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THE EFFECT OF PREY AVAILABILITY ON METABOLISM AND ACTIVITY IN THE TARANTULA *PHORMICTOPUS CANCERIDES* (ARANEAE: THERAPHOSIDAE)

by

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in

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Abstract

This study examined the effect of different periods of food deprivation on resting metabolic rates (RMR) and foraging activities in tarantulas (*Phormictopus cancerides).* Juvenile tarantulas were separated into two feeding groups and fed once either every 5 or 30 days. Monthly feeding trials were preceded by RMR measurements. During feeding trials I compared differences between the two groups in (1) prey capture rates, (2) time to prey capture, (3) locomotory activity, and (4) the predator's prey detection distance. RMRs increased for the well-fed group but remained consistent for individuals, fed only once a month. Time to prey capture decreased for food-limited individuals, and the proportion of individuals that ate in the 30-day group was higher than in the well-fed group, but the results for locomotory activity and detection distances were inconclusive. Overall, changes in metabolism and behavior were more noticeable in the well-fed group compared to individuals fed once a month.

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Introduction

All organisms rely on energy to perform functions necessary for life. Unlike plants, animals cannot utilize the sun to manufacture energy and therefore must obtain the energy needed from what they eat. Because energy is essential to sustaining life, organisms have developed many ways of accumulating the necessary means to fuel their bodies. What is stored as food caches by one animal is maintained as internal energy reserves by another. When these reserves begin to diminish, organisms must find ways to replenish them. As energy reserves diminish, predators may alter their normal foraging patterns to maximize the possibility of finding prey. Organisms that are normally less inclined to search for food have been found to increase their locomotory activity when faced with starvation (e.g., Hervant et al. 1997). Walker et al. (1999) found that the wolf spider, *Hogna helluo,* altered its predatory behavior to more actively search for prey when it was food limited. As well as alter behaviors, invertebrate ectotherms have been found to selectively forage on the basis of particular nutrients needed (Mayntz et al. 2005). These different behavioral strategies are both examples of efforts by organisms to minimize the risk of starvation.

To make use of the energy from the ingested food, the body must convert it to a usable product. The function of energy use related to the internal processes is collectively called metabolism. This total energy consumption is often measured as a function of time called metabolic rate (MR). Due to a high degree of variation in the three main factors affecting MR (temperature, mass, and phylogeny), disparities among metabolic characteristics of both species and individuals are common (Bennet 1988).

To compare the metabolic rates of different ectothermic organisms, resting metabolic rate (RMR) is most often used. RMR is the minimum MR that is needed by an organism to maintain life. When organisms are not at their RMR, they are expending more energy, thereby not giving a true indication of their minimal requirements for life. For example, the MR of an actively running eucalyptus-boring beetle is 72 times higher than a beetle at rest (Rogowitz and Chappell 2000), beetles forced to right themselves had a 7-12-times-higher MR than beetles at rest (May et al. 1986), and there is a 100-fold increase in MR during flight in moths as compared to their RMR (Reinhold 1999). Because there is such variability in the duration, intensity, and types of activities, the active MR does not give the most accurate and comparable results. MRs during activity are variable even among the same individuals. Repeatability of metabolic testing was not always found to be significant during repeated bouts of running wheel locomotion in beetles (Rogowitz and Chappell 2000). Because of the limitations of a standardized active MR, the RMRs of individuals in this study will be compared in an attempt to reduce the variability.

RMR has also been correlated to the availability of food. Bennet (1983) suggested that low RMR in vertebrate and invertebrate ectotherms may be an adaptation to extended periods with little food. For example, *sit-and-wait* strategists exhibit low RMRs because of the limited movement associated with the acquisition of food. Organisms, such as ticks, have been shown to sit and wait for more than a year in the hopes of contacting a meal (Lees 1964; Jaworski et al. 1984; Lighton and Fielden 1995). Lighton and Fielden (1995) further hypothesized that the effectiveness of a sit-and-wait strategy in ticks is due to a low ratio of actively respiring tissue to body mass. This might

also hold true for other sit-and-wait strategists who have physiological functions that allow them to have large, sporadic meals but do not require much physiological maintenance. Because prey are not always available, this tactic is often employed to maximize the probability of prey capture while minimizing energy costs associated with actively seeking out prey (Samu et al. 2003; Jackson et al. 2004).

A sit-and-wait strategist is not restricted to being parasitic. There are many sit-and-wait predators; however, these organisms do not employ only one mechanism for obtaining energy. A shift can be made from a sit-and-wait to a more active predation strategy. Wolf spiders that are generally sit-and-wait predators will alter this foraging behavior during periods of varying prey densities (Samu 1993). In response to environmental variation in prey availability, the wolf spider, *Pardosa agrestis*, will alter its "waiting-moving" continuum in order to maximize food capture (Samu et al. 2003). Many tarantulas also utilize a sit-and-wait strategy (Minch 1978; Stradling 1994; Shillington and Verrell 1997) for prey capture, but little is known about their foraging strategies. This study will examine their ability to wait for extended periods to obtain food. It is possible that tarantulas increase their activity levels in a food-limited environment.

Despite their notoriety, tarantulas (Aranea: Theraphosidae) are a poorly studied group of animals. Because of their sit-and-wait predation strategy, they are ideal candidates for this study because they can survive extended periods of starvation (Baerg 1958; Punzo 1989). This sit-and-wait strategy is also thought to affect the MR of tarantulas. In general, MR increases with the weight of an organism (see Schmidt-Nielsen 1997). However, as a group, spiders have a lower RMR compared to other

ectotherms of similar size (Anderson 1970; Greenstone and Bennett 1980). Specifically, Anderson (1970) determined that Theraphosids had between 31 and 35% of the expected RMR and further hypothesized that low RMR provides a selective advantage for spiders, enabling them to survive long periods without food.

By starving *Lycosa lenta* for 5 months, Anderson (1974) found that RMRs initially decreased with increasing periods of food deprivation and then plateaued while body weight continually declined. These reduced MRs likely increase the longevity of food-deprived spiders. Surprisingly, during periods without food, activity is not compromised, and in some cases, movement of starved spiders has been shown to increase as a function of food deprivation time (Anderson 1974; Provencher and Riechert 1991; Walker et al. 1999). This increased activity suggests that spiders may alter their foraging strategy in an attempt to regain much-needed energy by actively seeking food rather than waiting for it to pass by.

This study will utilize both MR and feeding regimens to examine the relationship between metabolics, activity, and hunger in tarantulas. I hypothesized that the following differences would be seen between the satiated and hungry groups: (1) there would be a change in foraging strategy in the hungry group, including higher levels of locomotory activity; (2) The hungry group would have an increased awareness of prey; and (3) The hungry group would have a lower RMR. Based on these hypotheses, I predicted that food deprived tarantulas would be more active in attempts to capture prey, indicated by a greater prey-detection distance and an increased locomotory activity level.

Material and Methods

Juvenile *Phormictopus cancerides* (n = 18) were used for this experiment. *P. cancerides* are considered to be aggressive, burrowing tarantulas from the Caribbean (Marshall, 1996). They are fast growers, making them ideal as test subjects. All spiders were from the same egg sac and were reared from the second instar in our laboratory (Batch 1) for approximately 10 months. Shortly after the experiment began, two subjects died, prompting us to seek additional spiders for the study. Individuals from the same egg sac were acquired and constituted Batch 2 (n = 30). For the duration of the study, *P. cancerides* were housed in separate, clear plastic containers (226.8 cm^3) in a laboratory under a natural photoperiod (14h:10h light:dark) at approximately 25 ˚C. Housing containers were lined with a substrate of crushed coconut shell and kept moist. While in the laboratory before experiments began, all tarantulas were fed crickets (*Acheta domestica*) once a week.

Two groups were formed randomly among the *P. cancerides*. Group 1 (n = 9 from Batch 1, n = 15 from Batch 2) was fed one cricket every five days for the four-month duration of the study. Group 2 (n = 9 from Batch 1, n = 15 from Batch 2) was fed one cricket every 30 days. Because spider growth within these two groups varied substantially, each spider received a cricket on the basis of its body weight. This proportion (prey:spider body weight) was maintained throughout the experiment.

