

TEMPERATURE, PREDATION RISK AND GRASSHOPPER BEHAVIOR

BIOS 569—Field Practicum in Environmental Biology

Molly Chambers

Wheaton College, Wheaton, IL 60187

Angela Laws

UNDERC 2003

ABSTRACT

A field experiment was conducted on an old-field at the University of Notre Dame Environmental Research Center in Gogebic Co., Michigan to study the effects of temperature and predation risk on the behavior of the grasshopper *Camnula pellucida*. Temperature was manipulated by shading enclosures for 4 or 6 hours in the morning, covering with plastic for a greenhouse effect for 2, 4, or 6 hours of the morning, or leaving untreated. Wolf spiders (*Lycosa spp.*) were added to half of the enclosures as predators. Increased temperature, within the range experienced during the experiment, had a positive effect on the proportion of grasshoppers visible, feeding, and active (moving or feeding) as shown by increases on warmer days, during warmer times of days and in warmer thermal treatments. Spider presence decreased visibility (an index of activity) and activity, but had no significant effect on feeding. Differences of spider effect in different thermal conditions were unclear and will require more study.

INTRODUCTION

As ectotherms, grasshoppers are dependent on thermal conditions and must behaviorally thermoregulate to maintain a suitable body temperature for activity and survival (Pitt 1999). Warmer conditions, relative to colder temperatures, have been shown to increase feeding time, leading to increased survival, while shade can limit grasshopper feeding time (Ritchie 2000, Chase 1996, Laws and Pendergast, unpublished data). Most grasshopper species are unable to feed at temperatures below 15°C, are killed by temperatures above 45°C and do the best between 35 and 42°C (Pitt 1999).

Prey species of all kinds must detect and respond to predation risk, changing activity, feeding behavior and habitat use to avoid being preyed upon, creating a pathway for non-lethal yet significant effects on food web dynamics (Lima 1998, Lima and Dill 1990). Grasshoppers respond to predation risk with changes in activity, diet (Schmitz et al. 1997, Schmitz and Suttle 2001, Belovsky and Slade 1993) and habitat use (e.g. height in vegetation at which grasshoppers spend more time, Pitt 1999). Birds, reptiles and mammals present predation risk for grasshoppers, but so do smaller predators like spiders (Pitt 1999). Spiders pose the greatest risk for nymphs, inducing diet and activity shifts in addition to higher mortality from direct predation (Belovsky and Slade, 1993, Schmitz et al. 1997, Schmitz and Suttle 2001). Increased risk to nymphs is due to the fact that the ability of a predatory spider to capture and consume a grasshopper is at least partially dependent on relative size, with spiders generally being able to capture grasshoppers of equal or lesser size (Schmitz et al. 1997, Schmitz 1993, Chase 1996, Schmitz 1994). This usually results in grasshoppers being vulnerable as nymphs, but not adults. According to Belovsky and Slade (1993) spiders must have an abdominal diameter greater than 5mm in order to be considered a predator of grasshoppers.

Trophic cascades, such as a predatory spider having a positive effect on vegetation by reducing the amount that grasshoppers consume, are possible in plant-grasshopper-spider systems (i.e. spiders are capable of inducing a trophic cascade, Schmitz 1994), but only when the system is under top-down controlled (Schmitz et al. 1997) and not in bottom-up (resource limited) systems. Trophic cascades can occur either because the density of the herbivorous prey species is lowered or because of behavior changes that reduce the amount of time spent feeding (Schmitz et al. 1997), and it is the potential for trait-mediated trophic cascades in spider-grasshopper-plant systems that gives reason for this study of behavior. Change in grasshopper behavior in the presence of a predator has the potential to induce a trophic cascade. Such has been shown by rendering the predator incapable of killing the grasshopper (Schmitz et al. 1997) and by observing a trophic cascade in which predation was compensatory (Schmitz 1998). In other cases the direct or indirect effect depends on the kind of spider. Schmitz and Suttle (2001), for example, found that sit and wait and sit and pursue spiders affected behavior, but active hunting spiders only affected density. The same study showed a shift from feeding on grass to herbs with some spiders, but not with small active spiders.

The effects of predators and thermal conditions on grasshopper behavior are not independent, as behavioral decisions to pursue favorable thermal and foraging conditions may conflict with the pursuit of continued life and trade-off decisions must be made (Lima and Dill 1990). Schmitz et al. (1997) found that under predation risk grasshoppers compressed the bulk of their activity to the middle of the day (1000-1300) when it is warmest and spiders are less active. Studies by Chase (1996) involving comparisons of shaded and unshaded conditions with and without spiders revealed that spiders are not affected by shade (behavior-wise) and shading grasshoppers under threat of predation together can reduce grasshopper density and time spent feeding.

This study sought to answer the question of how grasshopper behavior is affected by thermal conditions and predation risk from hunting spiders. The following 3 hypotheses were to be tested: (1) increased temperature leads to an increase in the time grasshoppers spend feeding or active until the temperature is too high for grasshopper activity at which point feeding time will decrease, (2) spider presence has a negative effect on grasshopper feeding and activity time, and (3) increased temperature has a positive effect on grasshopper feeding and activity time in the presence of a spider predator as the amount of time during the day warm enough for grasshoppers to eat and hot enough to decrease spider activity increases.

MATERIALS AND METHODS

Field Studies

Experiments to determine the effects of temperature and predation risk on grasshopper feeding time and behavior were conducted in enclosures at an old field at the University of Notre Dame Environmental Research Center in Gogebic Co., Michigan. Vegetation on the field consisted of a variety of grasses including *Phleum pratense* and forbs including *Chrysanthemum leucanthemum* and *Rudbeckia birta*. The enclosures were made of aluminum screening anchored with a buried metal base and wood stakes at the corners. The enclosures cover 0.5 m² of natural vegetation (for complete documentation see Belovsky and Slade 1993) and are separated by 1-2 m. Nymphs of the grasshopper *Camnula pellucida* were collected and 10 were and put in each enclosure at a 3:2 male to female ratio (6 males, 4 females).

Temperature was decreased by covering enclosures for 4 or 6 hours (starting at 0700) with 80% shade cloth on 2 sides to block morning sun or increased by covering for 2, 4, or 6 hours (starting at 0700) with plastic for a greenhouse effect. The controls were not covered with either material. Treatments will be referred to by their numbers, which are assigned in order of increasing thermal intensity (1: 6 hours shade, 2: 4 hours shade, 3: control, 4: 2 hours greenhouse, 5: 4 hours greenhouse, 6:6 hours greenhouse).

Wolf spiders (*Lycosa spp.*) were added to 4 enclosures of each thermal condition at a density of 1 per cage (2/m²) while another 4 enclosures for each thermal condition were left without spiders and serve as a control for spider effect.

Observations of grasshoppers were made for 3 enclosures for each thermal and predator treatment. During observation each enclosure was observed 3 times each hour between 0700 and 1600 and observed for 2 minutes. Activities of the visible grasshoppers were recorded (feeding, not moving on screen, moving on screen, not moving on vegetation or moving on vegetation, similar to feeding/moving/motionless categories of Chase 1996 and Schmitz and Suttle 2001). Grasshoppers on the leaf litter or ground, when exposed, were considered to be on the vegetation. In order to get the most accurate estimate of undisturbed behavior possible, the behavior of the easily visible grasshoppers on the screen was recorded as the observer approached (before disturbing them with human presence) but it was the behavior at the end of the 2 minute interval that was recorded for all other grasshoppers so that disturbed grasshoppers would have a chance to resume their activity. Chase (1996) has determined that the observer has little impact on grasshopper behavior. Each full observation required 4 observer days (9 cages per observer per day), so temperature data was collected from a weather station (temperature measured every 15 minutes) at the site so that ambient temperature could be compared between days. The temperature inside the enclosures of the different thermal treatments was also measured 1-3 times per hour on observation days. A partial observation (all spider-free and half of the with-spider enclosures) was done by one observer on June 25-27 and a full observation was done by 2 observers on July 12-13.

Analysis

Before other analyses were done, field temperatures were compared between observation days and enclosure temperatures were analyzed using an analysis of variance (ANOVA) followed by a Tukey post-hoc test to determine if multiple days of an observation could be pooled and if treatment was affecting cage temperature. Behavior was considered in terms of visibility (grasshoppers active enough to be seen by observer), activity (feeding and moving combined), and feeding, each as an arcsine square root transformed ratio (of number alive in cage for visibility or of the number visible for feeding and active). General linear model (GLM) analyses of feeding and general activity (feeding and moving on screen or vegetation combined) were done on arcsine square root transformed proportions of visible grasshoppers that were feeding or active. The number of grasshoppers visible as well as the arcsine square root transformed proportion of living grasshoppers that were visible were also analyzed using a GLM. Analyses of proportions feeding, active, and visible tested the effects of temperature (day and thermal treatment), time (through day) and predation risk (spider versus no spider). Spiders were observed during behavior observations in some cages that were supposed to be no-spider cages (were not necessarily *Lycosa spp.* and not necessarily capable of preying upon or causing a perceived predation risk for *C. pellucida*, but were out of place nonetheless), so those cages were not included in the analyses in which spider was a factor. At some times of day no grasshoppers were visible in some cages. These cages were excluded from behavior (feeding and active) analysis but included in analysis of visible grasshoppers. Some temperature data was analyzed by graphing in excel and all other analysis was done on SYSTAT.

