y							
species x		AO	CC	CV	FM	LL	SM	TN	TS
t	AO	0.364	0.044	0.134	0.142	0.139	0.196	0.143	0.116
	CC	0.080	0.721	0.107	0.051	0.159	0.242	0.157	0.196
	CV	0.118	0.173	0.467	0.098	0.077	0.096	0.100	0.081
	FM	0.128	0.044	0.043	0.262	0.096	0.006	0.049	0.129
	LL	0.167	0.018	0.227	0.223	0.206	0.060	0.172	0.215
	SM	0.040	0.000	0.000	0.057	0.140	0.305	0.073	0.007
	TN	0.014	0.000	0.009	0.039	0.110	0.055	0.202	0.009
	TS	0.088	0.000	0.012	0.129	0.073	0.039	0.105	0.247

		t + 1							
		species y							
species x		AO	CC	CV	FM	LL	SM	TN	TS
t	AO	0.000	0.158	0.251	0.193	0.174	0.283	0.179	0.154
	CC	0.126	0.000	0.202	0.069	0.200	0.348	0.197	0.261
	CV	0.186	0.621	0.000	0.133	0.097	0.138	0.125	0.107
	FM	0.202	0.156	0.081	0.000	0.121	0.009	0.062	0.171
	LL	0.262	0.065	0.425	0.302	0.000	0.087	0.216	0.286
	SM	0.063	0.000	0.000	0.077	0.176	0.000	0.091	0.010
	TN	0.022	0.000	0.017	0.052	0.139	0.079	0.000	0.012
	TS	0.139	0.000	0.023	0.175	0.092	0.057	0.131	0.000

**Table 2. 5** Pairwise species co-occurrence results for SE, SSD, and WHY sites.

Significant SES values are in bold. Negative values indicate species aggregation; positive values indicate species segregation.

	SE	SSD	WHY
AO CV		1.156	0.294
AO TN	-0.825	-0.972	0.248
CC AO	0.326		1.240
CC CV			-0.558
CC LL	0.612		
CC TN	<b>2.345</b>		<b>2.412</b>
CC TS	0.724		1.043
CV TN		0.904	-1.709
FM AO	0.398	0.915	
FM CC	0.731		
FM CV		0.368	
FM LL	0.730		
FM TN	1.539	<b>-2.687</b>	
FM TS	-0.850	0.935	
TN LL	<b>2.353</b>		
TS AO	0.379	0.772	0.348
TS CV		-0.203	0.707
TS LL	0.715		
TS TN	2.858	<b>2.580</b>	0.600

## Figure Legends

**Figure 1.** The relationship between experimental and field based dominance values for local (closed markers, solid line) and regional (open markers, dotted line) species sets. The local behavioral experiment relationship is significant ( $P=0.024$ ) whereas the regional relationships is moderately significant ( $P=0.092$ ).

**Figure 2.** Comparison of original (solid) and zero (hatched) Markov model predictions of relative abundance for the regional (A) and local (B) set of species.

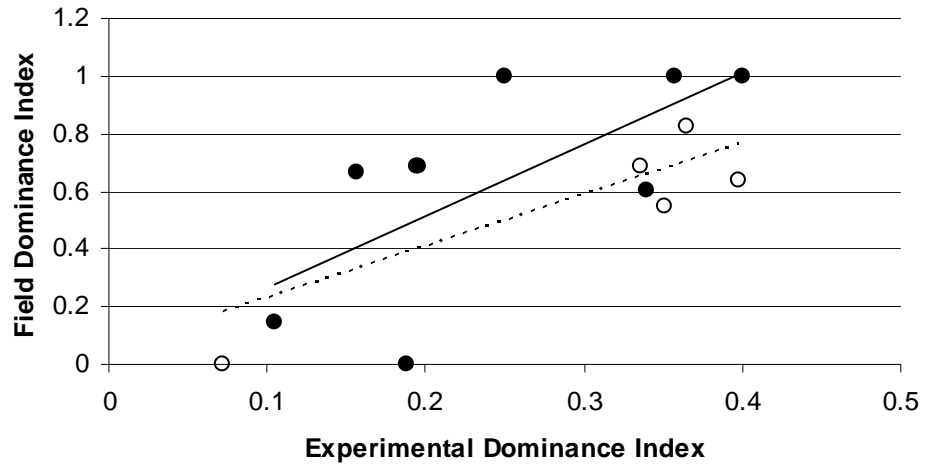
**Figure 3.** Markov model predictions of relative abundance (dark) and observed relative abundance (gray) for species occurring across regional sites. Original Markov model predictions vs. observed bait occupancy (A) and worker numbers per bait (B). Zero Markov model predictions vs. observed bait occupancy (C) and worker numbers (D). In all figures species are ordered in terms of increasing Markov model relative abundance prediction. In no case does the behavioral predictions of relative abundance accurately predict observed relative abundance of the community ( $F_{1,4}=2.261, 0.013, 4.549, 0.048$ , respectively,  $P>0.05$ ).

**Figure 4.** Markov model predictions of relative abundance (dark) and observed relative abundance (gray) for species occurring at a local site. Original Markov model predictions vs. observed bait occupancy (A) and worker numbers per bait (B). Zero Markov model predictions vs. observed bait occupancy (C) and worker numbers (D). In all figures species are ordered in terms of increasing Markov model relative abundance prediction. A significant negative relationship exists between the zero Markov model prediction and the observed local bait occupancy (Figure 5).

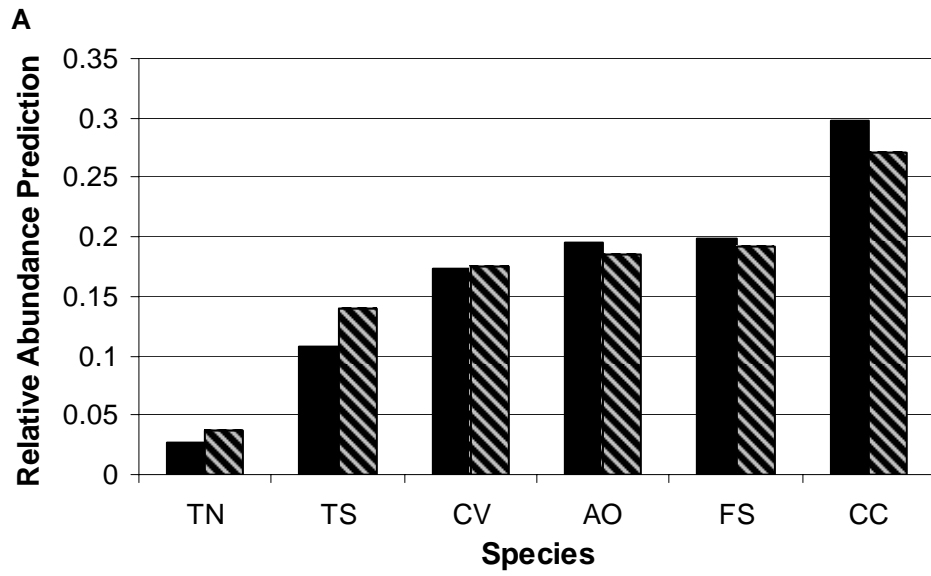
**Figure 5.** Observed relative abundance of local bait occupancy vs. zero Markov model relative abundance prediction ( $r^2=0.662$ ,  $F_{1,6}=11.77$ ,  $P=0.014$ ).

**Figure 6.** Typical relationship between experimentally-derived dominance measurements and co-occurrence values on baits in the field. Each point represents a unique species pair. Data from SE site during a single evening sampling period ( $r^2 = 0.006$ ,  $F_{1,13} = 0.082$ ,  $P = 0.779$ ).