All feedings and feeding trials were monitored to determine which spiders ate. Crickets not eaten were removed from the containers, and the spiders were not fed again until their next scheduled feeding time. All dates of spider molts were recorded. The

entire course of molting includes two processes, apolysis (separation of the old cuticle from the newly developing cuticle) and ecdysis (the shedding of the entire, old exoskeleton) (Foelix 1996). Once a spider has molted, its new exoskeleton is initially very soft. Fasting occurs during apolysis as well as the period following ecdysis while its new cuticle hardens (Foelix 1996). By monitoring which spiders ate at a particular trial, the pre- and postmolt fasting times were calculated. Due to the length of time between feedings of Group 2, the pre- and postmolt fasting times were only measured for Group 1.

Metabolic Rates

An open-flow respirometry system was used to determine metabolic rates (MRs) as rates of CO_2 ($\dot{V}_{CO2}$) production in postabsorptive animals. All subjects were weighed before being placed in the metabolic chamber. During MR measurement, tarantulas were placed in a small metabolic chamber. Six subjects and one baseline were run per 24-hour recording period. Air was pulled through a column of Drierite/Ascarite/Drierite to remove CO_2 and moisture from the air passing through the system and into the metabolic chamber. Air leaving the individual metabolic chambers passed through a CO_2 analyzer (LiCor 6251, LiCor Environmental Division, NE, USA), which transmits data to a computer running acquisition software (DATACAN, Sable Systems, NV, USA). The flow rate of air through the system was 25 mL/min. Using an eight channel multiplexer (Sable Systems, Nevada), we broke the 24-hour recording period into six 4-hour blocks. During each of the 4-hour blocks, the individual MRs were measured for 15 minutes after a period of 20 minutes to flush the system and reduce CO_2 buildup. The CO_2 produced by the subject in the chamber was quantified in parts per million.

The rate of CO_2 production ($\dot{V}_{CO2}$) was calculated on the basis of the equation from Withers (1977): $\dot{V}_{CO2}$ (mL/h) = (Fe_{CO2}- Fi_{CO2})* (flow rate in mL h^{-1}). Fe_{CO2} and Fi_{CO2} refer to the fractional concentrations of CO_2 leaving and entering the respirometry chambers. Because of the Ascarite's removal of all CO_2 entering the chambers, Fi_{CO2} was zero; therefore, $\dot{V}_{CO2}$ was simply the fractional rate concentration of CO_2 for a subject, multiplied by the flow rate. The RMR of an individual was considered the lowest 5-minute period over any of the six recordings per individual for the 24-hour recording. See Shillington (2005) for additional details about the experimental setup.

All metabolic rates were measured prior to the monthly feeding trial, when the animals were postabsorptive. To linearize the MR results, all data were $\log_{10}$ transformed. Because of the influence of mass on MR, the data were adjusted for body mass by regressing the logRMR on logMass. The residuals from this regression are considered mass-corrected RMRs and were used in all analyses (see Beaupre and Zaidan 2001; Shillington 2005). We compared differences between the groups and also determined individual trends over the entire experimental period, using a repeated-measures ANOVA. Tests for heterogeneity were performed to ensure that there was no significant difference between the slopes of the two feeding groups prior to using the mass-corrected RMR residuals.

As previously mentioned, two individuals died during the first month of testing, prompting us to acquire the second batch of individuals. The experimental design called for metabolic testing at the beginning and end of the 4-month study because the equipment was not available during the middle of the study. When the second batch

began their 4 months of testing, the metabolic equipment was not available; therefore, I did not obtain an initial, or starting, RMR for these individuals. The results of the metabolic measurements only include individuals from Batch 1.

Feeding Trials

Weight – At the start of each monthly feeding trial, the tarantulas were weighed. Differences in weight were compared for Groups 1 and 2 each month. The initial weights of the individuals (separated by batch) were compared using a *t* test. Because there were no differences within the groups at the start of the experiment, members of the same group but different batches were combined and compared with a one-way ANCOVA with the initial mass as the covariate. In addition, before all ANCOVAs were run, the data were tested for heterogeneity.

Test Apparatus – For all feeding trials, a 14 x 6 x 5.5 cm Plexiglass feeding arena was connected to the individual tarantula containers. Following the connection of the container to the arena, the prey item (cricket) was introduced at the opposite end. A 1-cm-square grid was placed on top of the arena so that quantitative measures of activity could be made from the video recordings.

All trials were recorded with a camera (Panasonic WV BP130) positioned above the chamber. Because all tarantulas were fed during daytime hours prior to the start of the study, all feeding trials were similarly run during the day to be consistent with pre-trial habituation. Each trial was timed from the introduction of the cricket into the arena until either it was captured by the tarantula or 5 minutes had elapsed. Preliminary tests indicated no difference in capture frequency after a 5-minute time period had elapsed (i.e., if a tarantula had not eaten within the 5-minute period, it would not eat even if the

cricket was left in the container for a 24-hour period). If there was no capture during the feeding trial, the cricket was removed from the spider container and no food was offered to the tarantula until the next feeding period, and the test was scored as *no response*. Feeding trials for both groups only occurred every 30 days, in accordance with Group 2's feeding schedule. During all 5-day feedings of Group 1, crickets were placed in the tarantulas containers; therefore, no group had more access to the testing arena than the other.

Detection Distance – The prey detection distance was measured in the feeding arena and is an attempt to quantify the ability of tarantulas to detect prey. Frame-by-frame analysis was completed on a Panasonic Desktop Editor VCR, and detection distance was determined when the spider made its first movement in response to the prey item and was measured as the distance between the spider cephalothorax and the cricket head at this time point.

In addition to prey detection and capture, the locomotory activity of tarantulas was logged. During the trial period, this was recorded as the number of spiders that left their container (located at the end of the feeding arena) and went into the feeding chamber arena. An ANOVA was used to determine if there were differences in willingness to leave their chamber between the groups.

Results

The spiders in this experiment were divided into two separate feeding groups. The individuals of Group 1 were fed once every 5 days, and those in Group 2 were fed once every 30 days. Within each group, spiders were divided into different batches. Although all individuals from the different batches came from the same egg sac, there was a difference in the sizes of the tarantulas on the basis of feeding from second instar until two months prior to the experiments. Batch 1 was reared in our laboratory from the second instar, and Batch 2 was initially reared by the breeder. Both batches were concurrently run in the experiment, with Batch 2 two months behind Batch 1. At the beginning of the experiment, the average weight of the individuals in Batch 1 was 1.31 ± 0.084 g (mean ± SE) and the average weight in Batch 2 was 0.22 ± 0.0068 g.

The initial weights of the spiders were compared at the beginning of the experiment to verify that there was no initial difference between the groups. We found no difference in the initial weights (Table 1) of the individuals in each feeding group within each batch (Batch 1: $t = -0.51$, $p = 0.62$; Batch 2: $t = 1.08$, $p = 0.30$). When the batches were combined, we again found no differences between the groups ($t = -0.40$, $p = 0.69$). Thus, unless otherwise indicated, each feeding group contained individuals from both batches.

The experiment began exclusively with Batch 1, but after the two deaths in Group 1 in the first month, which reduced the sample size to 7, Batch 2 was acquired and prepared for the experiment. In addition to the mortality in Batch 1, there was also one individual from Group 1 in Batch 2 that died during the trial (and was also removed from

analysis). The only mortality that occurred in the study was in Group 1, the well-fed group.

Feeding Trials

Weight Gain – Throughout the 4 months of this study, the average weights of both Group 1 and 2 increased (Fig 1). Although there was no difference in the average weights at Month 0 ($t = -0.4$, $p = 0.691$), Month 1 ($t = 0.33$, $p = 0.743$), and Month 2 ($t = 1.15$, $p = 0.256$), there were significant differences between the groups for the last two months of the study. At both Month 3 ($t = 2.1$, $p = 0.0211$) and Month 4 ($t = 3.65$, $p = 0.00071$), the average weight of Group 1 was significantly higher than that of Group 2. It should be noted that the average weight for Group 1 increased every month. Likewise, the average weight of Group 2 increased through Month 3 but decreased at Month 4. This decrease is an artifact of molting. There were 3 smaller individuals that were not included in the average weight calculated for Month 3 because they were in the process of molting. This gave an inflated average at Month 3, and, thus, Month 4 weights appeared to decrease. As the experiment progressed, there were differences that could be noted on visual inspection of the spiders. Although Group 2 did not appear to be starving, the members of Group 1 appeared to be satiated; they were less likely to eat, and their abdomens were visibly more distended.