RESULTS

Temperature

During observation 1 the field temperature differed between the days with the first day being an average 10.9°C warmer than days 2 and 3 ($p < 0.0005$), but days 2 and 3 were the same (averaged 16.0°C and 16.3°C, $F = 0.161$, $df = 1$, $p = 0.689$, Fig. 1). The temperatures inside the enclosures of different thermal treatments were significantly different ($p < 0.0005$), but this is because different assortments of treatments were observed on different days (Fig. 2 a,b). On day 1 there was no significant difference between temperature treatments ($F = 1.47$, $df = 3$, $p = 0.239$). Nor was there a significant difference in enclosure temperature between treatments on day 2 ($F = 1.69$, $df = 3$, $p = 0.186$). On day 3, however, temperature was different between the treatments ($F = 2.663$, $df = 4$, $p = 0.042$) with the greenhouse (increased) treatments being warmer than the shade (decreased temperature) and control treatments. All cages observed on days 1 and 2 were non-spider treatments and since treatment did not have an effect those days all thermal treatments were pooled within each day and day 1 (warmer) was compared to day 2 (cooler) with day considered a thermal treatment.

During observation 2 the ambient temperature was (mean \pm 1SD) 22.57 \pm 3.28 °C on day 1 and 24.54 \pm 3.28 °C on day 2, so the days were pooled (Fig. 3). Treatment had an effect on enclosure temperature during this observation ($F = 4.815$, $df = 5$, $p < 0.0005$) with treatments 5 and 6 being warmer than 1 and 2 (5:1 $p = 0.006$, 5:2 $p = 0.050$, 6:1 $p = 0.004$, 6:2 $p = 0.036$, all others $p > 0.05$, Fig 4). The effects of the treatments on temperature were only significant while the treatments were on the cages, creating a temperature difference from 0800 until 1300 ($p < 0.019$ 8:00 through 12:00 hours, $p > 0.149$ elsewhere, Fig. 4b). Although the temperature within the cages did not differ between days ($F = 1.787$, $df = 1$, $p = 0.183$), adding treatment to an analysis of cage temperature between days yielded a difference between days ($F = 7.489$, $df = 1$, $p = 0.007$), but treatment was more significant ($p < 0.0005$) and from Fig. 4a it is clear that the difference was because of the higher temperature in treatment

6 on day 2 relative to day 1 (post hoc test could not be done because of a lack of statistical power).

When temperature data from the two observations are combined (Fig. 5) it is clear that days 2 and 3 were cooler (ambient temperature) than days 1, 4 and 5 (observation 2 days 1 and 2 renamed 4 and 5 respectively). Behavior analysis of all days combined therefore involved “day” as a variable so that those differences would be accounted for in the models. Temperatures within the cages were different between days ($F=96.486$, $df=4$, $p<0.0005$) with days 1, 4 and 5 being warmer than days 2 and 3, thermal treatments ($F=13.849$, $df=5$, $p<0.0005$) with treatments 5 and 6 being warmer in the morning than the other treatments, and hours ($F=122.249$, $df=1$, $p<0.0005$, Fig. 6 a,b), changing with the field temperature through the day.

Behavior

Observation 1

During observation 1 visibility differed between the days ($F=175.486$, $df=2$, $p<0.0005$) with day 1 yielding higher visibility than days 2 or 3 (Fig. 7). More specifically more grasshoppers were visible on day 1, which was warmer than day 2 ($F=693.611$, $df=1$, $p<0.0005$, day 3 was not included in this analysis because different temperature treatments could not be pooled). Time spent feeding was not significant between the days ($F=0.437$, $df=2$, $p=0.646$) but activity was significantly higher on day 1 than on day 2 ($F=199.690$, $df=1$, $p<0.0005$, Figs. 8 and 9).

Observation 2

During observation 2 the proportion of living grasshoppers that could be seen was negatively affected by spider presence ($F=8.314$, $df=1$, $p=0.004$). Thermal treatment, time of day, and the treatment/spider interaction were all significant to the proportion of living grasshoppers visible (treatment: $F=4.365$, $df=5$, $p=0.001$, time: $F=219.998$, $df=1$, $p<0.0005$, treatment/spider: $F=4.839$, $df=5$, $p<0.0005$). Visibility increased for the first few hours of the day (Fig. 10a) and was lower in the greenhouse treatments than in the shade conditions (Fig. 10). Variation in grasshopper visibility among the thermal treatments in the presence of a spider can be seen in figure 10b (see discussion on visibility). Activity was negatively affected by spider presence ($F=5.99$, $df=1$, $p=0.015$), and activity changed over time ($F=16.62$, $df=1$, $p<0.0005$) and differed between treatments ($F=3.01$, $df=5$, $p=0.011$, Figs. 10, 11, and 12). The interaction of thermal treatment and spider presence was marginally significant ($F=2.01$, $df=5$, $p=0.075$), suggesting that the effect of spider presence on grasshopper activity may change between thermal conditions. Feeding was not significantly affected by spider presence ($F=1.48$, $df=1$, $p=0.224$) or time of day ($F=0.65$, $df=1$, $p=0.418$), but was affected by thermal treatment ($F=3.63$, $df=5$, $p=0.003$) with feeding tending to be higher in treatment 6 than in 4 or 2. The treatment/spider interaction was not significant for feeding ($F=1.53$, $df=5$, $p=0.176$).

Observations Combined

Overall treatment significantly affected the proportion of grasshoppers that were visible to the observer ($F=7.040$, $df=5$, $p<0.0005$) as did time of day ($F=392.856$, $df=1$, $p<0.0005$), day ($F=32.770$, $df=4$, $p<0.0005$) and spider presence ($F=17.376$, $df=1$, $p<0.0005$). Visibility was highest in control and shade conditions and decreased with increased greenhouse treatment, increased through the morning and leveled off midday, and was decreased in the presence of a predator. The raw number of grasshoppers visible was greatest on day 1, then 3, and least on days 2, 4 and 5, while the proportion visible was greatest on day 1, lowest on day 2, and increased through day 5 (Fig. 13). All treatment, spider and time interactions were significant for the proportion visible ($p\leq 0.003$) as well as number visible

($p \leq 0.002$) except for spider/time ($p = 0.497$, Fig. 14 a,b). Activity was affected by treatment ($F = 3.706$, $df = 5$, $p = 0.002$), spider ($F = 4.572$, $df = 1$, $p = 0.033$), time ($F = 16.651$, $df = 1$, $p < 0.0005$) and observation day ($F = 48.404$, $df = 4$, $p < 0.0005$). Thermal treatments 3 and 6 resulted in more activity than treatments 1 and 2, spiders decreased grasshopper activity, activity increased from 0700 to 1100 and leveled off for the rest of the day, and activity was greater in days 1, 4 and 5 than in days 2 and 3. Within each treatment, spider was only significant in the control (no shade or greenhouse, $F = 5.937$, $df = 1$, $p = 0.016$; $F = 7.837$), where activity was decreased in the presence of a spider. Time was significant in shade and control treatments ($p \leq 0.022$), but not in sun treatments ($p \geq 0.511$, Fig. 15 a,b). Feeding was affected by treatment ($F = 4.937$, $df = 5$, $p < 0.0005$) with more feeding in condition 6 than in 4 or 2, and by day ($F = 5.474$, $df = 4$, $p < 0.0005$) with the most feeding observed on days 4 and 5, the least on day 1, and intermediate feeding on days 2 and 3 (Fig. 16). Thermal treatment and spider effects interacted ($F = 2.859$, $df = 5$, $p = 0.014$) as did treatment, spider and time ($F = 2.388$, $df = 5$, $p = 0.036$). Within thermal treatments time was significant to feeding in treatment 2 ($F = 7.222$, $df = 1$, $p = 0.008$) and 6 ($F = 8.075$, $df = 1$, $p = 0.005$), and the time/spider interaction was significant or nearly so in treatments 3 ($F = 3.171$, $df = 1$, $p = 0.077$) and 6 ($F = 10.414$, $df = 1$, $p = 0.002$). Days were significant to treatment 6 ($F = 8.781$, $df = 2$, $p < 0.0005$) with day 4 higher than days 2 and 5 (Fig. 17 a,b).

DISCUSSION

The point of this study was to determine the effects of spiders and thermal conditions on grasshopper behavior, especially time spent feeding. Actually seeing a grasshopper eating was relatively rare because grasshoppers in the dense vegetation are difficult to see and the most visible grasshoppers are those moving or sunning in prominent places. Visibility and activity (feeding plus moving on screen or vegetation) were therefore the most viable options for getting a view of the effects of predators and temperature on grasshopper behavior. Proportions feeding would be the most desirable index of activity as it is directly related to the grasshoppers' fitness (survival and reproduction), but feeding was not observed commonly enough to compare temperature and spider treatments efficiently. Activity would probably be the next best index since moving grasshoppers are more likely than still grasshoppers to consume vegetation since both activity and feeding are limited by temperature and grasshoppers hiding from predators do best to remain still. The number or proportion of visible grasshoppers is probably even less dependable because it pools grasshoppers known to be active with those known to be still and compares that number to a group of grasshoppers for which there is no way of determining behavior (possibly hidden and feeding in the vegetation), but seeing as visibility increases through the morning, it may be a fair assumption that many of the unseen grasshoppers have not yet been active that day (still in protected places on ground or low in vegetation). Another issue with visibility as an index is that treatments probably affect visibility differently. Shade treatments appeared to force grasshoppers up on to the screen where they sunned on the warmest corner of the screen whereas greenhouse treatments made seeing the grasshoppers very difficult, especially for the first few hours when very few grasshoppers are active to start with, vision is blocked by the greenhouse (for the first 2-6 hours) and the fog on the observation window of the greenhouse (first 2-4 hours).

