The effect of prey availability on metabolism and activity in the tarantula *Phormictopus cancerides*

B.N. Philip and C. Shillington

Abstract: Spiders typically exhibit very low resting metabolic rates (RMR) and altered feeding behaviors as mechanisms to survive extended periods of limited food availability. We examined the effect of different periods of food deprivation on RMR and foraging activities in the Hispaniolan giant tarantula (*Phormictopus cancerides* (Latreille, 1806)) (Araneae: Theraphosidae). 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, we compared differences between the two groups in (*i*) prey capture frequency, (*ii*) time to prey capture, (*iii*) locomotory activity, and (*iv*) the predator's prey detection distance. Metabolic rates increased for the well-fed group but remained constant for individuals fed once a month. Time to prey capture decreased for food-limited individuals and the proportion of individuals that ate during each feeding trial was significantly higher in the 30-day group. Conversely, results for locomotory activity and detection distances were inconclusive.

Résumé : Les araignées utilisent généralement des taux de métabolisme au repos (RMR) très bas et des comportements alimentaires modifiés comme mécanismes pour survivre aux périodes prolongées de faible disponibilité de la nourriture. Nous examinons les effets de différentes périodes de carence de nourriture sur le RMR et les activités de recherche de nourriture chez une mygale (*Phormictopus cancerides* (Latreille, 1806)) (Araneae : Theraphosidae). Les jeunes mygales ont été séparées en deux groupes alimentaires et nourries respectivement une fois tous les 5 ou 30 jours. Les repas expérimentaux mensuels étaient précédés de mesures du RMR. Durant les essais alimentaires, nous avons comparé chez les deux groupes les différences dans (*i*) la fréquence de capture des proies, (*ii*) le temps écoulé avant la capture de proies, (*iii*) l'activité locomotrice et (*iv*) la distance à laquelle le prédateur perçoit sa proie. Les taux métaboliques ont augmenté chez le groupe bien nourri, mais sont demeurés constants chez les individus nourris une fois par mois. Le temps écoulé avant la capture de proies diminue chez les individus à alimentation limitée et le pourcentage d'individus qui mangent durant chacun des essais alimentaires est significativement plus élevé chez le groupe nourri aux 30 jours. Par ailleurs, les résultats de l'activité locomotrice et des distances de détection sont peu concluants.

[Traduit par la Rédaction]

Introduction

Energy is essential for sustaining life and organisms have developed many mechanisms to acquire the energy required for survival and reproduction. What is stored as food caches by one animal is maintained as internal energy reserves by another. As these reserves begin to diminish, organisms must find ways to replenish them. Predators, for example, may alter their normal foraging patterns to maximize the possibility of finding prey. Organisms that are normally less inclined to search for food increase their locomotory activity when faced with starvation (e.g., Hervant et al. 1997). Similarly, Walker et al. (1999) found that the wolf spider *Hogna helluo* (Walckenaer, 1837) altered its predatory behavior to more actively search for prey when it was food-limited. As well as altering behaviors, invertebrate ectotherms selectively forage based on particular nutrients needed (Mayntz et al. 2005). These different behavioral strategies are examples of efforts by organisms to minimize the risk of starvation.

Once food is ingested and assimilated, it must be converted within the body 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 and called metabolic rate (MR). Because of 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 (Bennett 1988).

To compare the MRs 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 and is measured when an animal is at rest and post-absorptive. Activities, such as locomotion and digestion, lead to significant increases above RMR. For example, the MR of an actively running beetle is 72 times higher than when 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 from RMR during flight in moths (Reinhold 1999). In inver-

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tebrates, increases in MR associated with feeding are typically 2- to 3-fold that of RMR levels (reviewed in Secor 2009).

RMR is also correlated to the availability of food. Bennett (1983) suggested that low RMR in 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, sporadically spaced 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).