During the trial, the number of times each spider ate was totaled and compared between the 2 groups. Although Group 1 was offered food every 5 days (for a total of 25 times), no individual ate all 25 offerings (Fig 2). On average, Group 1 consumed 13.6 meals (54% of the offerings), and the number of meals consumed ranged between 10 and

17. Group 2 was fed 5 times. The average number of meals consumed was 4 (80% of the offerings), and the number of meals consumed ranged from 2 to 5.

The percent of weight increase of individuals fed over the course of the experiment is shown in relation to the number of times they ate in Figure 3. Finding crickets that were the same proportion of the weights of both the larger spiders of Batch 1 and the smaller spiders of Batch 2 was very difficult on the basis of the availability of crickets. Therefore, individuals were fed according to their batch and the availability of crickets; Batch 1 generally received 25 ± 5% of their weights and Batch 2 received 50 ± 5 % of their weights. Thus, although the trends were consistent between the groups, in order to examine the weight gains, the spiders were separated into Batch 1 and Batch 2. For Batch 1, the number of meals was positively correlated to percent of weight increase ($r^2 = 0.82$, $p < 0.0001$). Similar to Batch 1, the number of meals consumed was positively correlated to percent of weight increase in Batch 2 ($r^2 = 0.83$, $p < 0.0001$). Figure 3 shows the rate (weight/ # of meals) of increase in both batches. Although both batches showed an increase in weight that was positively correlated to the number of feedings, this rate of increased weight was higher in Batch 2 than in Batch 1. The difference is probably due to the larger relative weight of the prey fed to Batch 2.

Throughout the experiment, there was variability in the number individuals that ate at each feeding trial. There was also variability in the number of individuals that were used at each feeding trial as a result of factors such as molting and death. To account for differences in the number of individuals in the feeding trials for the different groups, a 2 x 2 contingency table was used to compare the proportion of individuals that ate to the number of individuals at that trial rather than to the total number of spiders in the group.

At one month of separate feeding regimens, there was no significant difference between the two feeding groups in the proportions of individuals that fed (Month 1: $\chi_c^2 = 4.33*10^{-1}$, $p > 0.05$). The following three months all showed significant differences in the proportion of individuals who ate during the feeding trials (Month 2: $\chi_c^2 = 7.79$, $p < 0.01$, Month 3: $\chi_c^2 = 10.7$, $p < 0.005$, Month 4: $\chi_c^2 = 20.7$, $p < 0.001$), and Group 2 had a higher proportion in all three months (Fig. 4).

Trial Times – The average length of time for the individual feeding trials was compared for the two Groups (Fig 5a). There was no significant difference in the average trial length between Group 1 and Group 2 at Month 1 ($F = 0.119$, $p = 0.73$). During the feeding trials for Months 2, 3 and 4, Group 1 had significantly longer trial times compared to Group 2 (Month 2: $F = 13.794$, $p = 0.0006$; Month 3: $F = 12.013$, $p = 0.0013$; Month 4: $F = 137.44$, $p < 0.0001$). Following the trial times of Month 1, the average times for Group 1 and Group 2 went in opposing directions. Group 1 times increased from Month 1, and Group 2 trial times decreased in a linear fashion in respective months.

The average length of feeding trials was also compared within each group over the 4-month period. For Group 1, there were significant differences between the months ($F = 7.21$, $p = 0.0016$). Using pairwise comparisons of all of the trials, we found the trial lengths for Months 2 through 4 were all significantly higher when compared to the times at Month 1 (Month 2: $F = 18.44$, $p = 0.0006$, Month 3: $F = 5.16$, $p = 0.0383$, Month 4: $F = 24.03$, $p = 0.0002$) (Fig. 5a). There were no other significantly different pairwise comparisons. Although the average length of trials decreased throughout the experiment in Group 2, there was not as large a decrease in Month 2, compared to the increase seen

in Month 2 for Group 1. For Group 2, there were no significant differences between the months ($F = 1.72$, $p = 0.18$).

The average feeding trial times for both groups were heavily influenced by those individuals that did not eat. Therefore, all individuals that did not eat were removed and the data were reanalyzed (Fig. 5b). There was no significant difference between the average trial times for Groups 1 and 2 through Month 3 of the trial (Month 1: $F = 0.136$, $p = 0.72$; Month 2: $F = 0.177$, $p = 0.68$; Month 3: $F = 1.019$, $p = 0.32$). At Month 4, however, Group 2 had a significantly higher average trial time than Group 2 ($F = 43.617$, $p < 0.0001$).

Detection Distance and Locomotory Activity – After the cricket was placed into the feeding arena, the distance between predator and prey when the spider made its first movement was measured as the detection distance. There was not a particular movement that had to be made to be considered the detection distance. For some individuals, this initial movement coincided with a strike response, whereas for others it was merely a small twitch by one appendage. Of the 174 total feeding trials, 60 (34.4%) of the detection distances were measured as the spider grabbed the prey. The largest detection distance for the two groups was 15.2 cm for Group 1 and 16.2 cm for Group 2. In 8 % of the trials, the cricket approached the tarantula and then moved away. After the cricket moved further from the tarantula, the spider would then make its first movement. This generally occurred when the cricket was far away, thereby inflating the group's average detection distance. This was the spider's first movement but cannot be considered the detection distance because it is not known if the detection occurred at the closer distance or the distance after it moved away (Fig. 6). Data were thus analyzed by removing these

individuals. There were significant differences in detection distances at Month 1 (Group 1:2.12 ± 0.13 cm, Group 2: 3.45 ± 0.58 cm, F = 5.053, p = 0.308). The were no significant differences between the two group means for Month 2 (Group 1: 3.16 ± 0.30 cm; Group 2: 2.62 ± 0.20 cm; F = 2.425, p = 0.128), Month 3 (Group 1: 2.50 ± 0.31 cm; Group 2: 2.98 ± 0.49 cm; F = 0.661, p = 0.422) and Month 4 (Group 1: 5.5 ± 0.96 cm, Group 2: 3.7 ± 0.36 cm, F = 3.774, p = 0.591).

Locomotory activity was defined as the number of spiders that would leave their "home" boxes and venture into the 14-cm-long feeding arena during trials. Of the 45 individuals in the feeding trials, 31 (68.8 %) left their containers at least once during one of the four feeding trials. Of those 31 individuals, 22 (71 %) left their containers at more than one feeding trial. Of 174 total individual feeding trials, tarantulas left their containers during 58 (33.3 %) of the trials. Of these 58 occurrences, 36 (62%) were from Group 1, and 22 (38%) were from Group 2. Once again, a contingency table was used to determine if there was a difference in the proportion of individuals that left their boxes at any point during the feeding trials. During the first three months, there was no significant difference in the proportion of each group that left their boxes (Month 1: $X_c^2 = 1.78$, $p > 0.05$, Month 2: $X_c^2 = 0.55$, $p > 0.05$, Month 3: $X_c^2 = 0.61$, $p > 0.05$; Fig. 7), but there were a greater proportion of individuals in Group 1 (50%) that left the boxes than in Group 2 (16.7%) in Month 4 (Month 4: $X_c^2 = 4.16$, $p < 0.05$). In every trial, as soon as the spider grabbed and started eating, the trial was ended. Therefore, those individuals that ate were not given the full five minutes in the arena. Because there were spiders that both ate their prey and left their boxes, the 2 x 2 contingency table was recalculated by including only individuals that did not eat. During the four feeding trials, there was no

difference between the proportion of individuals in either group (that did not eat and) that left their boxes (Month 1: $X_c^2 = 0.0048$, $p > 0.05$, Month 2: $X_c^2 = 0$, $p > 0.05$, Month 3: $X_c^2 = 0.044$, $p > 0.05$, Month 4: $X_c^2 = 0.071$, $p > 0.05$).