Temperature Effect

Within the range of temperatures experienced during these observations, increased temperature had a positive effect on grasshopper visibility, feeding and general activity, as expected (Chase 1996, Ritchie 2000, Pitt 1999, Laws and Pendergast, unpublished data). The observation days and the summer in general was relatively cool compared to some of the

southwestern parts of the range (CA, UT, NV), and to other summers (Laws and Pendergast, unpublished data) so observation on warmer days, at higher thermal conditions, or in a hotter region should reveal a unimodal activity curve peaking between 35 and 42°C and declining sharply at higher temperatures as the grasshoppers' enzymes denature (Pitt 1999). Spider presence was not significant to the time grasshoppers spent feeding.

Spider Effect

Spider presence significantly decreased the visibility of grasshoppers in observation 2. A negative trend in activity in the presence of a spider was sometimes significant, but often interacts significantly with other factors. For a better idea of spider effect more replicates of fewer but more extreme temperatures should be used.

Time of Day and the Interaction of Effects

It may well be that the spider effect was not consistent because the spider effect interacted with temperature and time of day. As seen in figure 11(a and b), grasshopper activity is lowered during the morning hours when a spider is added, as would be expected from the results of Schmitz et al. (1997) who found that activity was restricted to the warmest part of the day in the presence of a spider. Spiders seem to interrupt the even, downward trend in visibility with increased thermal intensity but more study would be required to determine exactly what, if anything, causes such an interaction (Fig. 10b). Another aspect of time is that in general, activity, feeding and visibility increase through the morning hours and asymptotes in the afternoon (Fig. 10a). The analysis of all days together showed no significant effect of time on activity for greenhouse (increased temperature) enclosures. In this case the warmer conditions during the coldest parts of the observation probably even out the times of day in terms of temperature allowing activity for more of the day. This supports the hypothesis that activity increases with increased temperature and agrees with other temperature studies (Laws and Pendergast, unpublished data, Ritchie 2000, Chase 1996). As seen in figure 12, grasshopper activity throughout the day differs between thermal treatments. Activity appears to be greater in the higher thermal intensities than in the 6 hour shade treatment and morning activity tends to be higher in the greenhouse treatments than the shade or control treatments. The negative effect of predator presence is most clearly seen in the 4 hour greenhouse enclosures.

Temporal Patterns

The only evidence of change through the season is that feeding was highest overall on days 4 and 5, then 2 and 3, then day 1 (Fig. 16). Temperature-wise one would expect day 1 to be equivalent to days 4 and 5 or at least greater than days 2 and 3 which were colder. This could be a difference in behavior with developmental stage (more grasshoppers were adults on days 4 and 5 than days 1-3) but may also be the result of wet grass (rain stopped at 0655 on day 1) or difficulty in finding grasshoppers in grass (observer inexperience was greatest on day 1 and an experienced observer did half of the observations for days 4 and 5). Five of the 9 cages observed on day 1 also had to be thrown out because of out-of-place spiders, so further study would be required for any firm conclusions to be made regarding behavior change through the summer.

Application and Importance—Trophic Cascade Studies

If a trophic cascade is detected in this system (spiders having a positive effect on vegetation) and if it is not due to density (i.e. compensatory predation that does not lower the grasshopper density in spider cages relative to predator-free cages), the negative trends in grasshopper activity observed when spiders were present can be used to support the hypothesis that trait-mediated trophic cascades occur. Because an increase in grasshopper feeding and activity time was observed with increased temperature, there is potential for time

limitations to be replaced by resource limitations in a warmer climate. If such a limitation shift were to occur trophic cascades could not happen in the food web (Schmitz et al. 1997).

Future Studies

In future studies of temperature and spider effects on grasshopper behavior trends and differences among spider and thermal treatments would probably be more easily detected with fewer thermal conditions covering a broader temperature range (perhaps 6 hours shade, control, 3 hours greenhouse and 6 hours greenhouse) more efficient shading (sun is directly overhead by 11:30, rendering the shade-cloth on 2 sides ineffective). More full replicates at different points in the summer and consideration of the developmental stage of the grasshoppers along with spiders of known sizes would allow for better analysis of spider effect since adults are often too big for hunting spiders to capture (Schmitz et al. 1997, Schmitz 1993, 1994, Chase 1996). As comparable field temperatures are important to the utility of the data, finishing each observation within the fewest days possible would be desirable. Shifting observation by an hour so that it starts at 0800, 1 hour after treatments are put up, might allow for collection of more usable data (extension of afternoon observation) since very few grasshoppers are visible during the first hour and treatments are not always different just after application.

ACKNOWLEDGEMENTS

Thanks to Angela Laws for much help in the field and on analysis, to Kelly Stanton for weather station data and help setting up the experiment, and to Jennifer Jeffers for help setting up enclosures. Thanks to the University of Notre Dame and the Bernard J. Hank Family for funding.

LITERATURE CITED

- Belovsky, Gary E. and Slade, J.B. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos* 68: 193-201.
- Chase, Jonathan M. 1996. Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos* 77: 495-506.
- Lima, Steven L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48(1):25-35.
- Lima, Steven L. and Dill, Lawrence M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619-640.
- Pitt, William C. 1999. Effects of multiple vertebrate predators on grasshopper habitat selection: trade-offs due to predation risk, foraging, and thermoregulation. *Evolutionary Ecology* 13: 499-515.
- Ritchie, Mark E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology* 81(6):1601-1612.
- Schmitz, Oswald J. 1993. Trophic exploitation in grassland food chains: simple models and a field experiment. *Oecologia* 93: 327-335.
- Schmitz, Oswald J. 1994. Resource edibility and trophic exploitation in an old-field food web. *Proc. Natl. Acad. Sci. USA* 91: 5364-5367.
- Schmitz, Oswald J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *The American Naturalist* 151(4):327-342.
- Schmitz, Oswald J., Beckerman, Andrew P., and O'Brien, Kathleen M. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78(5): 1388-1399.
- Schmitz, Oswald, J., and Suttle, Blake K. 2001. Effects of top predator species on direct and indirect interactions in a food web. *Ecology* 82(7): 2072-2081.

FIGURES

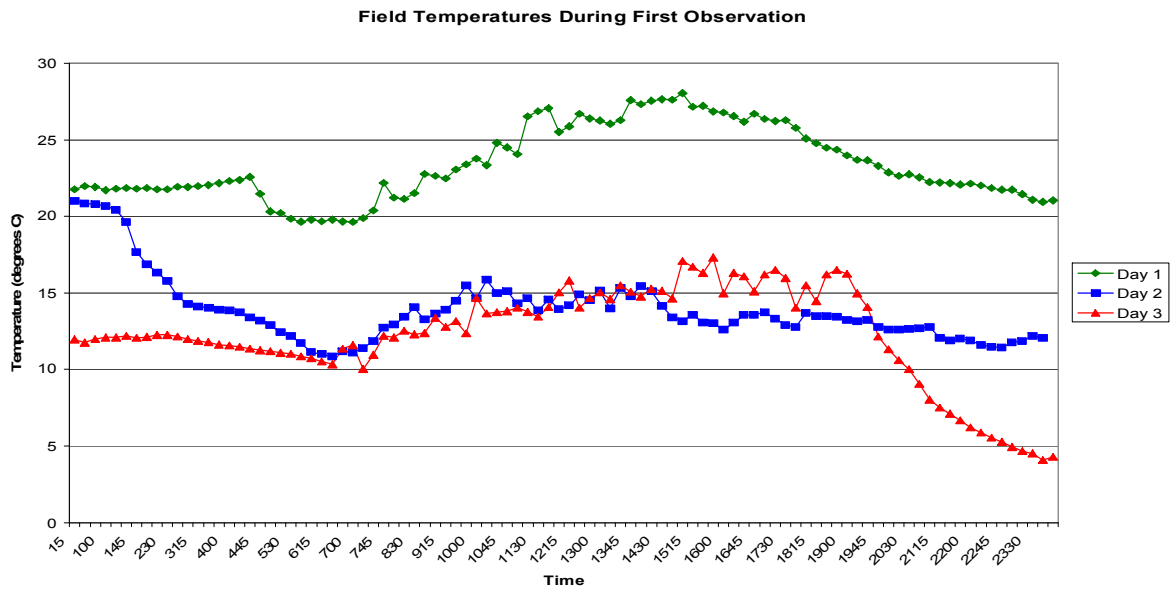


Figure 1
Ambient temperature (°C) is plotted against time of day for each day of observation 1.