Organisms do not employ only one mechanism for obtaining energy. A shift can be made from a sit-and-wait strategy to a more active predation strategy. In response to environmental variation in prey availability, the wolf spider *Pardosa agrestis* (Westring, 1861) will alter its "waiting–moving" continuum to maximize food capture (Samu et al. 2003). Although they are well-known predators, tarantulas (Araneae: Theraphosidae) are a poorly studied group of animals. They are typically sit-and-wait predators that attack unsuspecting prey from the proximity of their burrows and can survive extended periods of starvation (Baerg 1958; Punzo 1989). This sit-and-wait strategy is also likely to affect metabolic rates. In general, MR increases with the mass of an organism (see Schmidt-Nielsen 1997). However, as a group, spiders have a lower RMR compared with 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 the wolf spider *Lycosa lenta* (Hentz, 1844) for 5 months, Anderson (1974) found that RMRs initially decreased with increasing periods of food deprivation and then plateaued, whereas body mass continually declined. The reduction in MR likely increases 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 prey rather than waiting for prey to pass by.

In this study, we manipulated food availability to examine the effects of hunger on prey capture activities and metabolic rates in tarantulas. We hypothesized that food-deprived animals would exhibit the following: (*i*) a change in foraging strategy, (*ii*) an increased awareness of prey, and (*iii*) a lower RMR. We predicted that food-deprived tarantulas would have higher levels of locomotory activity and be more active in attempts to capture prey, indicated by a greater prey detection distance and an increased locomotory activity level. Also, we expected that those tarantulas experiencing longer periods without food would have lower RMRs than tarantulas feeding regularly.

Materials and methods

Juvenile Hispaniolan giant tarantulas (*Phormictopus cancerides* (Latreille, 1806)) (n = 48) were used for this experiment. These tarantulas are considered to be aggressive, burrowers from the Caribbean. They are fast growers, making them ideal as test subjects. Spiders were obtained from the same egg sac and were reared from the second instar in our laboratory for ~10 months (batch 1; n = 18). Shortly after the experiment began, two subjects died, prompting us to seek additional spiders for the study. We acquired additional individuals from the same egg sac and these individuals constituted batch 2 (n = 30). For the duration of the study, *P. cancerides* were housed in separate, clear plastic containers (~227 cm^3) in a laboratory under a natural photoperiod (14 h light : 10 h dark) at 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 house crickets (*Acheta domestica* L., 1758) once a week.

Tarantulas were randomly divided into two groups. Group 1 (n = 9 from batch 1, n = 15 from batch 2) was fed one cricket every 5 days for the 4-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 based on their body mass.

All feedings were monitored to determine which spiders consumed meals. Crickets not eaten were removed from the containers after 24 h, and the spiders were not fed again until their next scheduled feeding date. Dates of all 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). 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 premolt and postmolt fasting times were estimated. Because of the length of time between feedings of individuals in group 2, premolt and postmolt fasting times were estimated based on individuals in group 1.

Metabolic rates

MRs were determined as rates of carbon dioxide production ($\dot{V}_{CO_2}$) using an open-flow respirometry system in post-absorptive animals. All subjects were weighed before being placed in the metabolic chamber. Six subjects and one baseline were run per 24 h 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, Lincoln, Nebraska, USA), which transmits data to a computer running acquisition software (DATACAN; Sable Systems Inc., Las Vegas, Nevada, USA). The flow rate of air through the system was 25 mL/min. Using an eight-channel multiplexer (Sable Systems Inc., Las Vegas, Nevada, USA), the 24 h recording period was broken into six 4 h blocks. During each of the 4 h blocks, the individual MRs were measured for 15 min after a period of 20 min to flush the system and reduce CO_2 build-up. The CO_2 produced by the subject in the chamber was measured in parts per million.

The rate of CO_2 production ($\dot{V}CO_2$) was calculated from the fractional concentrations of CO_2 leaving (F_e) and entering (F_i) the respirometry chambers, using the equation from Withers (1977): $\dot{V}CO_2$ (mL/h) = ($F_eCO_2 - F_iCO_2$) × flow rate (mL/h). Because of the Ascarite's removal of all CO_2 entering the chambers, F_iCO_2 was zero; therefore, $\dot{V}CO_2$ 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 min period over any of the six recordings per individual for the 24 h recording. See Shillington (2005) for additional details about the experimental setup.