Molting

Group 1 was divided into the two batches for analysis of pre- and postmolt periods. Only Group 1 was included because Group 2 was not fed enough to determine if they would have eaten sooner than once every 30 days. Batch 1 included the larger spiders (1.26 ± 0.14 g), and Batch 2 contained much smaller individuals (0.22 ± 0.012 g). All of the individuals but one from Batch 2 molted more than once (maximum of 3 molts) during the study; therefore, only their first molt was used in comparison to accentuate any differences based on the sizes of the individuals. If a molt occurred early in the study and the spider had not eaten at all during the trial, there was no way to determine the length of time without food; therefore, the spider was only examined for postmolt fasting. Batch 1 had a significantly longer premolt fasting time (27.7 ± 3 days) than Batch 2 (13.3 ± 1.3 days; $t = 5.22$, $p < 0.0001$) (Fig 8). There was, however, no significant difference in the postmolt period for the 2 batches ($t = 1.76$, $p = 0.096$). Batch 1 (6.5 ± 1.1 days) took only slightly longer than Batch 2 (3.8 ± 0.9 days) to begin eating again after molting. Although not significant, it was interesting to note that there were four individuals in Batch 2 (25%) that ate on the same day that their molt was found. Although individuals from Group 2 were not included in this data, there were individuals that fasted for longer periods than did individuals in Group 1. One spider did not eat at the beginning of the trial through the first 90 days. Others in Group 2 would not eat at a feeding trial and would therefore not be given food again for another 30 days. During the feeding trials, it

became very evident which spiders were not going to eat and were perhaps beginning to fast before a molt. Their behaviors were much different from those of individuals that struck at and killed their prey. Those that were not interested in the cricket would often strike with their pedipalps and chase the cricket from their containers. When these behaviors were seen, it was evident that the tarantula would not eat during that trial.

Metabolic Tests

Because of the availability of the equipment, metabolic measurements were only completed for Batch 1 throughout the experiment. Thus, unless otherwise indicated, all analysis refers only to Batch 1. RMRs increased with body mass (Fig. 9) and the slope of the $\log_{10}$ body mass and $\log_{10}$ RMR were found to be homogeneous between the groups ($p = 0.66$); thus, the residuals of mass-corrected RMRs were used in all analyses. The Month ($F = 0.49$, $p = 0.62$) and Group*Month interaction ($F = 0.33$, $p = 0.72$) did not significantly affect RMR. In addition, although group did not have a significant effect on RMR ($F = 4.19$, $p = 0.061$), there was a surprising increase in RMRs for the well-fed group after the initial baseline recordings (Fig.10). This increase was consistent for both Month 1 and Month 4, whereas Group 2 RMRs showed little variation across all months. In addition, RMRs were compared within groups across all months. Although for Group 1 there was a slight increase after Month 0, these differences were not significant. Group 2 RMRs were very similar across all months (Fig. 10).

Discussion

The main focus of this study was to determine the effect of prey availability on the metabolism and foraging strategies of tarantulas. By reducing the amount of food given to one group of tarantulas, I expected that they would exhibit lower metabolism but a greater detection distance and activity level while foraging compared to well-fed tarantulas. However, the results were variable and did not clearly support the hypotheses. Although the RMRs for food-limited tarantulas were slightly lower than for well-fed individuals, much of this difference was due to an increase in RMRs in the well-fed group rather than a decrease in the RMRs of food-limited individuals. In addition, parameters associated with foraging (prey detection and locomotory activity) were not consistently different between the two groups.

Weight Gain

Being fed only once every 5 days may not appear to be enough food for many animals, but the result of the feeding trials showed that once every 5 days was more than adequate for *P. cancerides*. Before the experiment began and the spiders were separated into two different feeding groups, all individuals were fed on a weekly basis. The end of first month of the feeding trial is the last time both the 5- and 30-day feeding groups captured prey with the same frequency (Fig.4). By the time the second feeding trial was administered, there was a significant difference ($p < 0.01$) in the proportion of spiders in the two groups that ate. Thus, at some point after month 1, the majority of Group 1 became satiated, and only 20% of the group ate during the second feeding trial, compared to 66% of Group 2. This trend in the proportions of individuals that ate within the two

groups continued for the next two months of the trial, with an increasing divergence over time.

Before acquiring Batch 2, all spiders were being fed 25 ± 5 % of their body weight during feedings. After adding Batch 2 to the trials, it became very difficult to find crickets that measured 25 ± 5 % of their weight. Therefore, all individuals were fed on the basis of their batch: Batch 1 continued to receive 25 % of their weight, and Batch 2 received 50 % of their weight. Although individuals from Batch 2 received a higher percent of food on the basis of their body weight, the measure of percent gained/consumed accounted for the difference in food consumed. The difference in the percent weight gained/consumed is likely due to the temporal separation in the feeding of Group 2. Group 1 was consistently fed every 5 days and was able to store more energy from food. Group 2 was also able to store the nutrients from their food when fed but used some of these energy reserves over the following 30 days. Although their weight gain was not as high as that of Group 1, growth trends displayed by individuals in Group 2 were similar to previously published data. Bradley (1996) found that *Misgolas rapax* (Sydney brown trapdoor spider) needed approximately 4 meals in the period of one year to maintain a constant weight and 20 meals to double its weight. With four meals in four months, Group 2 increased their weight by 25%. Thus, to double their weight over a year, tarantulas in this experiment would need 16 feedings, similar to the 20 expected by Bradley (1996). Because tarantulas can survive greater than two years without food (Baerg 1958), feeding once a month provides them with enough energy to continue to grow and gain weight.

Because of the reduction in proportion of individuals in Group 1 that fed after Month 1, the average length of the trials markedly increased after Month 1 (Fig. 5a). Because the spiders were given a maximum of 5 minutes, the high number of individuals not feeding caused an increase in the average trial time for Group 1. These results are similar to what was seen by Bradley (1996), that spiders fed frequently will stop eating and responding to prey stimulus altogether. These behaviors were seen in individuals that did not eat during the feeding trial. They would often deliberately move away from the prey or raise their front legs in displays of aggression. These behaviors were not typical of tarantulas that were going to eat. When the individuals that did not eat were removed from the analysis of trial time, there was still a significant longer trial time for Group 1, but not until Month 4 (Fig. 5b).

Each spider had its container attached to the feeding arena during feeding trials, which provided a large, unfamiliar area. We did not have an accessible way to measure total distance moved, but we were able to directly observe if a spider left its container to venture into the feeding arena. The results showed that contrary to our expectations, the 5-day feeding group left the box more frequently (Fig.6). Although there were spiders that both ate the cricket and left the box (10 % of total that left their boxes), the majority of individuals that left the boxes did not eat. Because a greater proportion of individuals in Group 1 did not eat, this gave them a greater length of time to leave their containers during the 5-minute trial. Tarantulas will often explore unfamiliar areas given the opportunity (personal observation). Thus, the differences in frequency of locomotory activity may not be correlated with level of satiation as was seen by Walker et al. (1999).

In future experiments, it would be interesting to quantify activity levels in the feeding arena in separate trials without prey.

Detection Distance

Because of limited access to food, I predicted that Group 2 individuals would be more likely to actively pursue and capture the cricket and would also exhibit an increased prey detection distance, as was seen by Punzo (1989). Although a higher proportion of individuals in Group 2 ate compared to Group 1, Month 1 was the only month in which Group 2 had a significantly higher detection distance than Group 1 (Fig. 6). In all other months, either the mean of Group 2 was marginally larger than Group 1 or Group 1 displayed a higher detection distance. The detection distance for Group 2 in Month 1 was the highest that was recorded for the 4-month period. From Months 2 to 4, the averages were lower than for Month 1 and appeared to plateau.

According to Anderson (1974), during starvation of spiders, their normal capabilities generally remain intact. Although these spiders had been starved for a 1-month period, it appears that it did not decrease their detection distance. Although food deprivation did not decrease their detection distance, it was also not shown to increase, as was hypothesized. There are limitations to this measurement because it relies on the first movement of the spider to indicate when it detected the prey. Some of the subjects might have not been in a position conducive to striking for a sit-and-wait predator, whereas others may simply have known that the prey was close but were waiting for it to come closer before attacking. Although the results do not support the hypothesis that a greater detection distance would be seen in the less-fed group, it does show that the movement of the spiders in Group 2 remained fairly constant. As described by Punzo (1989),

tarantulas deprived of food for 72 hours were shown to capture prey at a greater distance and have a larger awareness field than those that had only been food deprived for 6 hours. Our experiment did not show a significant difference between the detection distance for either the 5- or 30-day feeding groups. It is possible that because individuals used by Punzo (1989) were all wild caught, they were naturally hungry (Anderson 1974; Wise 1975). All of the tarantulas used in this study were reared in the laboratory and very well fed. Differences in willingness to feed may be due to differences in feeding histories.