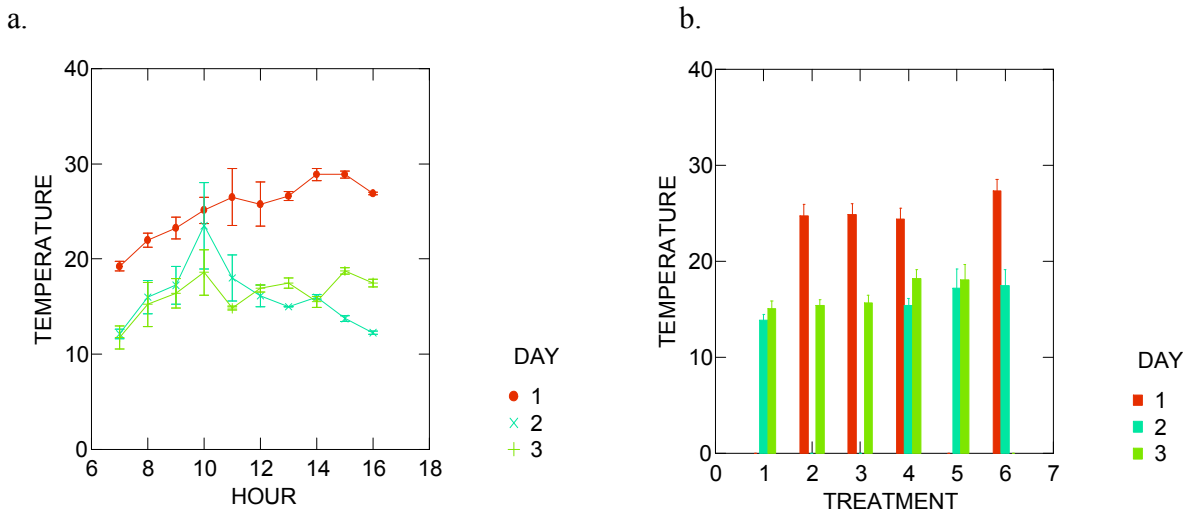


Figure 2
(a) Average temperature (°C) in enclosures is plotted against hour for each day of observation 1 (mean ± 1 SE). (b) Average temperature (°C) in enclosures is plotted against thermal treatment for each day of observation 2 (mean ± 1 SE).

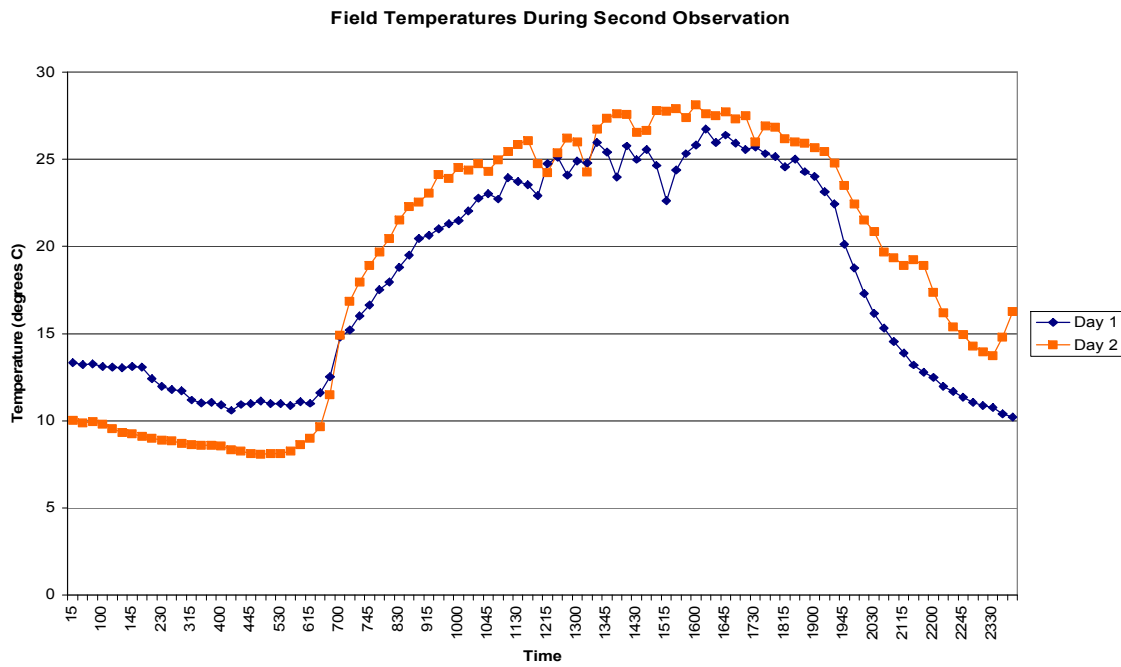


Figure 3
Ambient temperature (°C) is plotted against time of day for each day of observation 2.

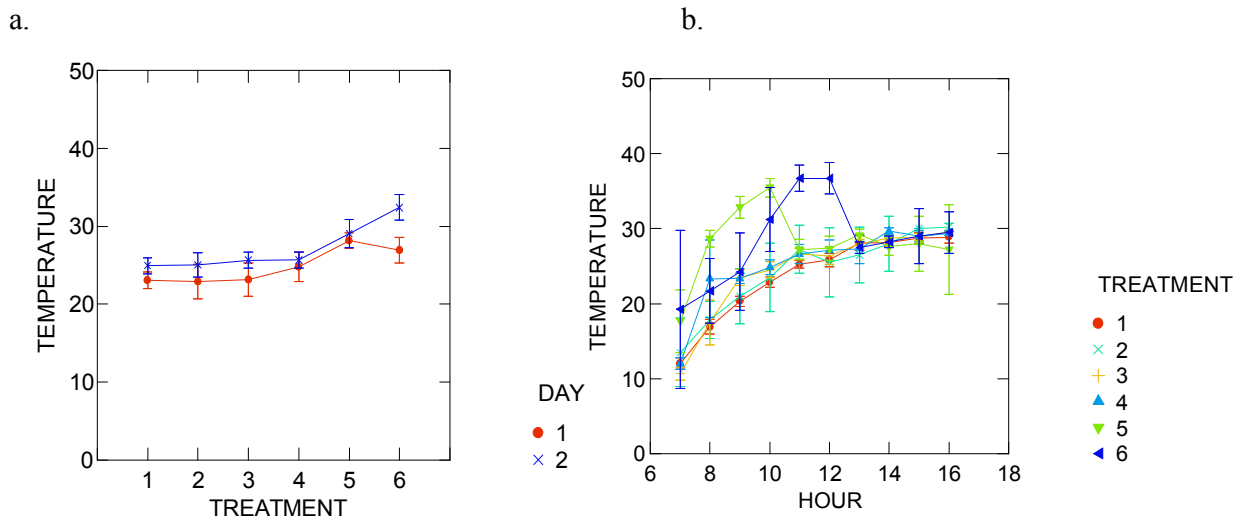


Figure 4
(a) Average temperature (°C) in enclosures is plotted against treatment for each day of observation 2 (mean \pm 1 SE). (b) Average temperature (°C) in enclosures is plotted against hour for each treatment for observation 2 (mean \pm 1 SE).

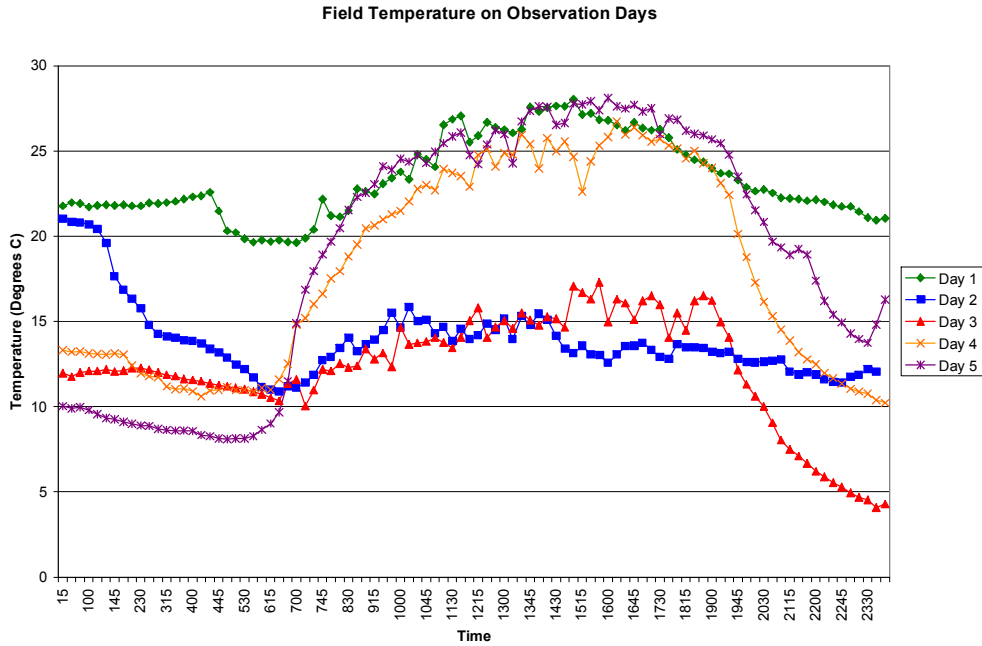


Figure 5
 Ambient temperature (°C) is plotted against time of day for each day of observations 1 and 2. Days 4 and 5 are days 1 and 2 of observation 2.