**Figure 2. 1**

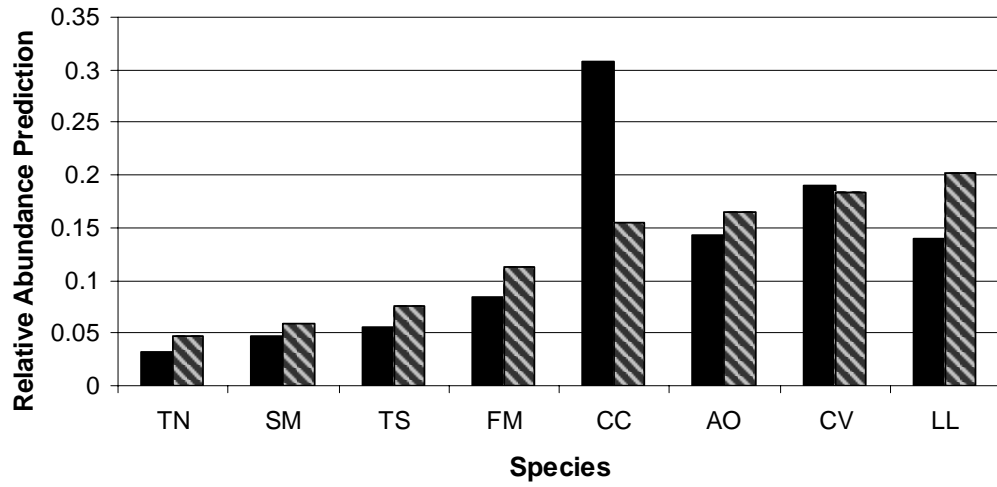


**Figure 2. 2**



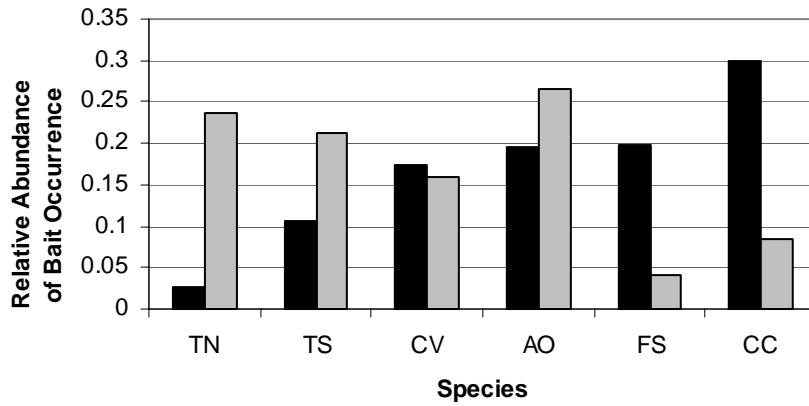


**B**

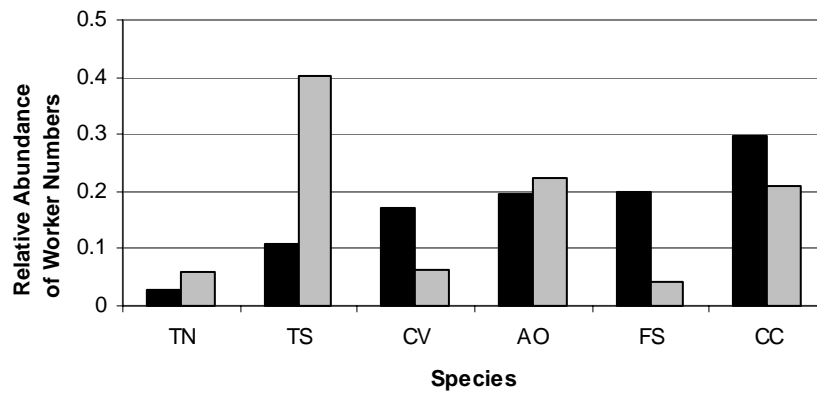


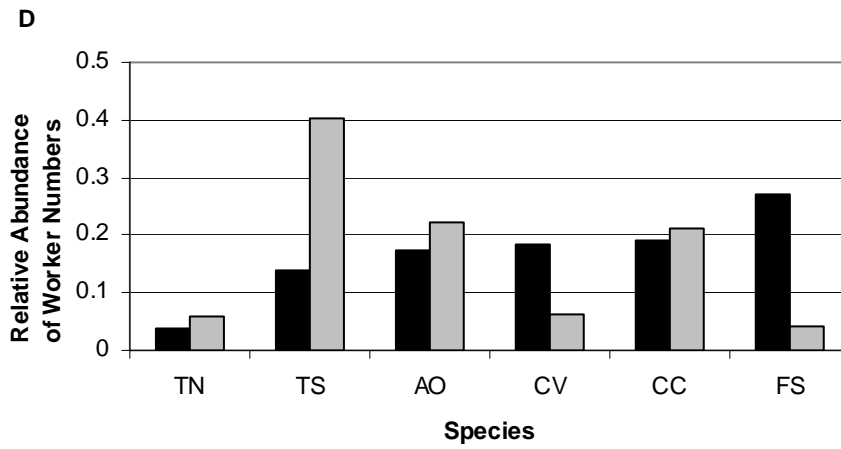
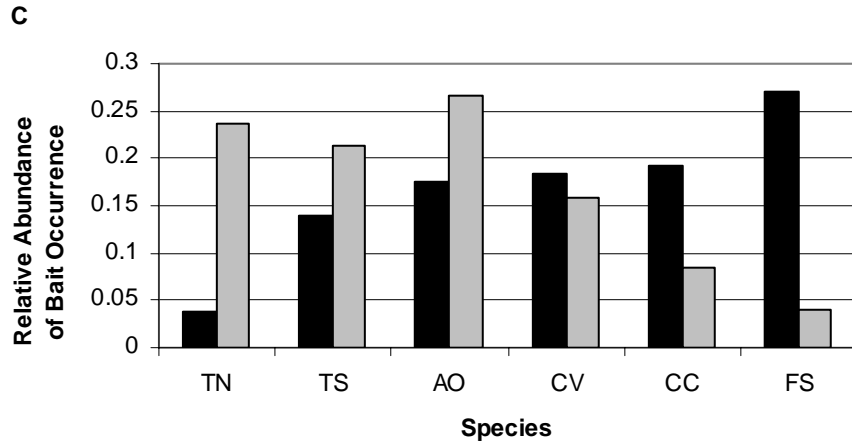
**Figure 2.3**

**A**

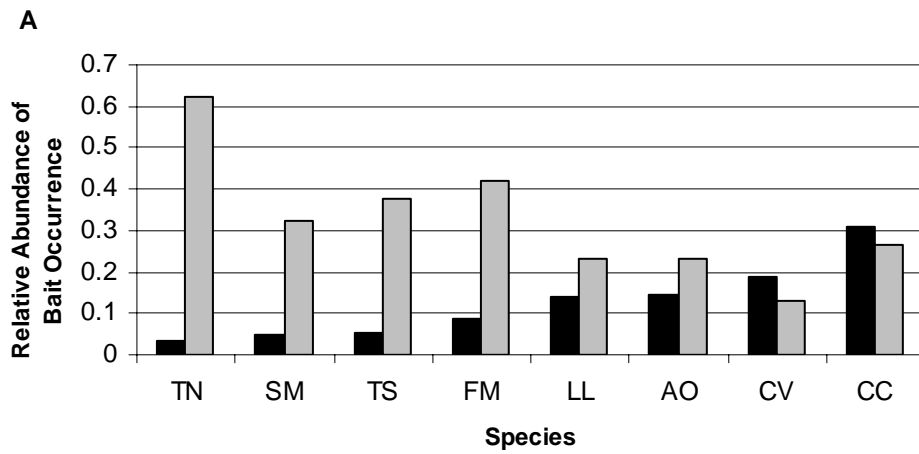


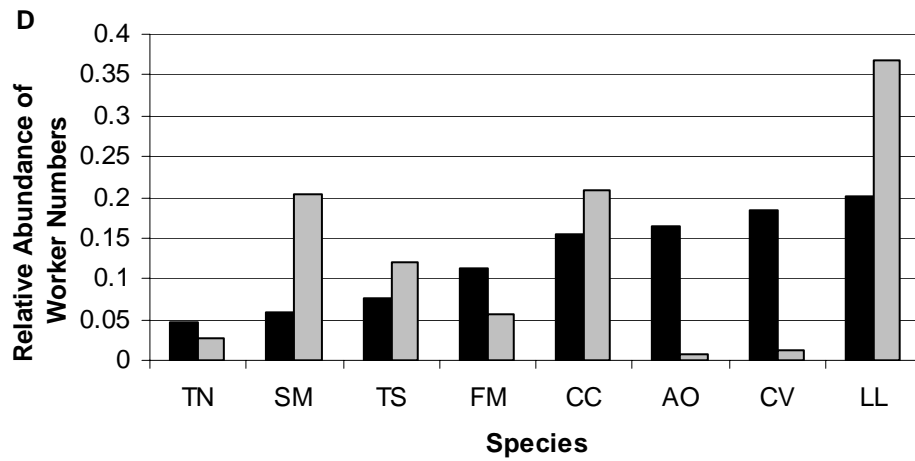
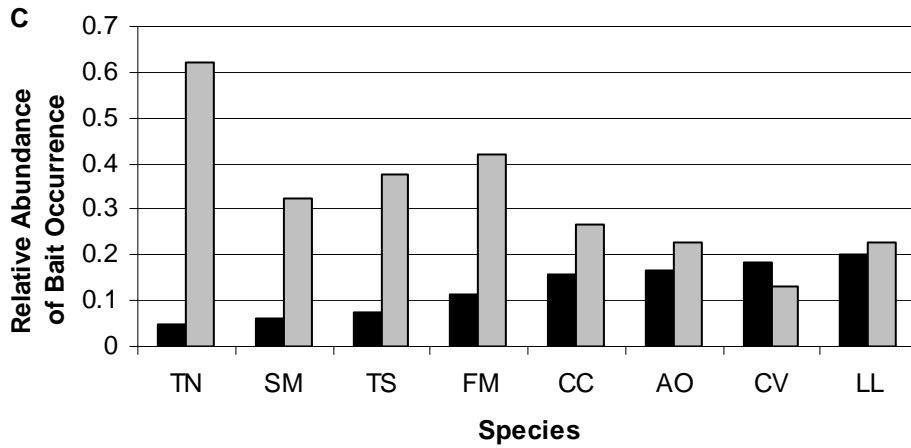
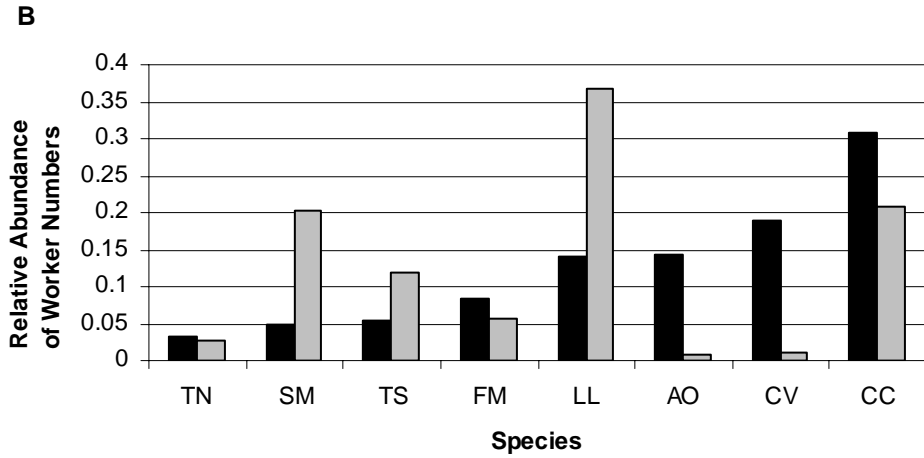
**B**