Metabolic rates for both groups were measured once a month prior to the group 2 feeding trial, when the animals were postabsorptive. To linearize the results, all metabolic data were $\log_{10}$-transformed. Because of the influence of mass on MR, the data were adjusted by regressing the log RMR on log mass. The residuals from this regression are considered mass-corrected RMRs and were used in all analyses (see Beaupre and Zaidan 2001; Shillington 2005). This mass-corrected or mass-independent variable was used because of concerns about using size-specific indices (Packard and Boardman 1999; Hayes 2001). 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. Unlike the behavioral studies, which include data from all individuals, metabolic measurements were only performed on individuals from batch 1.

Feeding trials

Feeding trials were conducted once a month for all individuals in both groups. Although group 1 was fed every 5 days, their behaviors were only observed once a month using a special arena setup (see Test apparatus below) along with group 2. Very little information is available about tarantulas feeding in their natural environment, so we used published information on other spider species and our discretion to determine the feeding rates for these trials.

Mass

At the start of each monthly feeding trial, all tarantulas were weighed. Differences in mass were compared for groups 1 and 2 each month. The initial mass of the individuals (separated by batch) were compared using a Student's *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 cm × 6 cm × 5.5 cm Plexiglas® feeding arena was connected to the individual tarantula containers. This meant that tarantulas would not be forcibly removed from their "home" territory, but could move out into a larger arena to capture prey. Following the connection of the container to the arena, the prey item (cricket) was introduced at the opposite end of the 14 cm run. A 1 cm × 1 cm square grid was placed on top of the arena so that quantitative measures of activity could be made from video recordings of the trials.

All trials were recorded with a camera (Panasonic WV BP130) positioned above the arena so that both the tarantula container and the feeding arena could be seen clearly. Because all tarantulas were fed during daytime hours prior to the start of the study, all feeding trials were likewise run during the day to be consistent with pretrial habituation. Each trial was timed from the introduction of the cricket into the arena until either the cricket was captured by the tarantula or 5 min had elapsed. Preliminary tests indicated no difference in capture frequency after a 5 min time period had elapsed (i.e., if a tarantula had not eaten within the 5 min period, it would not eat even if the cricket was left in the container for a 24 h period). If there was no capture during the feeding trial, the cricket was removed and no food was offered to the tarantula until the next feeding period (either 5 or 30 days), and the test was scored as "no response". Feeding trials for both groups only occurred every 30 days, in accordance with the feeding schedule of group 2. During all nontrial feedings of group 1, crickets were placed in the containers housing the tarantulas; therefore, no group had more access to the testing arena than the other.

Detection distance

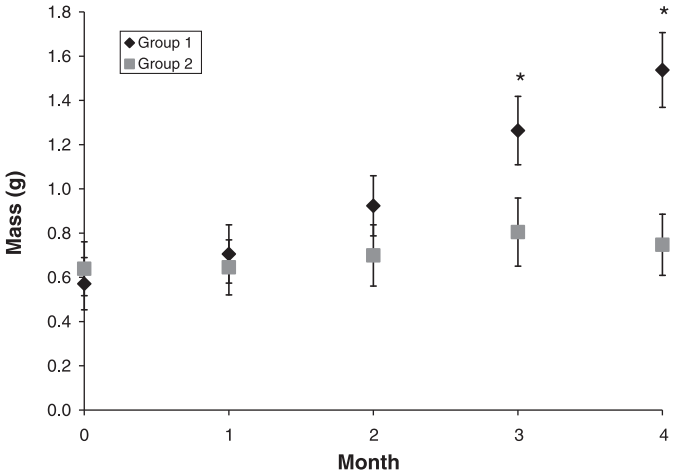
The prey detection distance was measured in the feeding arena to quantify the ability of tarantulas to respond to prey. Frame-by-frame analysis was completed on a Panasonic Desktop Editor VCR where detection distance was determined when the spider made its first movement in response to the prey item 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 arena. An ANOVA was used to determine if there were differences in willingness to leave their container between the groups.

Molts

The molting records of all individuals were maintained

Fig. 1. Mean mass of individual Hispaniolan giant tarantulas (*Phormictopus cancerides*) throughout the 4-month study. There is a significant difference between group 1 and group 2 at month 3 (Student's *t* test, $t = 2.1$, $p = 0.0211$) and month 4 ($t = 3.65$, $p < 0.001$).



throughout the study. We only recorded and compared premolt and postmolt fasting periods for group 1 because group 2 was not fed frequently enough to measure accurate fasting periods.