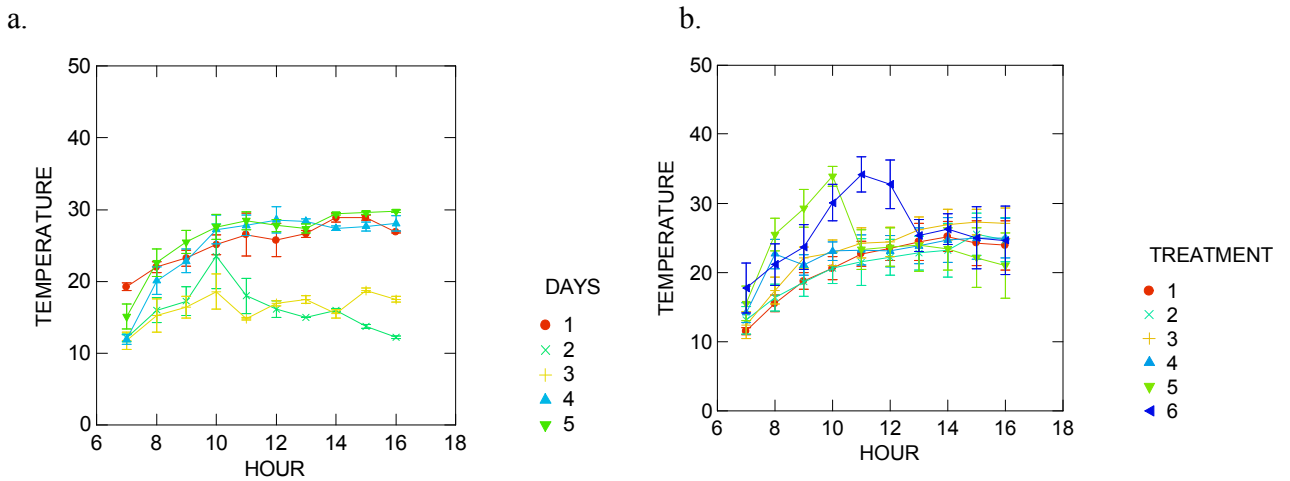


Figure 6
 (a) Average temperature (°C) in enclosures is plotted against hour for each day of observations 1 and 2 (mean \pm 1 SE). (b) Average temperature (°C) in enclosures is plotted against hour for each treatment of observations 1 and 2 (mean \pm 1 SE).

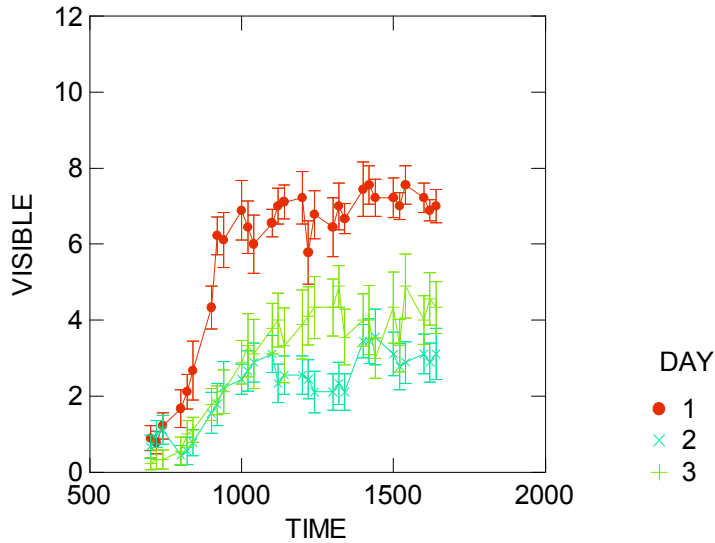


Figure 7

Number of visible grasshoppers plotted against time for each day of observation 1 as a mean \pm 1 SE (n=9). Each enclosure had 10 grasshoppers during this observation.

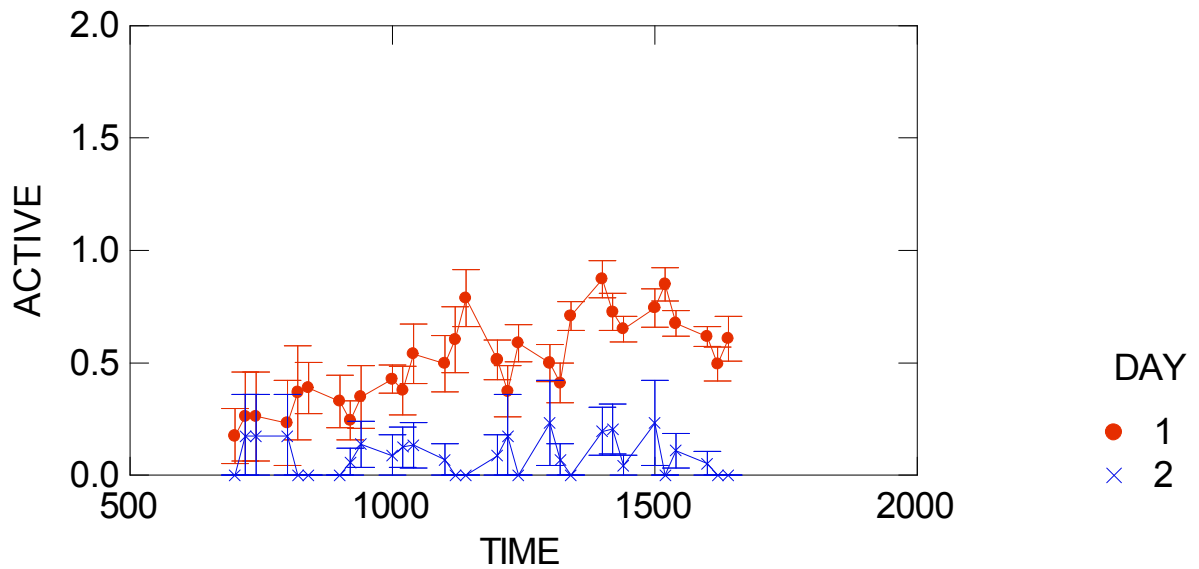


Figure 8

Proportion of grasshoppers active on days 1 and 2 of observation 1 as means of transformed proportions \pm 1 SE. Both days are non-spider treatments. Day 1 is warmer than day 2. Activity is graphed as transformed proportion of those visible.

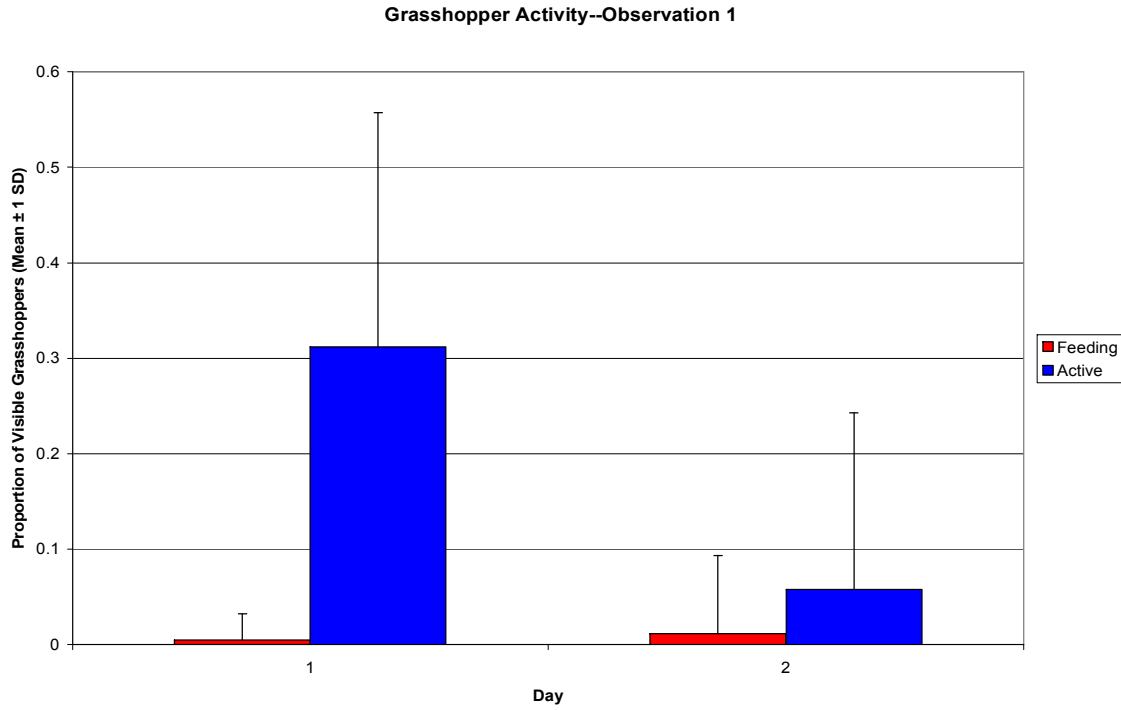


Figure 9
Proportion of grasshoppers active during observation 1 as mean \pm 1 SD.