One major confounding factor in the experiment was molting. Because feeding response to limited food access was being measured, the pre- and postmolt fasting by individuals was difficult to separate from a spider's choice to not eat. The feeding schedule of Group 1 enabled measurement of the pre- and postmolt fasting times because the frequency of their 5-day feeding schedule allowed for more exact measurements than that of Group 2. Our results indicate that premolt fasting time is correlated to the size of the tarantula (or instar), not to age. Although the spiders in Batch 1 and 2 were from the same egg sac and were thus the same age, there was a significant difference in the non-feeding premolt period. Though our average premolt fasting time in Group 1 was similar to the 30 days stated by Deevey (1949), we found that there were individuals that fasted for much longer than this 1-month period. The average length of premolt fasting, ranging from 5 to 40 days in Group 1 and up to 90 days in Group 2, made it difficult to consistently measure some of the behavioral parameters (detection distance, leaving box, etc.) because a large portion of the 120 days of the trial was spent fasting. It might be easier to use mature tarantulas in future feeding experiments because their intermolt periods are substantially longer.

Resting Metabolic Rate

Resting metabolic rate (RMR) has been shown to decrease in spiders that are food deprived (Anderson 1974). We expected that by reducing the amount of food given to tarantulas, their RMRs would be lower than those of well-fed individuals. Although the results of this study supported my hypothesis, the magnitude of the change was different from what I had predicted: RMRs for food-deprived individuals remained constant but increased for well-fed individuals. RMRs for the well-fed group increased after one month and remained consistently higher than those for Group 2 in the last month (Fig. 10). This suggests that RMR is correlated with prey availability, but in this case, individuals show increased metabolic activity after periods of prey abundance. Although wolf spiders show a decrease in RMR after one month of starvation (Anderson 1974), because of their ability to survive long periods without food (Baerg 1958), a longer food-deprivation time may be required to see similar responses in tarantulas.

In conclusion, feeding once a month did not appear to significantly affect tarantulas. Individuals continued to gain weight, there were no significant changes in their behaviors, and RMRs remained constant throughout the 4-month study period. In contrast, individuals fed every five days reached satiation after one month, and prey capture rates significantly decreased, whereas the RMRs increased. It appears likely that the feeding parameters must be greatly exaggerated before significant changes in foraging activities and metabolic rates are observed

Table 1. Average weights at start and end of trial, with individuals separated by group and batch

Group	Batch	Sample Size	Average Start Weight (g)	Average Final Weight (g)	Average Weight Gain (g)
1	1	7	1.26 ± 0.14	2.437 ± 0.159	1.18 ± 0.075
2	1	9	1.35 ± 0.11	1.52 ± 0.16	0.17 ± 0.073
1	2	14	0.23 ± 0.012	1.09 ± 0.11	0.86 ± 0.11
2	2	15	0.21 ± 0.007	0.28 ± 0.014	0.071 ± 0.01

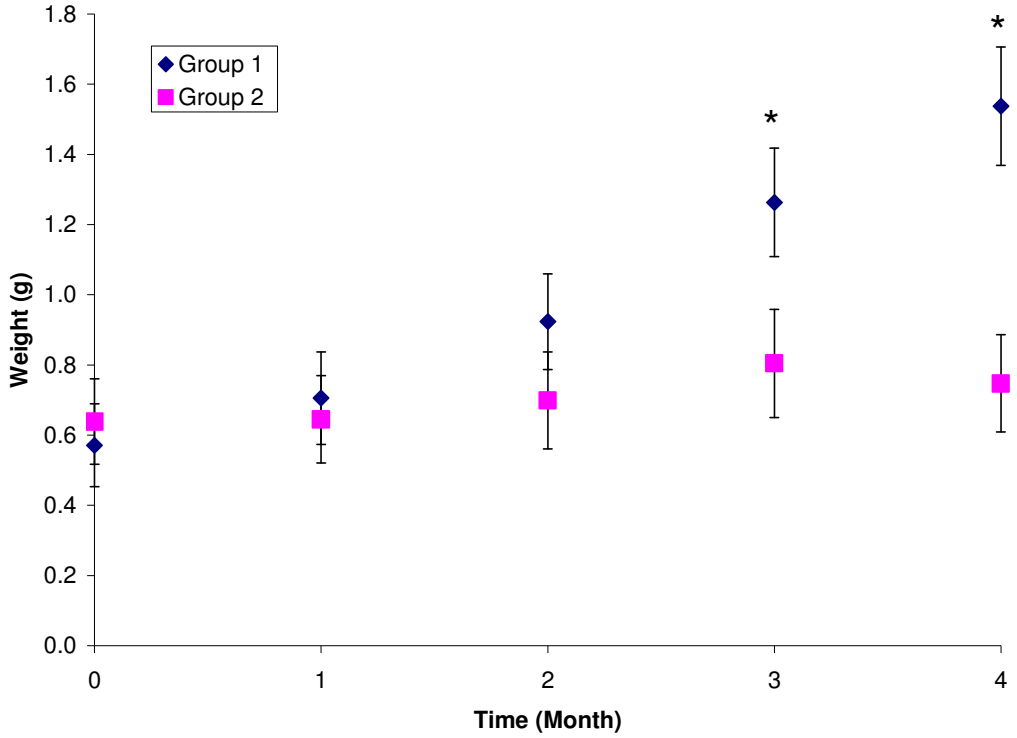


Figure 1. Average weight of individuals throughout the 4-month study. There is a significant difference between Groups 1 and 2 at Month 3 ($t = 2.1$, $p = 0.0211$) and Month 4 ($t = 3.65$, $p = 0.00071$).

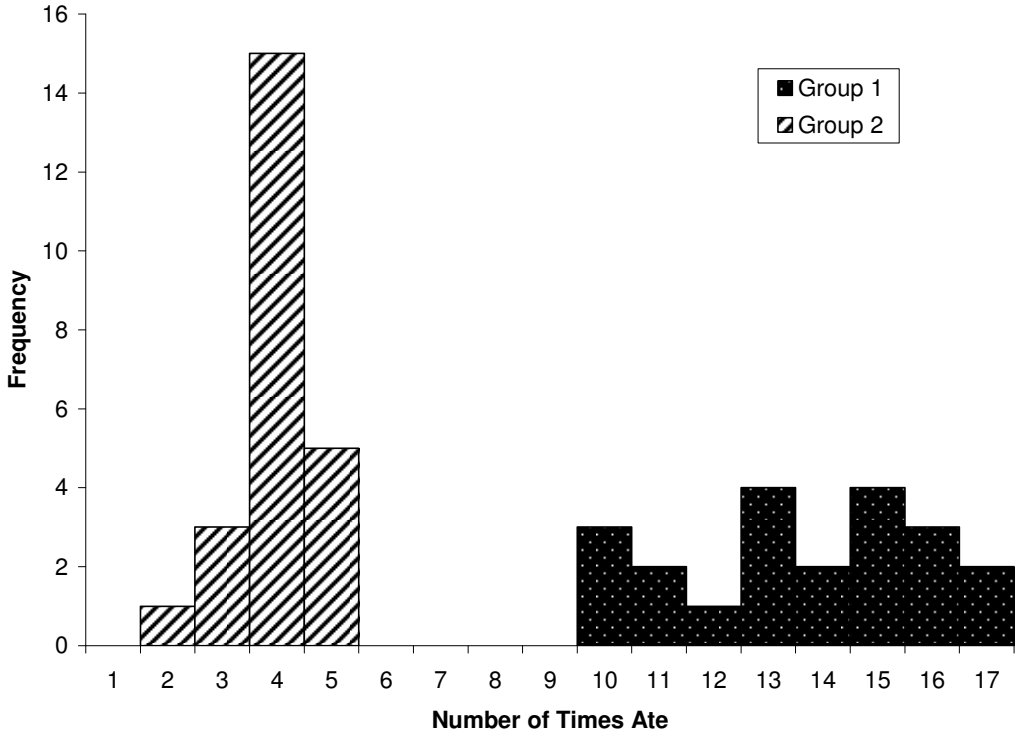


Figure 2. Histogram of the number of individuals in Groups 1 and 2 that ate during the 4 months of feeding trials. Group 1 was offered food 25 times, and Group 2 was offered food 5 times.