Results

The initial mass of the spiders were compared at the beginning of the experiment to verify that there was no initial difference between the groups. Although there were differences in the size of individuals within each batch (batch 1 = 1.31 ± 0.084 g (mean ± SE); batch 2 = 0.22 ± 0.0068 g), we found no difference in the mean initial mass between the two feeding group (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, each feeding group contained individuals from both batches.

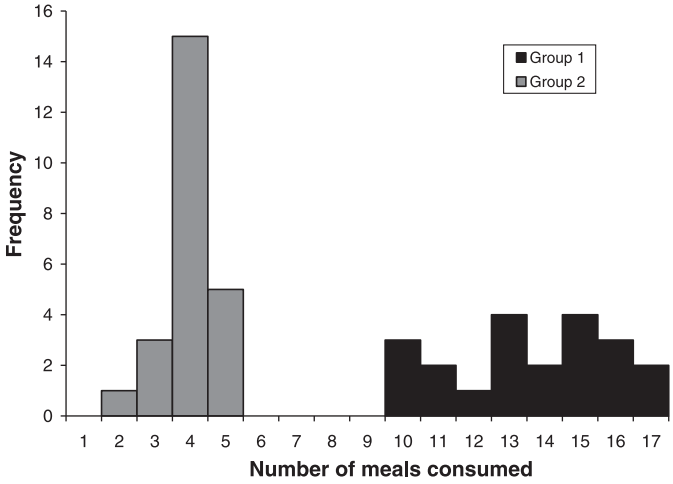
Over the course of the experiment, four individuals from group 1 died. The cause of death is unknown; however, all individuals were in group 1, the well-fed group.

Feeding trials

Mass gain

Throughout the 4 months of this study, the mean mass of both group 1 and group 2 increased (Fig. 1). Although there was no difference in the mean mass 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 mean mass of group 1 was significantly higher compared with the mean mass of group 2. It should be noted that the mean mass for group 1 increased every month. Likewise, the mean mass of group 2 increased through month 3 but decreased at month 4. This decrease is an artifact of molting. There were three smaller individuals that were not included in the mean mass calculated for month 3 because they were in the process of molting. This gave an inflated mean mass at month 3, and thus, the mean mass at month 4 appeared to decrease.

Fig. 2. Histogram of the meals consumed by individual Hispaniolan giant tarantulas (*Phormictopus cancerides*) in groups 1 and 2 during the 4 months of feeding trials. Group 1 was offered food 25 times and group 2 was offered food 5 times.



During the entire experiment, the number of times each spider ate was totaled and compared between the two 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 for different individuals. Group 2 was offered food five times over the course of the study. The mean number of meals consumed was four (80% of the offerings), and the number of meals consumed ranged from 2 to 5 for each individual.

The percent mass gain of individuals fed over the course of the experiment correlates with the number of meals they consumed (Fig. 3). Finding crickets that were the same proportion to the mass of both the larger spiders of batch 1 and the smaller spiders of batch 2 was very difficult. Therefore, individuals were fed according to their batch and the availability of crickets; batch 1 generally received 25% ± 5% of their mass and batch 2 received 50% ± 5% of their mass. Although the trends were consistent between the groups, to examine the mass gains the spiders were separated into batches. For batch 1, the number of meals positively correlated to the percent mass increase ($r^2 = 0.82$, $p < 0.0001$). Similar to batch 1, the number of meals consumed also positively correlated to the percent mass increase in batch 2 ($r^2 = 0.83$, $p < 0.0001$). Although both batches showed an increase in mass that was positively correlated to the number of feedings, the rate of mass gain (mass/number of meals) was higher in batch 2 than in batch 1. The difference is likely a result of the larger relative mass of the prey fed to batch 2, rather than a difference in the number of meals consume by spiders in batch 1 and batch 2 (Fig. 3).