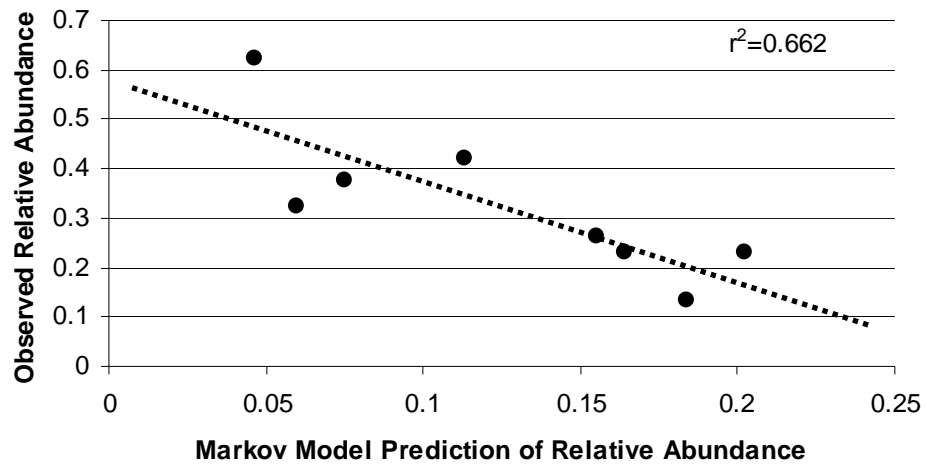


**Figure 2. 4**

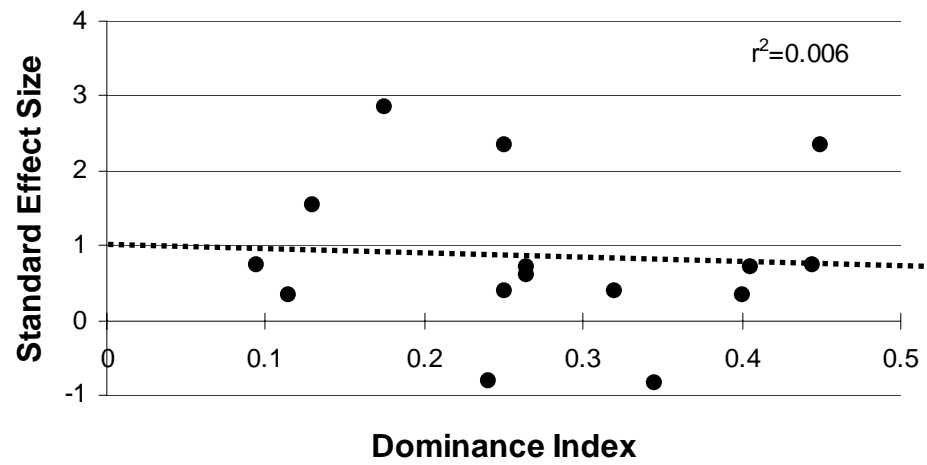




**Figure 2. 5**



**Figure 2. 6**



## Chapter 3

### **Disentangling competitive and thermal drivers of ant community structure.**

#### **Abstract**

Many areas of ant community ecology research conclude that competitive and thermal environments interact to drive ant community structure; however, no studies have manipulated these factors simultaneously and used physiological experiments to predict species response. I conducted a shade experiment to investigate how species respond to an altered thermal environment and then associated their changes in abundance to results from physiological thermal tolerance experiments. I then conducted a fully-factorial shade and removal experiment of a widespread behaviorally dominant species, *Formica moki*, to investigate if species respond directly to changes in the thermal environment or if abundance is an indirect effect of behaviorally dominant species activity. The addition of shade tables greatly reduced temperatures in the field. One species, *Temnothorax nevadensis*, consistently exhibited lower abundance in shade treatments. Decreased abundance of *T. nevadensis* in shade treatments was not an indirect effect of *F. moki*, or likely any other species activity in shade plots. Physiological thermal tolerance was strongly associated with changes in abundance in shade treatments: the lower a species thermal tolerance, the greater its positive change in abundance after shade additions. The only species with a strong foraging response to *F. moki* removal was *T. nevadensis*, a species who was often co-occurred with *F. moki* on baits. I did not find evidence for the interaction of competition and temperature, and it appears as though physiological differences strongly influence the foraging activity of Siskiyou ant communities.

## **Introduction**

Although the role of competition in structuring communities has been controversial (see reviews in (Gotelli and Graves 1996, Weiher and Keddy 1999), interference competition is widely held to exert strong control over ant communities (Hölldobler and Wilson 1990). However, a growing body of work suggests that the influence of competition may be strongly modulated by the abiotic environment, especially temperature. For example, competition may only be evident during cooler time periods which may occur either seasonally (Retana and Cerda 2000, Albrecht and Gotelli 2001) or diurnally (S. Wittman, unpublished data, Chapter 1).

The interaction between competition and temperature has been explored within several areas of ant community ecology research. This interaction is implicated in the maintenance of local diversity, as increasing temperature can switch competitive dominance hierarchies (Cerda et al. 1997) and explains temporal changes in diversity (Retana and Cerda 2000). Temperature's effect on competitive interactions is also invoked in dominance-diversity patterns on continental scales (Andersen 1992, Parr et al. 2005) in which the relative impact of dominant species is tempered by the abiotic, often thermal, environment. These continental wide patterns have led to classifications of ant functional groups (Andersen 1995, 1997), many of which relate species competitive ability and interaction with their abiotic environment (e.g. "Dominant Dolichoderinae," "Climate Specialists," etc.). The interaction of ants' competitive and thermal environments has also formed the framework which describes how ants communities respond to disturbance (Andersen 1991, York 2000, Farji-Brener et al. 2002) the success

and spread of invasive species (Holway et al. 2002, Krushelnycky et al. 2005) and management implications of agroforestry (Perfecto and Vandermeer 1996, Armbrrecht et al. 2005).

Surprisingly, very few studies have experimentally altered the thermal or competitive environment to investigate community response, and none, to my knowledge, have manipulated these factors simultaneously. Additionally, few studies have investigated how species physiological differences interact with their competitive environment to explain species abundance patterns in animal communities (Dunson and Travis 1991).

Through a shading experiment, physiological thermal tolerance experiments, and a factorial shade and species removal experiment, I address the follow questions: How does altering the thermal environment affect species foraging activity? Is there a difference in species physiological thermal tolerances, and if so, does thermal tolerance predict species response to changes in the thermal environment? Does shade or a behaviorally dominant species have a greater effect on species foraging abundance? Do competition and the thermal environment exert interactive effects upon the community?

## **Methods**

### **Study Area**

This study was conducted at a single site during June – August in 2004 and 2005 in the Siskiyou National Forest near Kerby, Oregon, USA (42.49°N, 123.78°W, elevation 430m). This area is part of the Siskiyou-Klamath ecoregion which has a Mediterranean climate, with cool winters (mean January minimum temperature = 0 °C) and warm dry

summers (mean July maximum temperature = 31.7 °C; mean annual precipitation = 154 cm, with only 4 cm falling between June and August). Forests are mostly open stands of *Pinus jeffreyi* with other sclerophyllous trees reduced to a shrub layer. Neither mean July maximum temperature nor precipitation in 2004 or 2005 differed significantly from their long-term average values.

### **Shade Experiment**

The shade experiment was conducted during June – August, 2004. Fifteen pairs of shade and no shade stations were established throughout the site in a randomized block design. Each pair was located in a relatively homogenous environment, and treatments were randomly assigned within the pair. Treatments consisted of small, table-like structures, 0.5m x 0.5m in area. Shade treatment included tarps taped to the tops of 10” metal stakes; control stations treatments were only the four metal stakes. Five meters separated the shade and control station in each pair, and blocks were separated by 15 - 25 meters.

Sampling occurred once every five weeks in a BACI design (Before-After-Control-Impact, Gotelli and Ellison 2004). The control stations were observed over all five weeks while the treatment stations were observed before (2 weeks) and after (3 weeks) shading (= “impact”) (Figure 1). Shade treatments had covers added the night before sampling and removed the morning after.

On sampling days, I set baits at 07:30 and observed 7 times throughout the day (3 morning, 1 afternoon, and 3 evening). Periods started at 08:15, 14:30, and 18:15; periods



sampled more than once were separated by 45 minutes. Baits consisted of a 3x5” laminated index cards with approximately 5 g of tuna in oil. At each sampling period I recorded the number and identity of each species and measured the soil surface temperature under and around each bait station to the nearest 0.1 °C using a Raytek® Raynger ST20 XB hand-held infrared thermometer (Santa Cruz, CA USA).