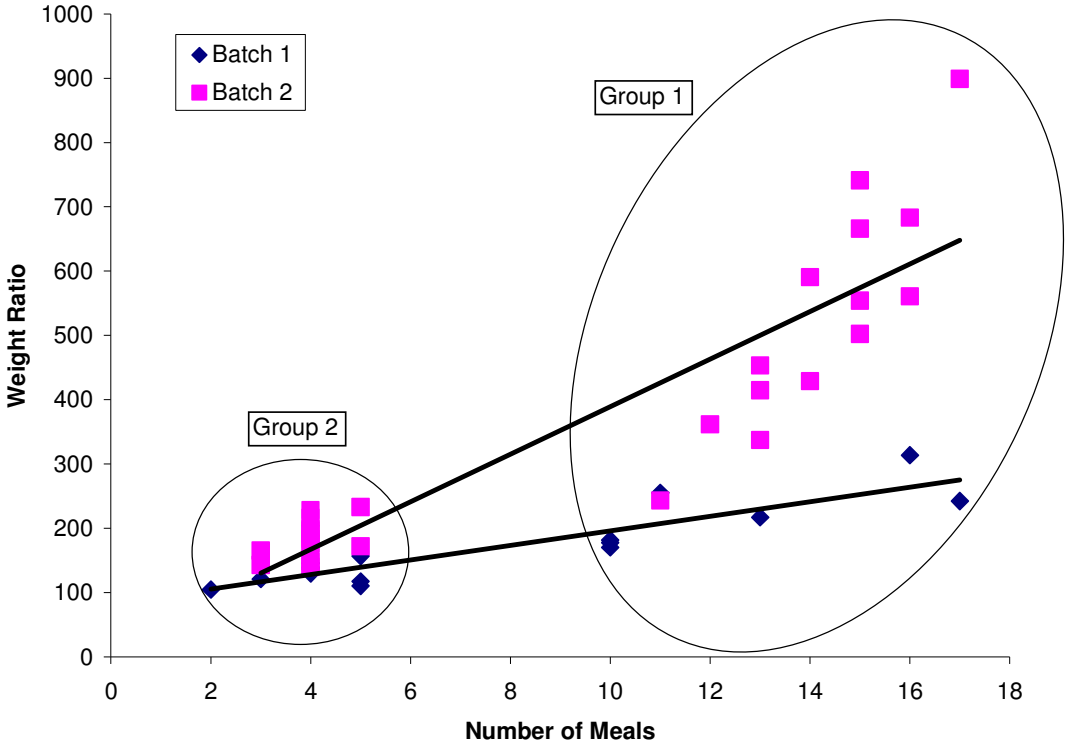


Figure 3. The number of meals consumed by each spider compared to its weight ratio. The weight ratio is the ratio of the final to the initial weight. Both Batch 1 and Batch 2 show positive correlations (Batch 1: $r^2 = 0.82$, $p < 0.0001$; Batch 2: $r^2 = 0.83$, $p < 0.0001$.

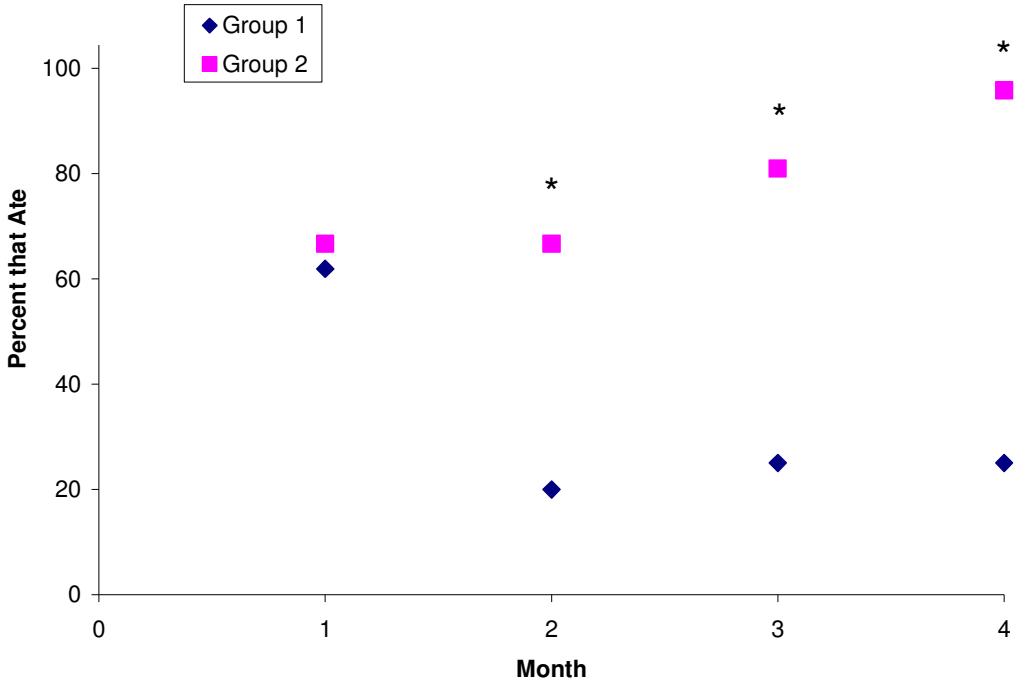
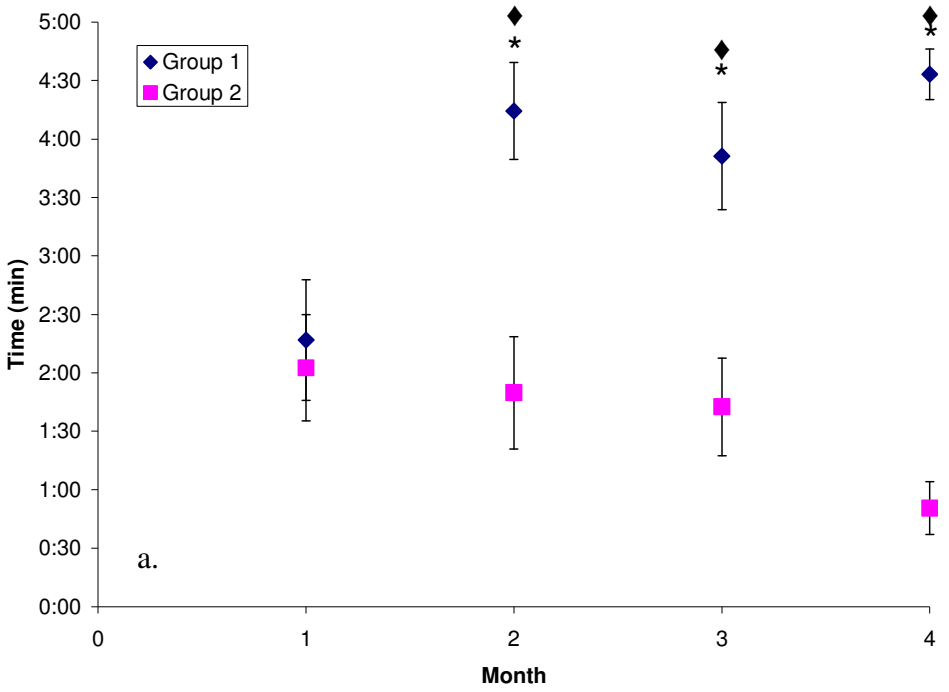


Figure 4. Proportion of individuals from Groups 1 and 2 that ate during the feeding trial. Based on the number of individuals that were offered food, the proportions only include those who ate during the feeding trial. Month 1: χ_c^2= 4.33*10^-1, p > 0.05; Month 2: χ_c^2= 7.79, p< 0.01; Month 3: χ_c^2= 10.7, p< 0.005; Month 4: χ_c^2= 20.7, p< 0.001.