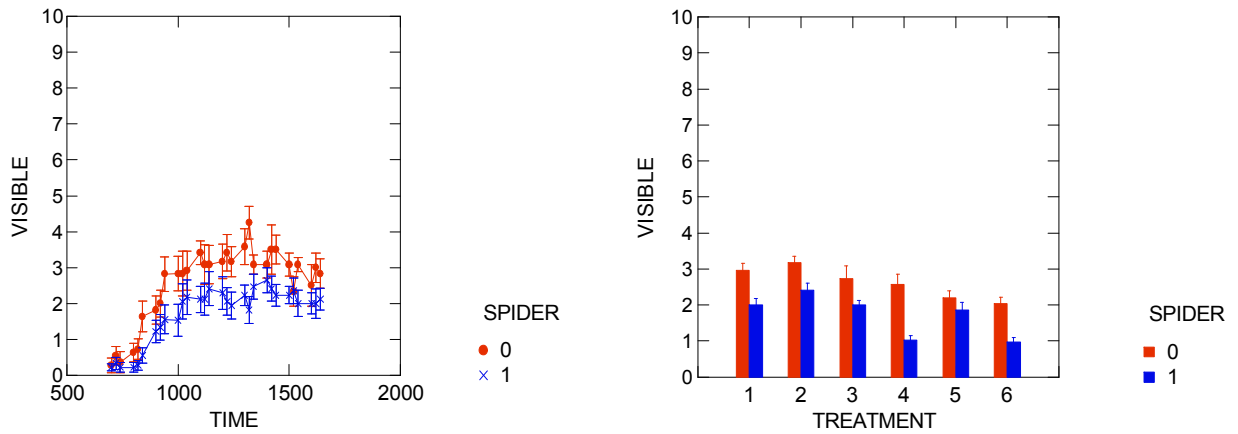


Figure 10
(a) Number of grasshoppers visible plotted against time with and without spiders for observation 2 as a mean \pm 1 SE. (b) Number of grasshoppers visible plotted against thermal treatment with and without spiders for observation 2 as mean \pm 1 SE.

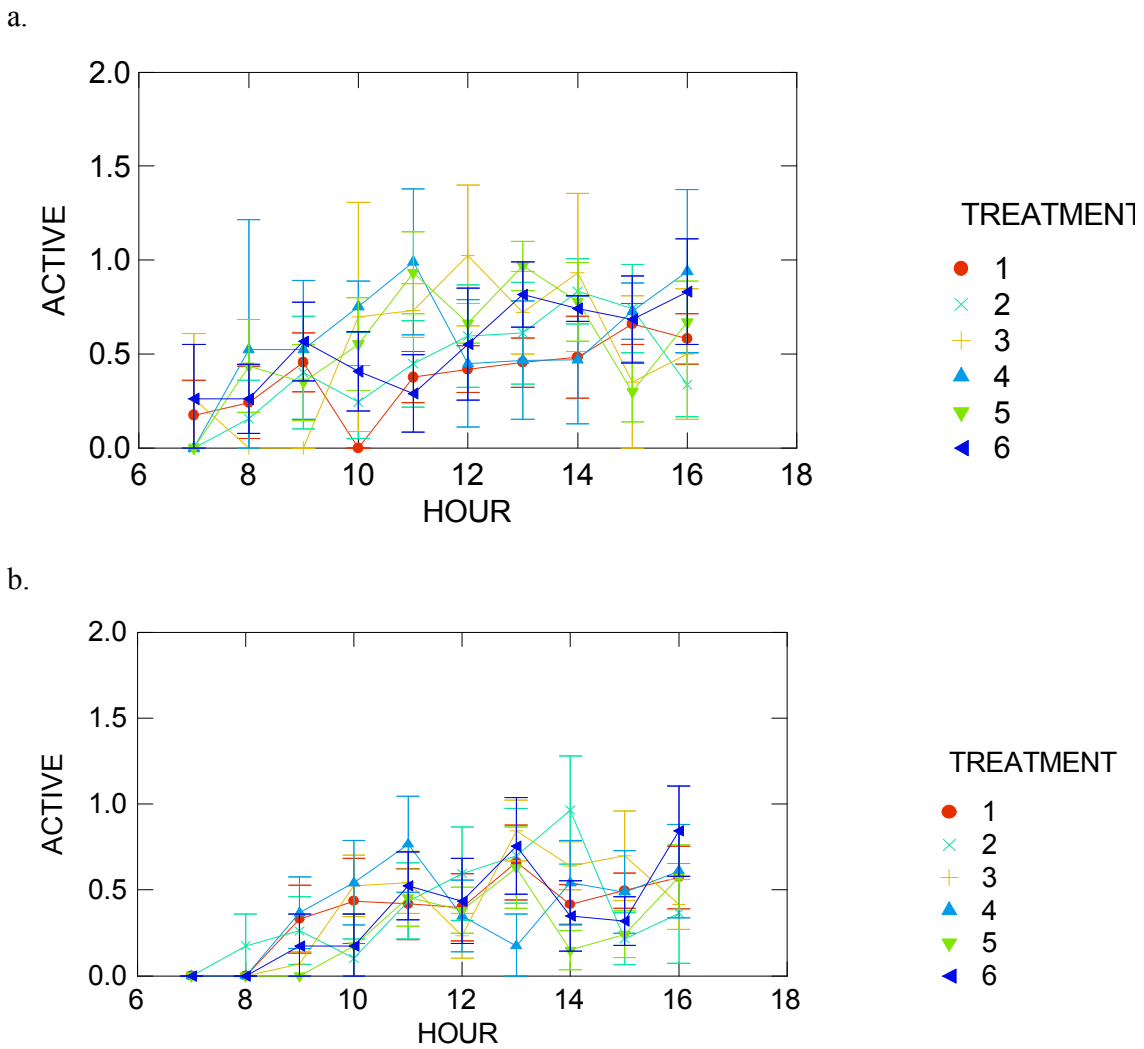
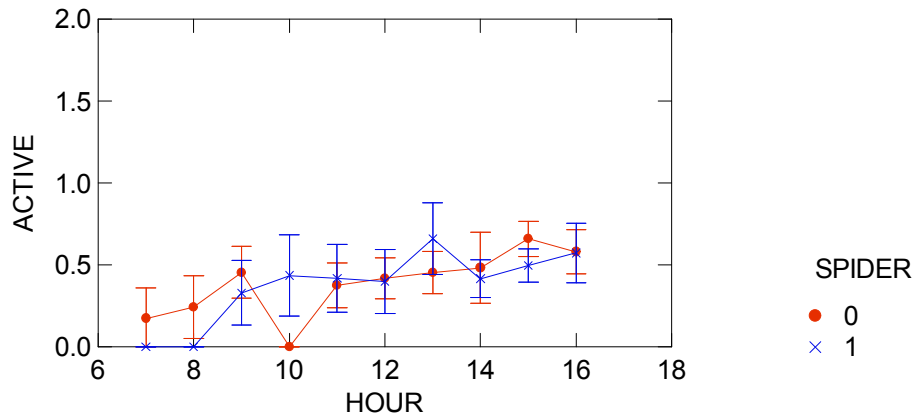


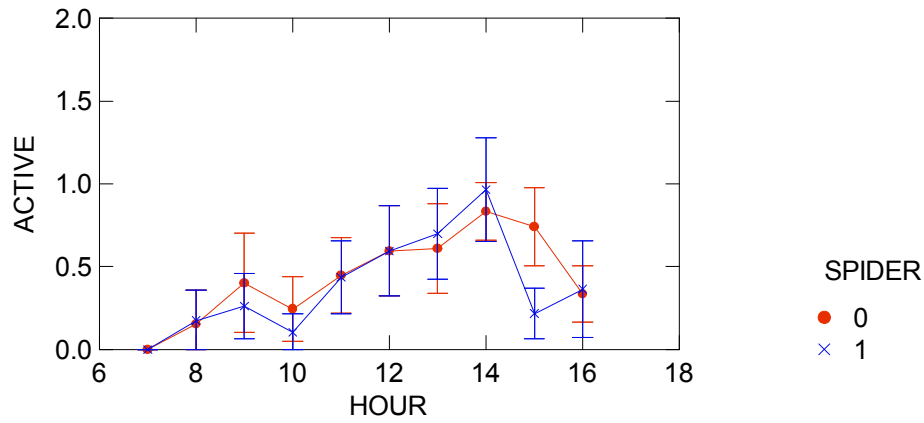
Figure 11

Proportion of grasshoppers active without (a) and with (b) spiders as transformed proportion plotted against hour for each thermal treatment during observation 2. Error bars represent 1 SE about mean.