I also recorded any behavioral interactions observed while sampling the baits.

Interactions were categorized into one of two categories (*sensu* Fellers 1987): attacks and avoidances. An attack consisted of active participation of at least two individuals in which one individual either bit, chased, lunged, or used chemical warfare to cause the other individual to retreat, which most often consisted of running away. Occasionally the attack would result in a severe injury or death. Avoidance behavior occurred when one species retreated (i.e. ran off card) after making contact with another without being attacked. Species were considered dominant if it attacked or if its presence elicited avoidance behavior in another individual. I determined the dominance index of each species by calculating the percentage of times it was dominant during all instances of its attacks and avoidances (Fellers 1987).

Individual workers were collected at the end of the observation period if they could not be readily identified in the field. Phil Ward at the University of California, Davis confirmed the species identifications.

## **Thermal Tolerance**

I conducted physiological thermal tolerance experiments on all species observed during the shading experiment (Table 1). I exposed workers to slowly increasing temperatures in a heat block (VWR heat block, VWR Scientific, Univar, USA). Eight workers were placed into their own 1.5 mL microcentrifuge tube and randomly assigned to a well within the heat block. Temperature exposure began at 40°C and increased by 2° intervals to 50°C. Individuals were exposed to each temperature for 10 minutes, and the temperature was recorded when individuals died or lost permanent muscle coordination. The mean death temperature for six replicates per species was calculated. Ants were used within 4 hours of field collection.

## **Shade and Removal Experiment**

The shade and removal experiment was conducted during June – August, 2005, at the same site as the shade experiment. Because *Fomica moki* was the most widespread behaviorally dominant species which interacted with most species (Table 1), it was the focal removal species in this experiment. I first located *F. moki* nests by baiting with Pecan Sandies™ and following workers to their nest. After locating 24 nests, I randomly assigned areas around nests to one of the four treatments of the fully factorial shade X removal experiment. Shade treatments consisted of the same shade stations used in the 2004 shading experiment. Shade tarps remained in place throughout the duration of the experiment (i.e. they were not added and removed only on sampling days). *Formica moki* workers were denied access to removal stations by constructing fencing and setting separate “distraction” baits close to the nest entrance(s) (Figure 2). Once treatments

were in place I sampled a total of 7 days; each sampling day was separated by 2-3 days. I set tuna baits at 07:30 and sampled stations every hour from 08:00 until 11:00.

Three stations were removed from the analysis. Upon further observation throughout the experiment, I discovered the some nests (with multiple entrances) were designated for both a control and a removal station. Thus, I removed two control stations from the analysis because they were affected by the “distraction” baits used in the removal experiment. One removal station was eliminated because I could not adequately quarantine *F. moki* workers.

### **Analysis**

Differences in thermal tolerances were evaluated with a one-way Analysis of variance, and group differences were compared with Tukey’s HSD.

To evaluate species foraging response to the 2004 shade experiment, differences in abundance among treatment groups were evaluated with a one-way ANOVA. Shade was analyzed as fixed effect, and analyses were run separately for each week. Abundance was measured in terms of both bait occurrence and worker numbers. Bait occurrence values record the number baits visited by different species. If a species had at least one forager on a bait during the sampling period, it counted as one bait occurrence. While bait occurrence recorded the number of visited baits, worker numbers describe the accumulation of foragers on those baits. Worker numbers were log transformed to satisfy assumptions of normality. I ran analyses on abundance values for all species combined as well as separately for one species, *T. nevadensis*. *Temnothorax nevadensis* was the

only species that occurred at sufficient baits within blocks to be analyzed in the randomized block design.

To compare if species physiological tolerance were associated with their response to the shade experiment, I computed Kendall's Tau b coefficient of concordance. Species response to the shade experiment was expressed as the percent increase or decrease in worker numbers from the week I-II average to the week III-V average in the treatment plots. Because the shade experiment was administered over time, changes in abundance in the shade treatments also incorporate any natural changes in abundance over time. Changes in species abundance over time were expressed as the percent increase or decrease in worker numbers from the week I-II average to the week III-V average in the control plots. I compared the ranks of species thermal tolerance to their ranks of shade response and to their ranks of time response.

To evaluate shade and removal treatment effects on abundance, I used a two-way ANOVA with shade and removal as fixed effects. I used the same abundance metrics, bait occurrence and worker numbers, as I did in the shade experiment. I log transformed worker numbers to satisfy assumptions of normality. I performed a two-way ANOVA on bait occupancy and worker numbers for all species combined, as well as separately on *F. moki* and *T. nevadensis* log transformed worker numbers.

I used a two-factor factorial nominal logistic model to investigate *F. moki* removal and shade addition on bait occupancy. Analyses were run separately on each of the four

sampling periods and conducted on each species separately. *Crematogaster coarctata* and *L. luctuosum* were only observed at one bait station and thus were excluded from the analysis. All analyses were conducted in JMP, version 4.0.2 (SAS Institute, Cary, North Carolina, USA).

## Results

### Thermal Tolerance

The eight species differed in their mean death temperatures ( $F_{7,40}=53.87$ ,  $P<0.001$ ). Ants fell into one of four distinct groups, ranging from 44.0 to 48.1°C. *Aphaenogaster occidentalis* was the least thermally tolerant, followed by *C. vicinus*, *S. molesta* and *T. sessile*. *Formica moki* fell into the third most tolerant group. *Crematogaster coarctata*, *L. luctuosum*, and *T. nevadensis* were the most thermally tolerant (Figure 3).

### Shade Experiment

The addition of shade addition tarps dramatically reduced soil surface temperature, especially during the middle of the day (Figure 4).

Bait occupancy was not significantly different in control vs. treatment plots for any week. Worker numbers, however, were greater in treatment plots during the fourth week (mean log workers number  $\pm$  SE =  $1.34 \pm 0.14$  in control plots,  $1.77 \pm 0.13$  in shade plots;  $F_{1,14} = 5.36$ ,  $P=0.039$ ), and there was a trend for greater workers numbers in treatment plots during the final week ( $1.33 \pm 0.14$  in control plots,  $1.67 \pm 0.13$  in shade plots;  $F_{1,14} = 4.42$ ,  $P=0.057$ ).

*Temnothorax nevadensis* recruited fewer workers to treatment baits during all (week III:  $F_{1,10}=222.00$ ,  $P<0.001$ ; week IV:  $F_{1,10}=7.07$ ,  $P=0.045$ ; week V:  $F_{1,10}=7.57$ ,  $P=0.04$ ) shaded weeks. There was no difference in *T. nevadensis* abundance between control and treatment baits during the initial, unshaded two week period (week I:  $F_{1,10}=1.52$ ,  $P=0.272$ ; week II:  $F_{1,10}=0.12$ ,  $P=0.741$ ; Figure 5).

There was significant agreement of the rankings of species thermal tolerances and their response to the shade treatment ( $W = 0.714$ ,  $P = 0.024$ ) while rankings of thermal tolerance were not associated with species response in control plots over time ( $W = 0.143$ ,  $P = 0.652$ ; Figure 6).

### **Shade and Removal Experiment**

Overall, more baits were occupied in the removal treatments ( $F_{1,17} = 4.752$ ,  $P=0.043$ ) than in the controls. There were no differences in bait occupancy ( $F_{1,17} = 0.100$ ,  $P=0.757$ ) between shade and control treatments. There was no interaction of the shade and removal experiment ( $F_{1,17} = 0.002$ ,  $P=0.965$ ) on bait occupancy. Worker numbers did not differ in either the shade ( $F_{1,17} = 2.18$ ,  $P=0.158$ ) or removal ( $F_{1,17} = 2.99$ ,  $P=0.102$ ) treatments, and there was no interaction effect ( $F_{1,17} = 0.334$ ,  $P=.571$ ).

Removal treatments were successful, as fewer *F. moki* workers were present at removal baits than at control baits (mean log workers number  $\pm$  SE =  $2.22 \pm 0.39$  in control plots,  $-0.38 \pm 0.40$  in removal plots;  $F_{1,15} = 20.29$ ,  $P<0.001$ ). There was no effect of shade (mean log workers number  $\pm$  SE =  $0.69 \pm 0.36$  in control plots,  $1.41 \pm 0.42$  in shade

plots;  $F_{1,15} = 3.49$ ,  $P=0.139$ ) or treatment interaction ( $F_{1,15} = 3.48$ ,  $P=0.139$ ).

*Temnothorax nevadensis* recruited more workers to removal baits ( $F_{1,13} = 18.58$ ,  $P<0.001$ ) and fewer workers to shaded baits ( $F_{1,13} = 8.92$ ,  $P=0.015$ ; Figure 7). There was no interaction of shade and removal treatments ( $F_{1,13} = 1.22$ ,  $P=0.290$ ).

Not surprisingly, *F. moki* was less likely to occupy baits in removal plots in all periods but the first, likely because most foragers didn't find baits until the second period (Table 2). *Aphaenogaster occidentalis* was more likely to occupy baits in the shade treatment during periods one and two, and there was no removal effect. Bait occupancy by *Solenopsis molesta* was equally probable among treatments across all sampling periods. *Temnothorax nevadensis* was less likely to occupy shaded baits in the first two periods and more likely to occupy removal baits in periods two through four. Baits were more likely to be occupied by *T. sessile* in the removal treatment during periods one and three (Table 2).