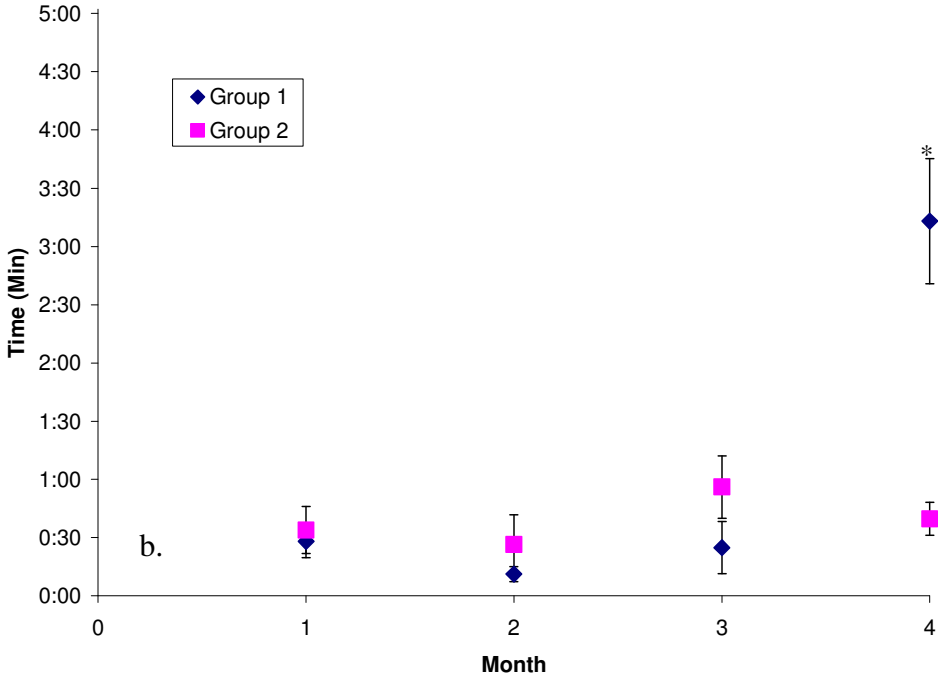


Figure 5 a and b. Trial times for Groups 1 and 2 by month. a. All individuals are included (eaters and non-eaters). There was no significant difference in the average trial length between Group 1 and Group 2 at Month 1 ($F = 0.119$, $p = 0.73$). There were, however, significant differences in the next 3 months (Month 2: $F = 13.794$, $p = 0.0006$; Month 3: $F = 12.013$, $p = 0.0013$; Month 4: $F = 137.44$, $p < 0.0001$). * = Significant difference between Group 1 and Group 2. ♦ = Significant difference compared to Month 1 for Group 1. b. Only includes individuals that ate during trial. There was no significant difference between the average trial lengths until Month 4 ($F = 43.617$, $p < 0.0001$).

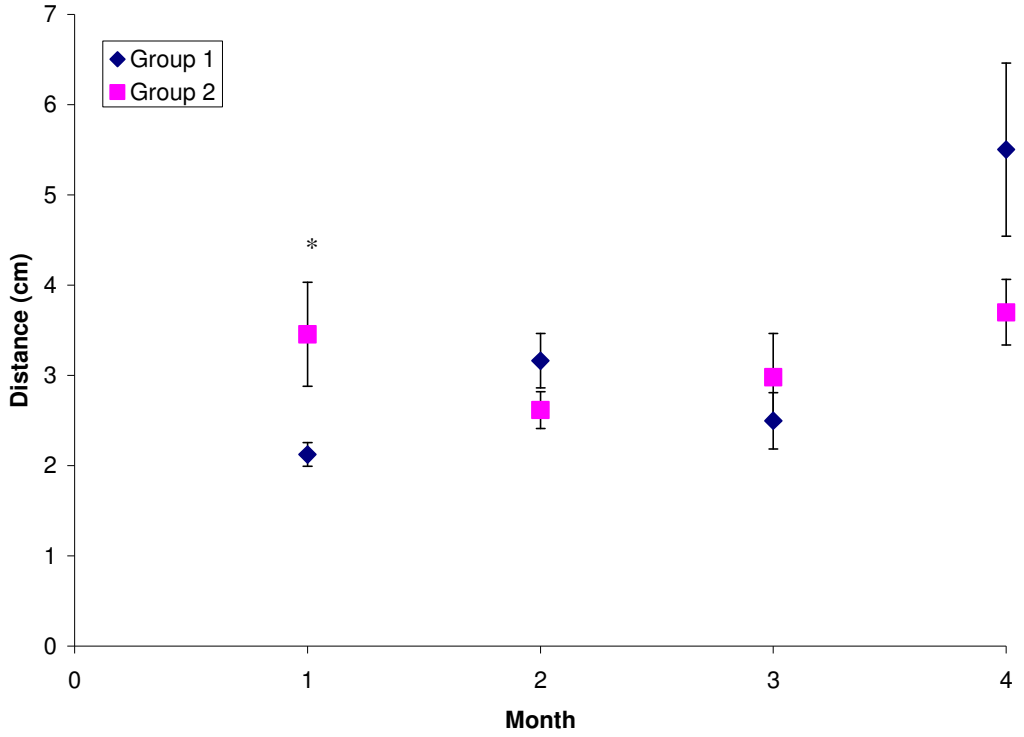


Figure 6. Detection distance of prey by spiders during feeding trials that only include trials in which cricket was not closer than detection distance before spider moved. There were trials where cricket would move close, retreat and then the spider would move. This removed all occasions in which the cricket was further at the time of the spider's first movement than it had previously been during the trial. Month 1: Group 1: (mean ± 1 SE) 2.12 ± 0.13 cm, Group 2: 3.45 ± 0.58 cm, F=5.053, *p = 0.308; Month 2: Group 1: 3.16 ± 0.30 cm, Group 2: 2.62 ± 0.20 cm, F = 2.425, p = 0.128; Month 3: Group 1: 2.50 ± 0.31 cm, Group 2: 2.98 ± 0.49 cm, F = 0.661, p = 0.422; Month 4: Group 1: 5.5 ± 0.96 cm, Group 2: 3.7 ± 0.36 cm, F =3.774, p = 0.59.

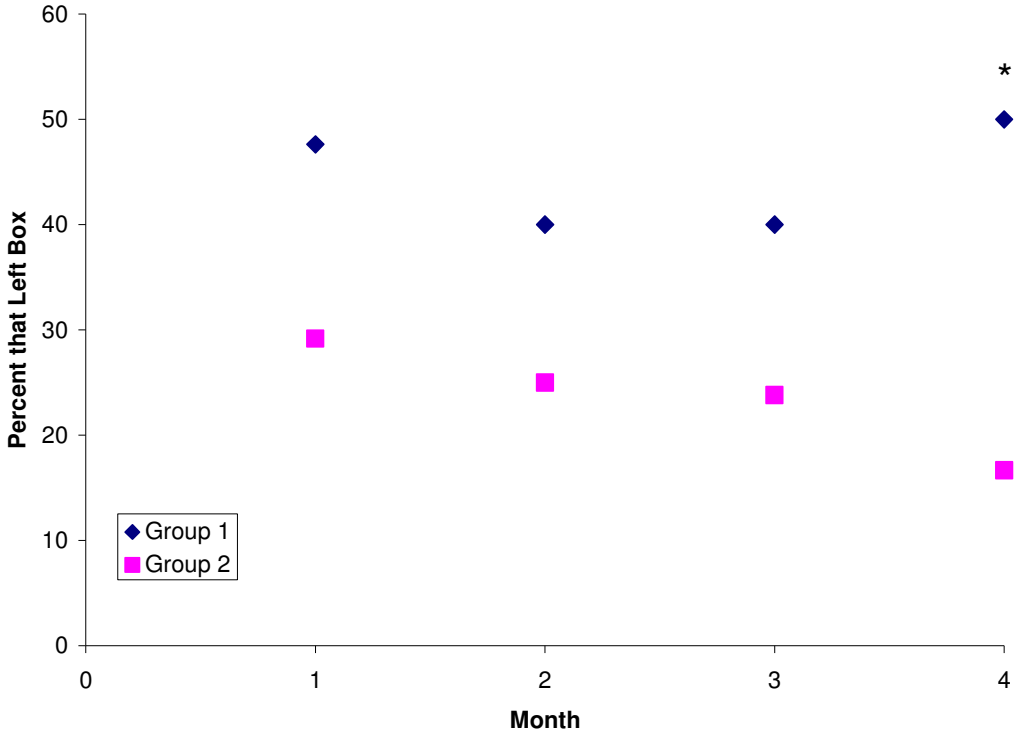


Figure 7. Proportion of individuals that left their boxes during the feeding trial. This includes all spiders that left their boxes, regardless of whether they ate or not. Month 1: $X_c^2 = 1.78$, $p > 0.05$; Month 2: $X_c^2 = 0.55$, $p > 0.05$; Month 3: $X_c^2 = 0.61$, $p > 0.05$; Month 4: $X_c^2 = 4.16$, $p < 0.05$.