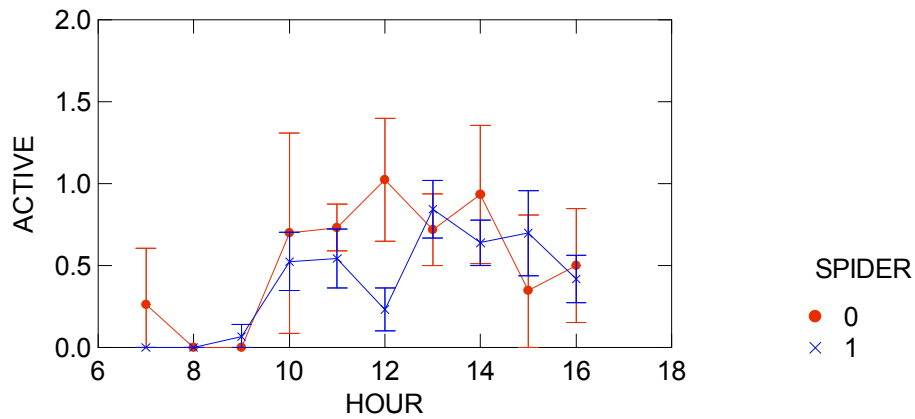
a. 6 hours shade



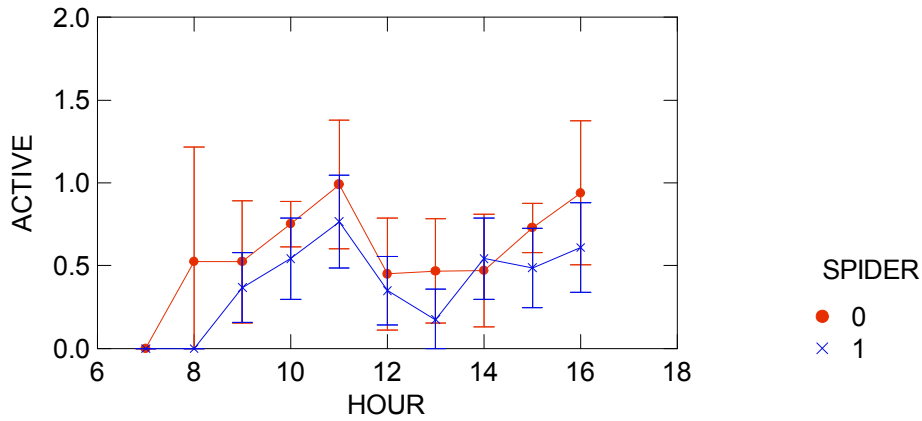
b. 4 hours shade



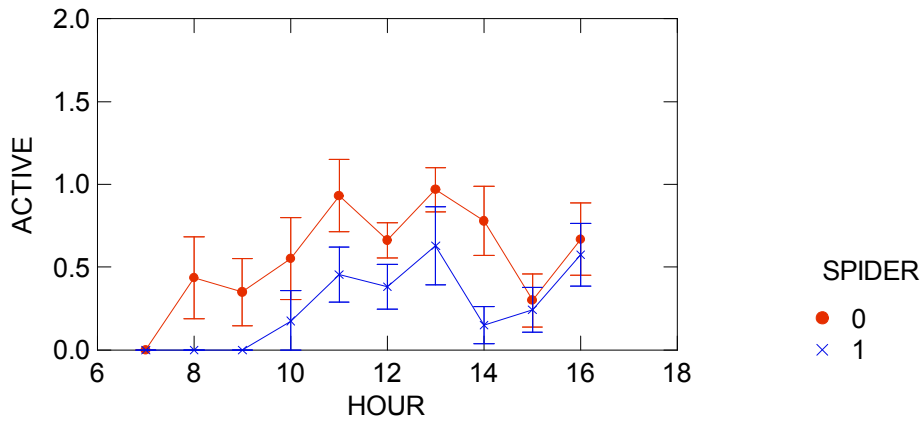
c. control



d. 2 hours greenhouse



e. 4 hours greenhouse



f. 6 hours greenhouse

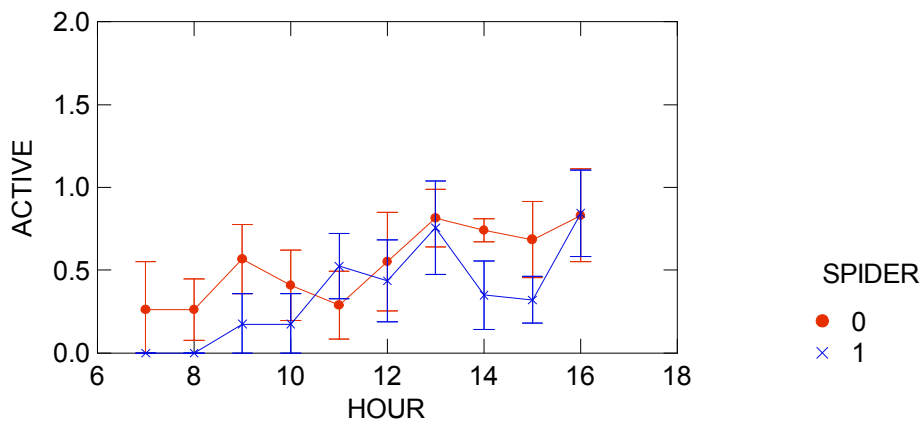


Figure 12

Transformed proportion grasshoppers active plotted against hour with and without spiders by treatment (a-f) for observation 2 as mean \pm 1 SE.

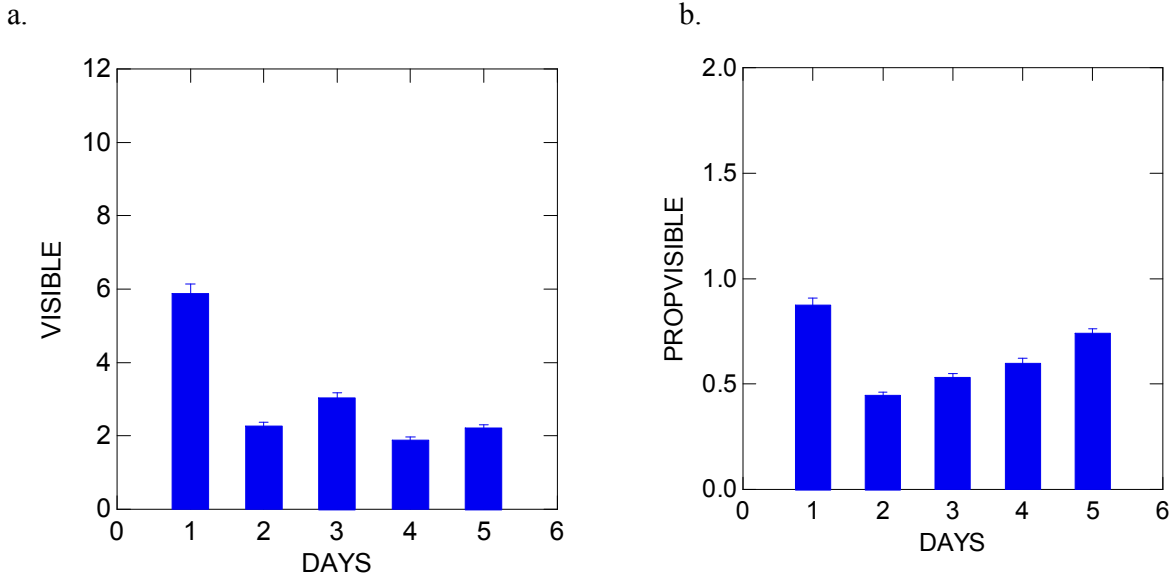


Figure 13
Number (a) and transformed proportion (b) of grasshoppers visible plotted against day for observations 1 and 2 combined as mean \pm 1 SE.

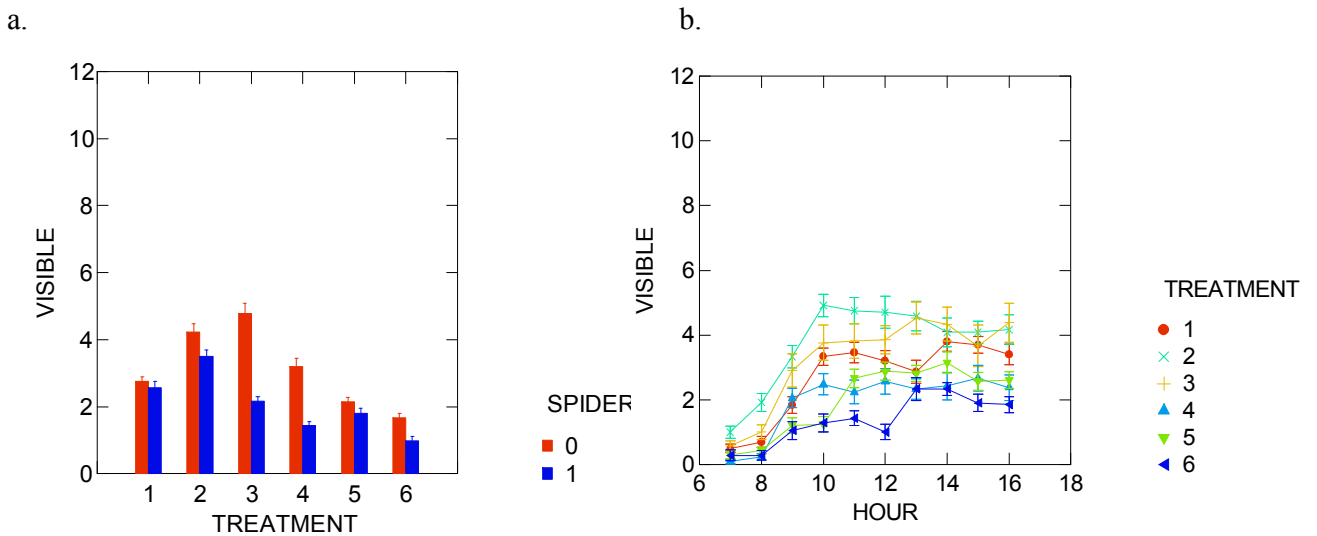


Figure 14
(a) Number of grasshoppers visible plotted against treatment with and without a spider for observations 1 and 2 combined as mean \pm 1 SE. (b) Number of grasshoppers visible plotted against hour for each treatment for observation 1 and 2 combined as mean \pm 1 SE.