## **Discussion**

Overall, these experiments provide support for the abiotic control of foraging activity in Siskiyou ant communities. The abundance of *T. nevadensis* was consistently affected by alterations to its thermal environment. *Temnothorax nevadensis* abundance decreased every week treatment baits were shaded in the 2004 shade experiment (Figure 5) as well as at shade treatments in the shade and removal experiment (Figure 7). Additionally, *T. nevadensis* was less likely to occupy baits in shaded plots (Table 2). Although *T. nevadensis* recruited more workers to removal baits (Figure 7), its decreased abundance in shade plots was not due to an indirect effect of the increased abundance of *F. moki*.

*Formica moki* is the most likely candidate because 1) during the 2004 shade experiment it was the most behaviorally dominant species to occur at the most bait stations (Table 1), 2) *T. nevadensis* interacted with *F. moki* in the majority (8/14) of its interactions (Appendix), and 3) during the shade and removal experiment all stations were placed within the foraging range of *F. moki*. However, *F. moki* abundance, while greater in shade plots, was not significantly so. Additionally, if *T. nevadensis* decreased abundance in shade plots was a result of increased *F. moki* activity, I would expect the interaction of removal and shade treatments to be significant. The interaction of removal and shade treatments was not significant for either *T. nevadensis* worker numbers (Figure 7) or bait occupancy (Table 2).

Although the decreased abundance of *T. nevadensis* at shaded baits was not due to indirect effects of *F. moki* activity, perhaps a different behaviorally dominant species was suppressing *T. nevadensis* abundance at shaded baits. The most behaviorally dominant species, *Camponotus vicinus*, *Crematogaster coarctata* and *Liometopum luctuosum*, are unlikely candidates because they occurred at few baits and interacted with few species during the 2004 shade experiment (Table 1). *Camponotus vicinus* was not observed during the shade and removal experiment, and *C. coarctata* and *L. luctuosum* only occurred at a single bait station.

Another possible candidate is *Aphaenogaster occidentalis* because during the shade and removal experiment it was more likely to occupy shaded baits while *T. nevadensis* was less likely to occupy baits during the same time periods (Table 2). However, during the



2004 shade experiment the two species only interacted once, and *T. nevadensis* was the dominant species. During the shade and removal experiment, the two species co-occurred on one of ten shaded bait stations and were never observed to interact. Thus, it is likely that *T. nevadensis* was responding directly to changes in its thermal environment.

The most striking evidence for abiotic control of species foraging activity is the concordance of species thermal tolerance rankings and their response to the shade treatments (Figure 5). Because shade treatments were administered through time, species response to shade also includes any natural changes in abundance over time. However, when the rankings of species thermal tolerance were compared to changes in abundance over time, there was no longer a significant association (Figure 5). These results are somewhat surprising, given that 1) competition interactions would be expected to alter abundances as well, 2) bait stations were only 0.25m<sup>2</sup> in area and, in most cases, did not cover ant nests (S. Wittman, unpublished data), and 3) species thermal tolerances did not vary by a large margin (~4°C). Although not uncommon to find temperature is a cue to prompt ants to leave the nest to forage (Muser et al. 2005, Azcarate et al. 2007) or that ants forage within a general thermal range (Garcia-perez et al. 1994, Cerda et al. 1997, Pol and de Casenave 2004), this is the first time that response to the thermal manipulations of ants foraging environment has been so closely tied to their physiology.

In previous studies (S. Wittman, unpublished data, Chapter 1), I found significant overlap in bait occupancy throughout the day, and species co-occurrence aggregated within

temperature intervals. However, I also found that peak foraging activity was evenly spaced, suggesting that species may be responding directly to variations in their thermal environment. Alternatively, species foraging activity may be a bi-product of their competitive and thermal environment. That is, some species may only obtain maximum activity on baits thermally distinct from those occupied by dominant species. If species were responding only to the thermal environment, then I would expect a significant treatment effect of shade and a non-significant shade X removal interaction. If foraging was determined by interactions with dominant species, and secondarily with the thermal environment, I would expect a significant shade treatment effect and a significant shade X removal interaction. Because, at least for *T. nevadensis*, the interaction of shade and removal treatments was not significant, and the community responded to shade additions in a manner so closely tied to its physiology, this study supports the hypothesis that species are responding directly to changes in their thermal environment.

Although *T. nevadensis* was the only species which exhibited decreased abundance in the presence of *F. moki*, and *T. nevadensis* and *T. sessile* were the only species more likely to occupy baits in removal plots, I cannot rule out the possibility that *F. moki* does not compete with other species observed during this study. By design, the removal experiment was conducted within the foraging areas of *F. moki*. *Crematogaster coarctata* and *L. luctuosum*, for example, were only observed at one bait station during the shade and removal experiment. Perhaps these species cannot persist within the foraging area of *F. moki*, or perhaps *C. coarctata* and *L. luctuosum* compete for nest sites

with *F. moki* during colonization. Alternatively, these species may not overlap with *F. moki* due to different abiotic requirements, i.e. due to habitat segregation.

A recent meta-analysis of natural communities with different taxa at multiple scales found that species tend to co-vary positively, not negatively, with each other, supporting a common response to abiotic factors, such as temperature and precipitation, and not competition (Houlahan et al. 2007). In open habitats, ant activity may be more influenced by temperature than by competition by dominant species (Cerda et al. 1998, Retana and Cerda 2000). In the Siskiyou Mountains, it appears as though physiological differences strongly influence the foraging activity of species, and this may underlie regular spacing of species peak foraging activity along the temperature niche axis. Although competition certainly influences ant community structure, much can be gained by “bridging the gap of physiological and community ecology” (Dunson and Travis 1991) to understand the mechanisms by which abiotic factors may drive community patterns.

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**Table 3. 1** Summary results of behavioral bait observations during the 2004 shade experiment. Entries display the number of bait stations each species visited (max=30), the total number interactions, the number of dominant behaviors exhibited during those interactions, and the number of species with which each species interacted (max=7). The dominance index is the percentage of all interactions in which a species was dominant. Abbreviations used in subsequent Tables and Figures use the first initial of the genus and species (e.g. *Formica moki* = FM).

<b>Species</b>	<b>No. Bait Stations</b>	<b>Total No. Interactions</b>	<b>No. Dominat Interactions</b>	<b>No. Species Interacted</b>	<b>Dominance Index</b>
<i>Formica moki</i>	14	18	12	6	67
<i>Temnothorax Nevadensis</i>	26	14	2	4	14
<i>Tapinoma sessile</i>	10	5	0	2	0
<i>Aphaenogaster occidentalis</i>	5	5	3	3	60
<i>Crematogaster coarctata</i>	4	5	5	2	100
<i>Solenopsis molesta</i>	9	3	2	1	67
<i>Camponotus vicinus</i>	2	1	1	1	100
<i>Liometopum luctuosum</i>	4	1	1	1	100



**Table 3. 2** Results of nominal logistic analysis on bait occurrence data collected during four separate sampling periods (08:00-11:00). Analyses were run separately for each species. *Crematogaster coarctata* and *L. luctuosum* did not occur at sufficient baits for the analysis. Significant p-values are in bold. Highlighted values indicate a greater chance of bait occupancy while boxed values indicate a lesser chance of bait occupancy in a given treatment.

Species	Period 1			Period 2			Period 3			Period 4		
	Removal	Shade	R*S	Removal	Shade	R*S	Removal	Shade	R*S	Removal	Shade	R*S
AO	0.162	<b>0.046</b>	0.162	0.167	<b>0.004</b>	0.494	1.000	1.000	0.935	0.958	0.945	0.958
CC	.	.	.	.	.	.	.	.	.	.	.	.
FM	0.570	0.767	0.932	<b>0.002</b>	1.000	1.000	<b>0.047</b>	0.999	0.999	<b>0.000</b>	0.063	0.999
LL	.	.	.	.	.	.	.	.	.	.	.	.
SM	0.328	0.328	0.394	0.098	1.000	1.000	0.098	1.000	1.000	0.345	0.262	0.206
TN	0.307	<b>0.019</b>	0.307	<b>0.034</b>	<b>0.034</b>	0.451	<b>0.046</b>	0.162	0.162	<b>0.014</b>	0.932	0.570
TS	<b>0.047</b>	0.999	0.999	0.887	0.887	0.582	<b>0.047</b>	0.999	0.999	0.098	1.000	1.000

## Figure Legends

**Figure 1.** Experimental design of 2004 shade experiment.

**Figure 2.** Shade and removal experimental field plots. Example of removal (A) and removal and shade (B) plots.

**Figure 3.** Mean death temperature of all species observed during 2004 shade experiment site. Species with the same letters are not significantly different from each other.