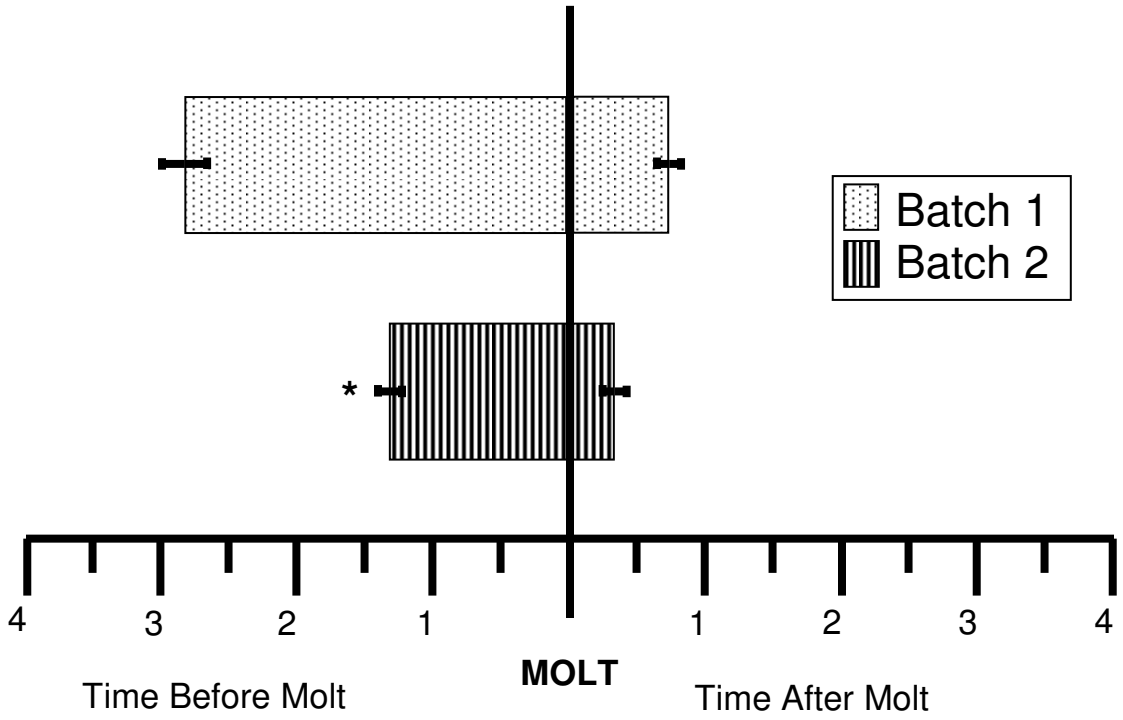


Figure 8. The days before and after molting that individuals from Group 1 did not eat. Because of a large weight difference in Group 1, it was separated into Batch 1 (mean ± 1 SE; 1.26 ± 0.14 g) and Batch 2 (0.22 ± 0.012 g) for comparison. There was a significant difference between the times prior to molting that the tarantulas did not eat when comparing the two batches ($t = 5.22$, $p < 0.0001$). There was, however, no significant difference between the times after molting until feeding began for the 2 batches ($t = 1.76$, $p = 0.096$).

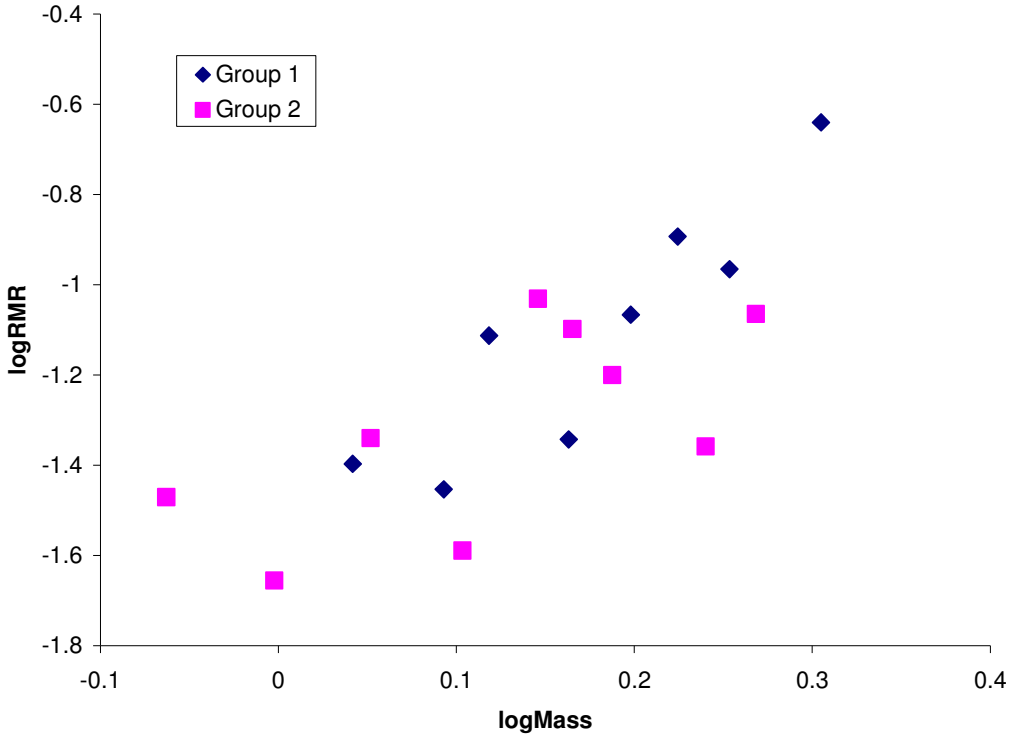


Figure 9. logRMR increases with logMass. These are the unadjusted RMRs at Month 0. All months showed a similar trend; therefore, this figure was included as a representative of the data.

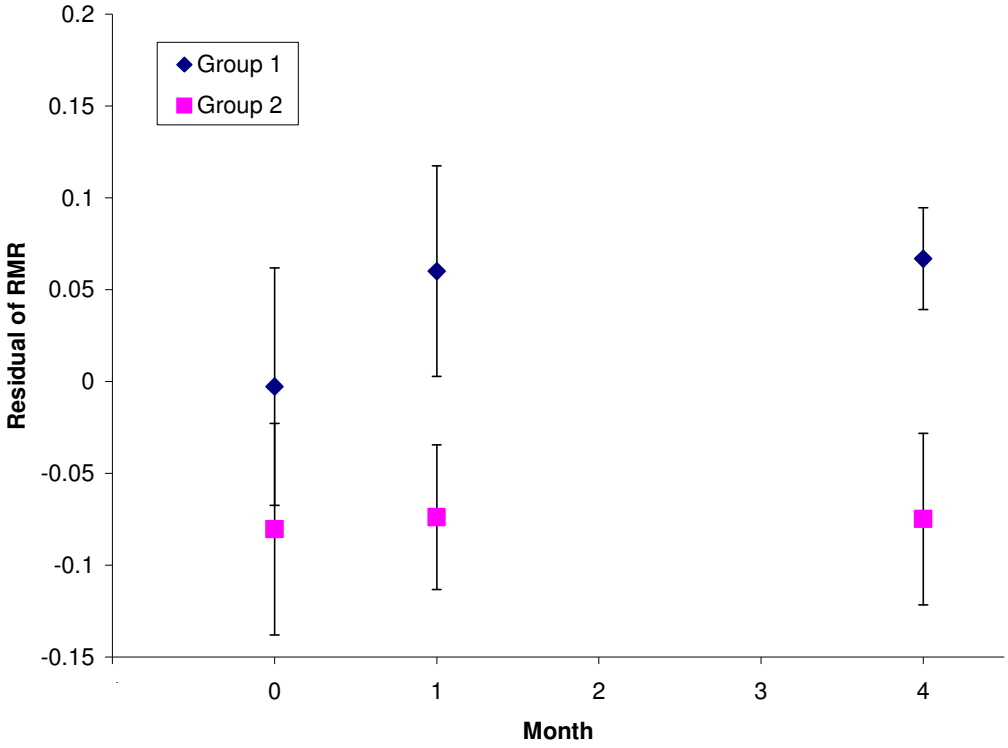


Figure 10. The residuals of logMass* logRMR for Batch 1. There was no difference between Group 1 and Group 2 at Month 0 ($t = 1.05$, $p = 0.30$), Month 1 ($t = 1.81$, $p = 0.081$) or Month 4 ($t = 1.92$, $p = 0.066$). There were no significant inter-group differences between any months.

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