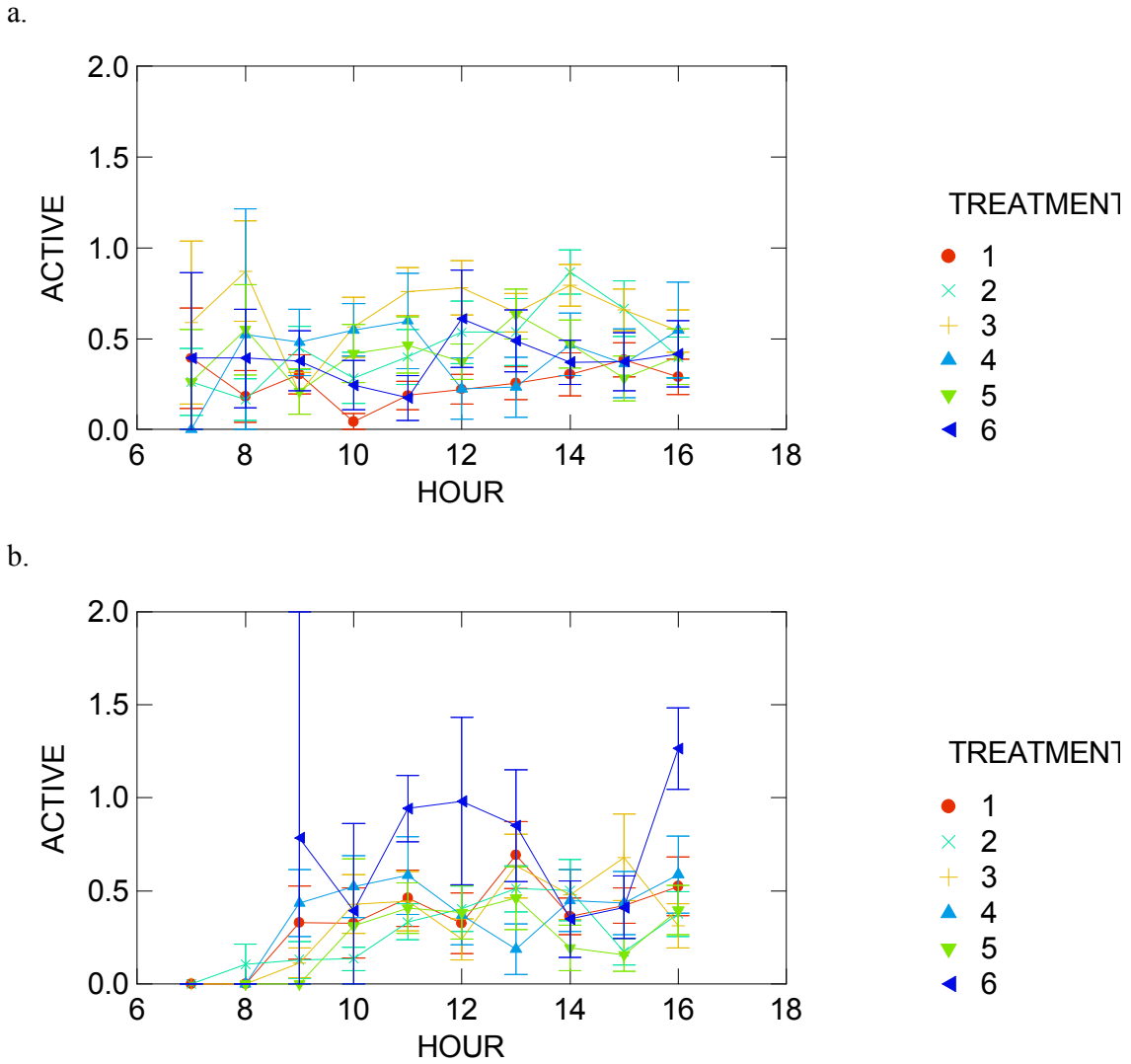


Figure 15

Transformed proportion grasshoppers active plotted against hour for each treatment without (a) and with (b) spider as a mean \pm 1 SE.

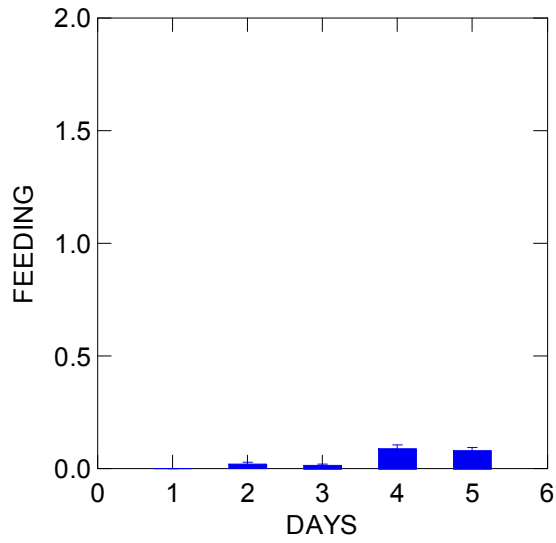


Figure 16

Transformed proportion feeding plotted against day during both observations combined as mean \pm 1 SE.

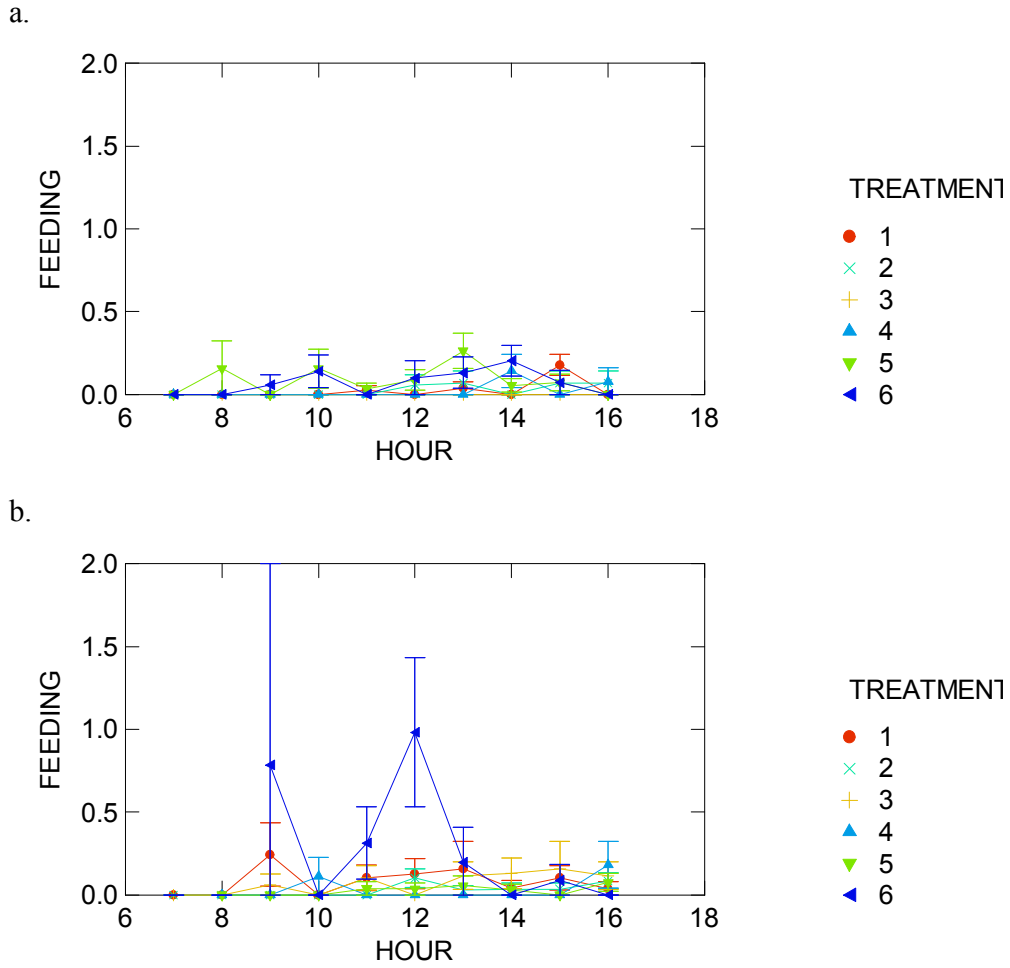


Figure 17
 Transformed proportion feeding plotted against hour for each treatment without (a) and with (b) a spider as mean \pm 1 SE.