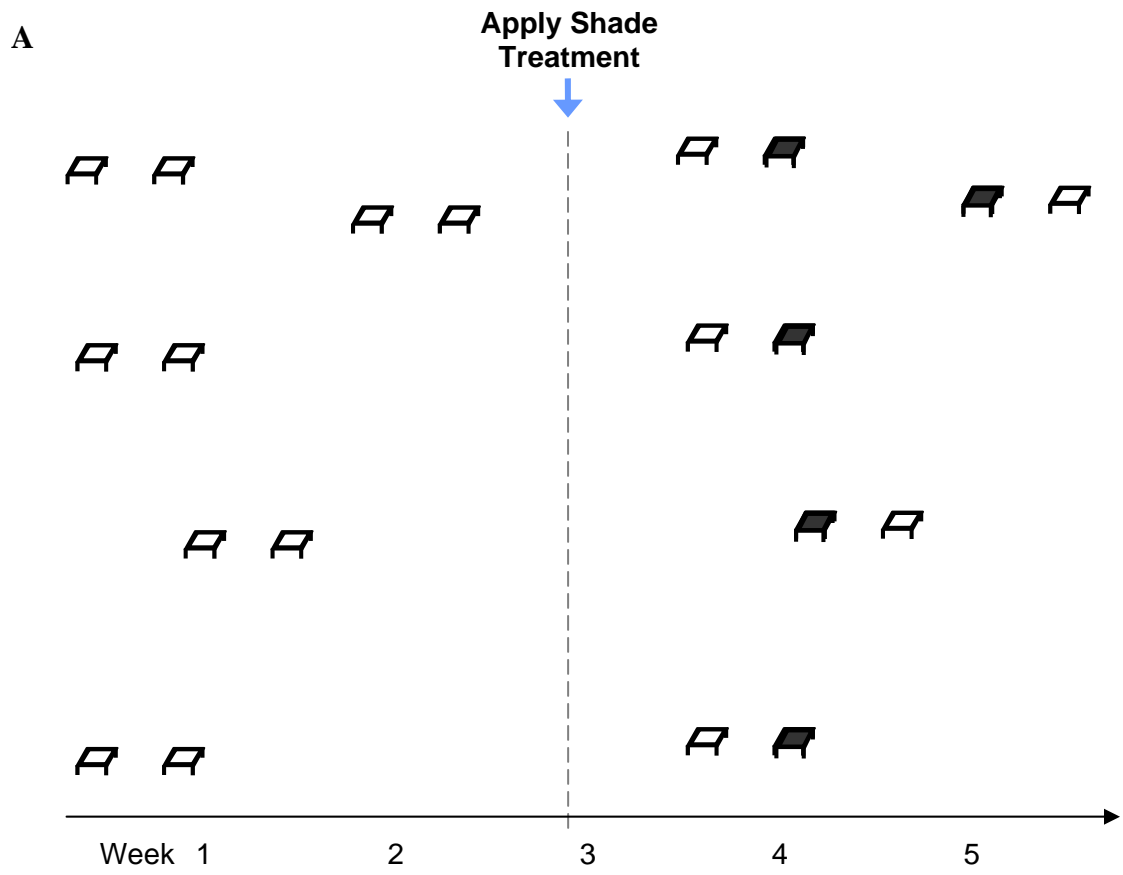
**Figure 4.** Average temperature difference inside vs. outside sampling plots. Circles denote control plots (never shaded). Squares represent treatment plots. Light markers display early week values, while darkened markers display later values when shade tarps were applied to treatment plots. The seven sampling periods (three morning, one afternoon, and three evening) are displayed.

**Figure 5.** *Temnothorax nevadensis* worker response to the shade experiment. Error bars represent standard error values. Closed symbols represent treatment baits; open symbols are control baits. Dotted, vertical line denotes application of shade treatments. Fewer workers visited shaded baits during weeks III, IV and V (\*,  $P < 0.05$ ).

**Figure 6.** Comparison of rankings of species thermal tolerance and their response to either the shade treatment or over time in the control plots. Species thermal tolerance is significantly associated with their response to shade ( $W = 0.714, P = 0.024$ ) but not with time ( $W = -0.143, P = 0.652$ ).

**Figure 7.** *Temnothorax nevadensis* worker numbers in the shade (dark markers) and no shade (light markers) treatments in areas where *F. moki* was removed and not removed. Adding shade decreased workers numbers on baits while removing *F. moki* increased *T. nevadensis* abundance.

Figure 3. 1



**Figure 3. 2**



Figure 3. 3

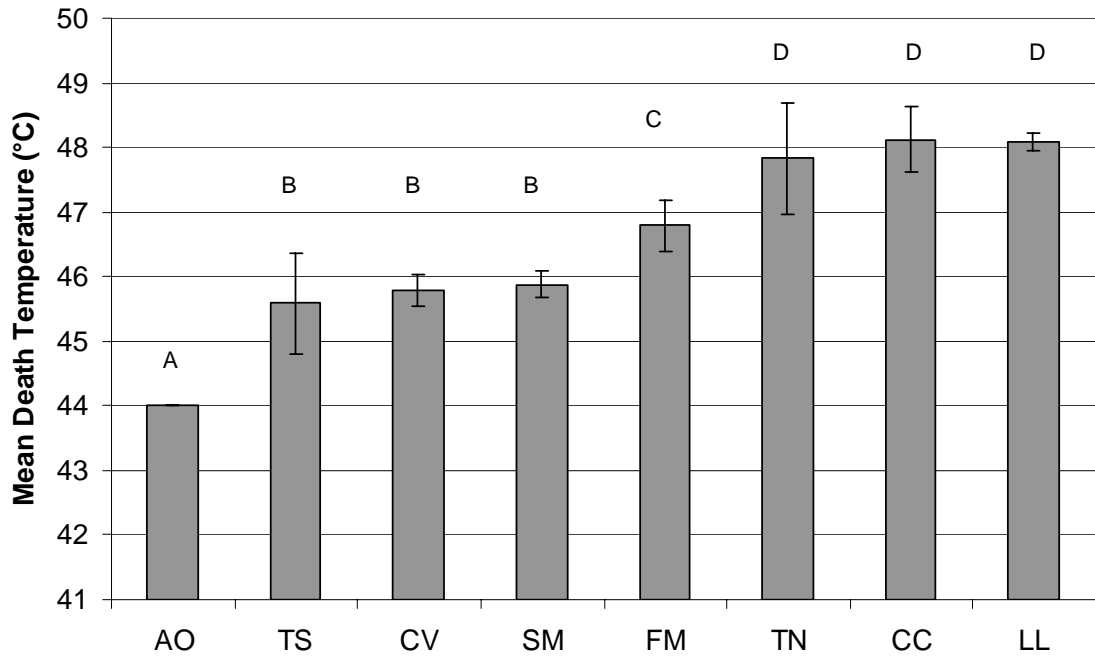
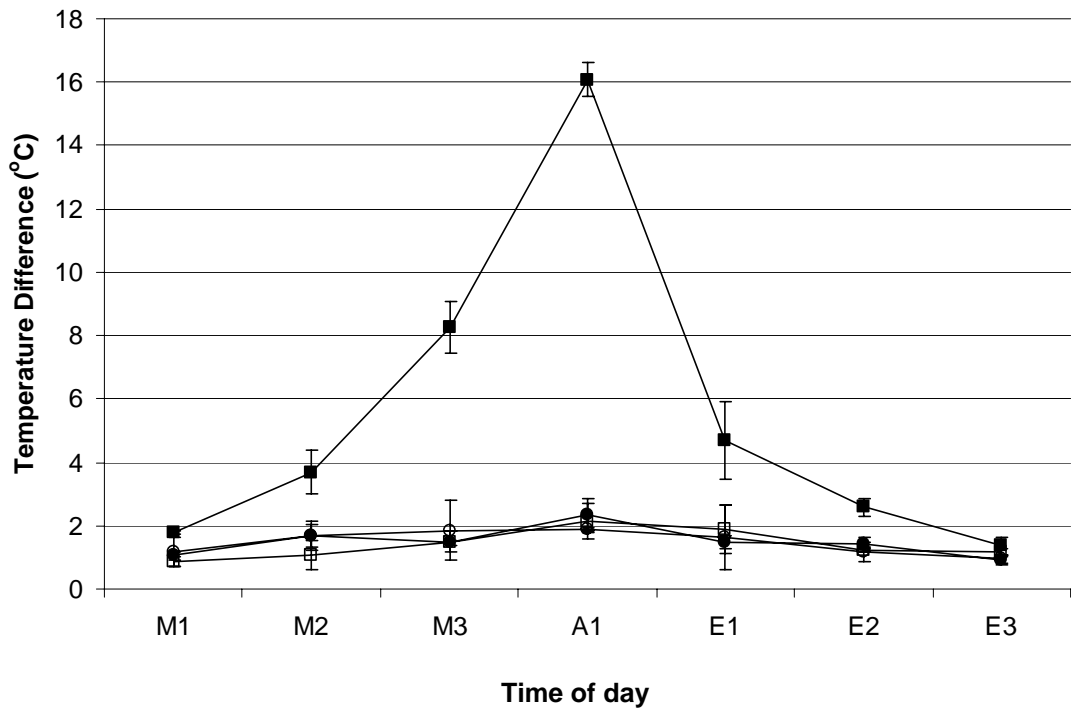
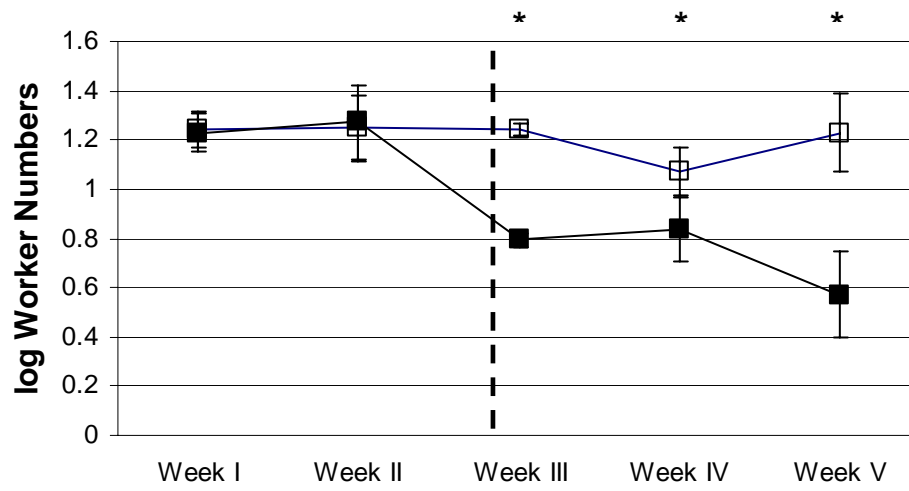


Figure 3. 4



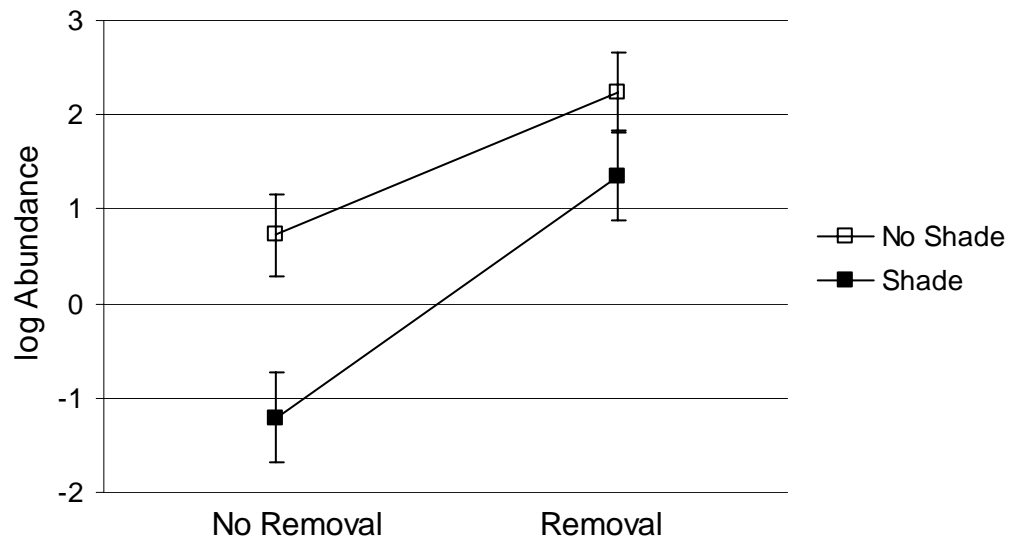
**Figure 3. 5**



**Figure 3. 6**

	<b>Shade Response</b>	<b>Thermal Tolerance</b>		<b>Thermal Tolerance</b>	<b>Time Response</b>	
greatest positive change	AO	AO	least thermally tolerant	AO	AO	greatest positive change
	SM	TS		TS	CC	
	FM	SM		SM	TN	
	TS	FM		FM	FM	
	LL	TN		TN	LL	
	TN	LL		LL	TS	
least positive change	CC	CC	most thermally tolerant	CC	SM	least positive change

**Figure 3.7**





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## Appendix A.

For each of the three sampling periods (MORN, AFTER, EVE) at each site, the worker numbers of each species are listed for each of the 25 bait stations. The three sampling periods began at 08:30 (MORN), 13:00 (AFTER) and 18:30 (EVE). Each sampling period was sampled three times (once every 30 minutes). Entries are the worker numbers of each species summed over the three sampling times within each sampling period.

Site	Period	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
023	AFTER	<i>T. sessile</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>A. occidentalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	30	0
		<i>C. coarctata</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. nevadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
		<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0







MORN	<i>T. sessile</i>	0	0	0	0	0	89	4	0	0	30	0	11	0	150	0	0	21	56	5	40	0	9	10	93	44
	<i>A. occidentalis</i>	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nevadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	5	0	0	0	1	4	0	2	11	1	0	0	0	0	0	2	1	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CDR AFTER	<i>T. sessile</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>A. occidentalis</i>	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nevadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0



	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. subelongata</i>	4	0	3	9	4	3	1	0	0	2	2	0	3	0	0	0	1	0	0	0	0	1	0	1	
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. subpolita</i>	1	7	0	0	0	0	0	0	0	0	11	0	0	11	8	0	5	0	0	6	14	4	0	7	19
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
EVE	<i>T. sessile</i>	0	11	0	166	31	47	1	104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>A. occidentalis</i>	6	1	26	0	0	0	0	0	6	52	0	0	0	0	0	0	15	87	0	0	16	0	0	0	
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. nevadensis</i>	4	3	0	3	6	0	1	0	2	1	8	0	3	1	0	0	0	3	0	0	0	1	0	0	0
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subelongata</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	<i>F. subpolita</i>	2	2	0	0	0	1	0	0	0	0	48	1	0	28	11	3	9	8	0	19	49	4	7	26	29
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MORN	<i>T. sessile</i>	0	2	0	133	5	27	0	77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>A. occidentalis</i>	0	0	1	0	1	0	0	0	1	4	0	0	0	0	0	0	2	10	0	0	16	0	0	0	
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	86	0	0	0	0	
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. nevadensis</i>	1	0	0	0	3	1	0	0	0	2	0	0	4	0	0	0	0	1	0	0	1	1	0	0	0
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	10	0	0	0	1
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
DCH AFTER	<i>T. sessile</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>A. occidentalis</i>	0	0	0	0	6	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	149	28	0	0	0	0	1	0	3	10	
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. nevadensis</i>	0	0	0	0	3	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	2
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subelongata</i>	0	0	0	0	1	1	1	1	0	0	0	0	2	7	2	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
EVE	<i>T. sessile</i>	0	0	0	0	0	9	0	0	0	0	32	0	0	0	0	2	0	0	0	0	0	0	0	0	0	
	<i>A. occidentalis</i>	0	0	30	73	11	13	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. coarctata</i>	1	26	0	0	196	0	1	0	0	0	0	29	0	25	9	252	390	22	32	22	0	20	6	71	386	
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. vicinus</i>	1	0	0	1	7	3	0	0	8	10	0	0	0	0	1	3	0	0	2	0	0	9	2	0	1	
	<i>T. nevadensis</i>	6	7	1	0	1	1	0	15	0	0	1	10	8	4	9	0	1	1	8	2	1	0	0	8	0	
	<i>T. nitens</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	













		<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. subelongata</i>	0	0	2	1	1	0	0	0	0	0	0	0	0	2	2	0	3	6	0	0	0	0
		<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SHT	AFTER	<i>T. sessile</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	12	2
		<i>A. occidentalis</i>	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. nevadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0
		<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. subelongata</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0







	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MORN	<i>T. sessile</i>	0	1	0	2	65	0	0	0	0	0	0	0	0	21	0	0	0	0	0	3	17	34	87
	<i>A. occidentalis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nevadensis</i>	0	0	0	2	0	0	0	1	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0
	<i>T. nitens</i>	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. moki</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DGF AFTER	<i>T. sessile</i>	0	0	43	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	3	0

	<i>A. occidentalis</i>	0	2	2	2	0	0	0	1	0	0	14	0	0	0	0	0	0	0	0	0	0	3	0		
	<i>C. coarctata</i>	2	0	0	0	0	3	7	29	27	0	0	63	46	0	18	124	47	0	50	74	70	116	51	17	48
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nevadensis</i>	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	4	7	0	0	0	0	7	0	0
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	2	13	1	2	2	0	0	0	0	14	5	0	1	7	0	0	0	1	0	5	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EVE	<i>T. sessile</i>	78	0	5	0	0	0	1	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>A. occidentalis</i>	0	7	29	8	4	16	8	14	0	0	12	0	0	48	16	24	0	24	0	0	2	0	0	0	0
	<i>C. coarctata</i>	0	0	0	0	0	194	1	84	25	10	47	65	135	0	16	171	85	0	28	65	40	175	60	37	220
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	1	4	4	1	21	0	0	0	0	0	0	1	0	0	0	0	0	2	0	11	6	0	
	<i>T. nevadensis</i>	0	0	0	1	5	0	8	1	0	0	1	0	0	3	5	0	4	7	2	1	0	0	3	1	3
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0











	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
EVE	<i>T. sessile</i>	18	67	290	0	10	5	0	0	80	4	48	26	12	0	251	0	18	61	32	50	43	17	3	140	629
	<i>A. occidentalis</i>	0	70	0	56	229	64	0	27	0	0	0	0	7	9	0	168	2	0	0	0	3	18	133	0	0
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
	<i>T. nevadensis</i>	71	13	22	0	0	9	48	13	7	22	12	21	24	32	3	1	27	53	9	4	4	5	0	2	0
	<i>T. nitens</i>	0	0	4	0	0	4	1	1	0	8	0	2	0	2	0	0	3	1	1	1	0	1	0	2	6
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MORN	<i>T. sessile</i>	25	0	0	1	15	0	0	0	19	2	40	10	0	0	61	0	0	0	125	59	14	108	0	60	0
	<i>A. occidentalis</i>	0	37	0	13	5	10	0	17	0	0	0	0	11	0	0	19	0	0	0	0	0	12	147	0	0
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	<i>T.nevadensis</i>	8	6	2	1	4	8	2	3	16	12	3	20	7	11	3	0	1	26	4	4	2	0	1	0	12
	<i>T. nitens</i>	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	0	0	0	3	8	1	0	0	0	1	0	17	1	0	2	0	0	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F.accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LM2	AFTER	<i>T. sessile</i>	0	0	0	0	0	0	0	0	0	0	9	0	0	2	0	0	0	0	0	0	0	0	0	0
		<i>A. occidentalis</i>	0	0	9	4	0	0	0	8	0	0	0	0	9	19	4	1	0	1	0	0	4	2	0	7
		<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>C. vicinus</i>	0	0	0	2	19	1	0	0	0	0	0	0	0	0	0	7	3	0	1	1	6	0	1	1
		<i>T.nevadensis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. nitens</i>	0	0	6	1	2	1	1	0	0	0	4	4	0	0	2	0	0	0	0	5	3	0	0	4
		<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	<i>F. subelongata</i>	1	0	1	2	1	2	2	0	0	0	0	1	3	3	0	0	0	0	0	7	5	1	2	2	
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	1	0	0	7	0	0	0	
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
EVE	<i>T. sessile</i>	1	0	5	0	3	0	0	0	0	0	0	2	0	4	0	0	0	0	0	0	0	1	0	0	
	<i>A. occidentalis</i>	0	0	3	6	0	3	0	0	1	0	1	0	0	1	0	0	0	3	0	1	0	1	1	0	
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>P. imparis</i>	0	0	0	0	0	0	3	0	0	0	0	17	0	0	3	0	0	0	0	1	0	1	0	0	
	<i>C. vicinus</i>	6	2	5	68	12	10	8	6	6	3	6	0	0	4	10	3	0	2	0	0	8	8	3	1	9
	<i>T. nevadensis</i>	29	15	6	0	2	7	4	8	1	1	9	0	0	0	3	10	2	1	0	2	0	0	0	7	9
	<i>T. nitens</i>	3	2	25	1	0	0	0	0	0	3	0	3	6	6	1	1	1	1	0	1	8	1	0	0	1
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	68	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subelongata</i>	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	4	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0





	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
MORN	<i>T. sessile</i>	22	0	0	110	0	2	0	0	0	0	0	0	1	168	188	3	161	0	37	62	14	0	3	458
	<i>A. occidentalis</i>	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nevadensis</i>	2	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	1	0	0	0	0	2	0	0	0	17	0	0	0	0	0	0	0	7	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0



SSD AFTER	<i>T. sessile</i>	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	72	0	0	0	0	0		
	<i>A. occidentalis</i>	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	2	0	0	11	1	0	0	
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. vicinus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	
	<i>T. nevadensis</i>	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
EVE	<i>T. sessile</i>	0	0	7	18	2	31	3	12	5	20	0	0	0	7	0	0	7	0	1	28	0	2	0	0	0
	<i>A. occidentalis</i>	0	0	0	2	53	6	56	0	0	0	0	0	13	1	49	19	9	1	0	0	0	22	21	1	0
	<i>C. coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	1	1	3	0	0	0	2	3	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
	<i>T. nevadensis</i>	0	0	0	0	2	0	0	0	0	0	0	4	2	1	3	4	1	1	0	0	1	1	1	4	16
	<i>T. nitens</i>	0	0	0	1	0	0	0	0	0	0	0	4	1	0	1	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0







	<i>L. occidentale</i>	0	0	0	0	0	0	0	7	0	0	70	5	10	1	11	65	10	2	14	130	168	44	2	3	13
	<i>F. moki</i>	0	0	1	0	5	0	0	2	0	2	1	1	0	0	1	0	0	0	5	5	1	8	3	4	12
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. accreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subpolita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>S. molesta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. neogates</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. laevigatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WHY AFTER	<i>T. sessile</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>A. occidentalis</i>	0	1	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. coarctata</i>	124	0	0	0	2	7	0	0	0	0	162	0	0	0	0	0	0	0	25	28	28	23	47	0	0
	<i>P. imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. vicinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nevadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. nitens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rudis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. lasiodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>B. depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. occidentale</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. moki</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. sp</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. subelongata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. rugatulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>T. sp. Ca-03</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>C. essigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>F. argentea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>L. pallitaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0





## Appendix B.

Summary tables for each unique species combination found at the local site (SE). Each table records the total number of attacks, total number of retreats, the number of attacks which resulted in a retreat, the total number of non-retreats, and the total number of encounters of the species pair. Entries are summed over the 10 replicate trials for each species pair. Species abbreviations: *Aphaenogaster occidentalis* (AO), *Camponotus vicinus* (CV), *Crematogaster coarctata* (CC), *Formica moki* (FM), *Liometopum luctuosum* (LL), *Tapinoma sessile* (TS), *Temnothorax nevadensis* (TN), *Solenopsis molesta* (SM).

	<u>AO</u>	<u>CV</u>	<u>AO</u>	<u>CC</u>	<u>AO</u>	<u>FM</u>
# ATTACKS	0	23	0	0	0	0
# RETREATS	27	25	12	4	34	46
# ATT -> RET	0	7	0	0	0	0
# NON-RETREATS	80	82	58	66	90	78
TOTAL # ENCOUNTERS	107		70		124	
	<u>AO</u>	<u>LL</u>	<u>AO</u>	<u>TN</u>	<u>AO</u>	<u>SM</u>
# ATTACKS	0	20	2	0	34	7
# RETREATS	46	57	2	30	5	29
# ATT -> RET	0	16	0	0	27	1
# NON-RETREATS	83	72	64	36	53	29
TOTAL # ENCOUNTERS	129		66		58	
	<u>AO</u>	<u>TS</u>	<u>CV</u>	<u>CC</u>	<u>CV</u>	<u>FM</u>
# ATTACKS	0	0	3	11	58	19
# RETREATS	17	28	15	18	13	44
# ATT -> RET	0	0	1	5	9	0
# NON-RETREATS	73	62	65	62	159	128
TOTAL # ENCOUNTERS	90		80		172	
	<u>CV</u>	<u>LL</u>	<u>CV</u>	<u>TN</u>	<u>CV</u>	<u>SM</u>
# ATTACKS	50	65	25	0	76	0
# RETREATS	74	46	2	32	0	24
# ATT -> RET	16	38	50	0	26	0
# NON-RETREATS	113	141	50	0	26	0
TOTAL INXS # ENCOUNTERS	187		63		41	
	<u>CV</u>	<u>TS</u>	<u>CC</u>	<u>FM</u>	<u>CC</u>	<u>LL</u>
# ATTACKS	2	0	0	0	64	24
# RETREATS	1	10	3	7	2	43
# ATT -> RET	0	0	0	0	27	0
# NON-RETREATS	45	36	50	46	83	42
TOTAL # ENCOUNTERS	46		53		85	



	<u>CC</u>	<u>TN</u>	<u>CC</u>	<u>SM</u>	<u>FM</u>	<u>LL</u>
# ATTACKS	10	0	6	0	2	40
# RETREATS	0	23	0	16	89	47
# ATT -> RET	6	0	6	0	1	24
# NON-RETREATS	46	23	26	10	64	106
TOTAL # ENCOUNTERS		46		26		153

	<u>FM</u>	<u>TN</u>	<u>FM</u>	<u>SM</u>	<u>FM</u>	<u>TS</u>
# ATTACKS	2	0	3	3	7	0
# RETREATS	9	14	9	1	36	37
# ATT -> RET	0	0	0	2	7	0
# NON-RETREATS	80	75	52	60	71	70
TOTAL # ENCOUNTERS		89		61		107

	<u>CC</u>	<u>TS</u>	<u>LL</u>	<u>TN</u>	<u>LL</u>	<u>SM</u>
# ATTACKS	1	0	37	3	11	2
# RETREATS	0	39	35	55	45	15
# ATT -> RET	0	0	88	0	71	0
# NON-RETREATS	74	35				
TOTAL # ENCOUNTERS		74		71		65

	<u>LL</u>	<u>TS</u>	<u>TS</u>	<u>TN</u>	<u>TN</u>	<u>SM</u>
# ATTACKS	53	11	0	0	6	0
# RETREATS	21	52	1	14	10	6
# ATT -> RET	37	0	0	0	5	0
# NON-RETREATS	69	38	41	28	33	37
TOTAL # ENCOUNTERS		90		42		43

	<u>SM</u>	<u>TS</u>
# ATTACKS	1	10
# RETREATS	5	1
# ATT -> RET	0	3
# NON-RETREATS	45	49
TOTAL # ENCOUNTERS		50

## Appendix C.

List of all behavioral interactions observed during the 2004 shade experiment. Observations were categorized into one of two categories: attacks and avoidances (sensu Fellers 1987). An attack consisted of active participation of at least two individuals in which one individual either bit, chased, lunged, or used chemical warfare to cause the other individual to retreat, which most often consisted of running away. Occasionally the attack would result in a severe injury or death. Avoidance behavior occurred when one species retreated (i.e. ran off card) after making contact with another without being attacked. Species were considered dominant if it attacked or if its presence elicited avoidance behavior in another individual.

Behavior	
Dominance	Avoidance
AO	FM
AO	TS
AO	TS
CC	FM
CC	FM
CC	FM
CC	TN
CC	TN
CV	FM
FM	AO
FM	TN
FM	TN
FM	TN
FM	TN
FM	TN
FM	TN
FM	TN
FM	TN
FM	TS
FM	TS
FM	TS
LL	FM
SM	TN
SM	TN
TN	AO
TN	SM