Throughout the experiment, there was variability not only in the number individuals that ate at each feeding trial, but also in the number of individuals that were used at each feeding trial because of molting and death. Only the number

Fig. 3. The number of meals consumed by each Hispaniolan giant tarantula (*Phormictopus cancerides*) compared with its final mass (% of initial mass). The percent change in mass was calculated by dividing the final mass by the initial mass of the spider. Both batch 1 and batch 2 are positively correlated (batch 1: $r^2 = 0.82$, $p < 0.0001$; batch 2: $r^2 = 0.83$, $p < 0.0001$).

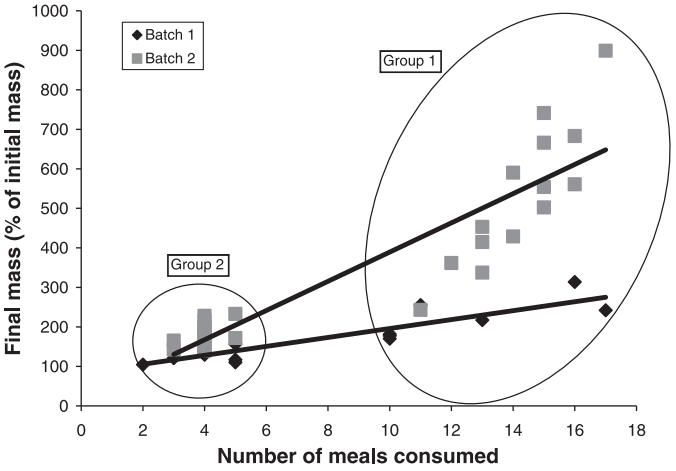
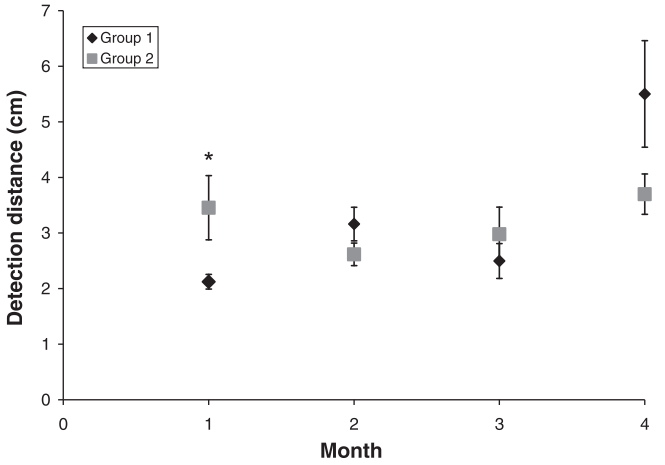


Fig. 4. Detection distance of prey by Hispaniolan giant tarantulas (*Phormictopus cancerides*) during feeding trials as measured by the first movement of the spider. There were trials when crickets would move close and retreat before the spider moved; however, these trials were omitted from the analysis. The only significant difference between the two groups occurred in month 1 ($F_{[1,36]} = 5.053$, $p = 0.0308$).



of individuals used in a specific feeding trail was included when calculating the percentage of spiders that consumed meals. After 1 month of separate feeding regimens, there was no significant difference, based on a contingency table, between the two feeding groups in the proportions of individuals that fed at the feeding trials (month 1: $\chi^2 = 0.433$, $p > 0.05$). Conversely, the following three months all showed significant differences in the proportion of individuals who ate during the feeding trials (month 2: $\chi^2 = 7.79$, $p < 0.01$; month 3: $\chi^2 = 10.7$, $p < 0.005$; month 4: $\chi^2 = 20.7$, $p < 0.001$), and group 2 had a higher proportion in all three months.

Trial times

The mean 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 mean time to prey capture was calculated. There was no significant difference between the mean trial times for groups 1 and 2 through month 3 of the trial (month 1: $F_{[1,26]} = 0.136$, $p = 0.72$; month 2: $F_{[1,17]} = 0.177$, $p = 0.68$; month 3: $F_{[1,20]} = 1.019$, $p = 0.32$). At month 4, however, group 2 had a significantly higher mean trial time than group 1 ($F_{[1,26]} = 43.617$, $p < 0.0001$).

Detection distance and locomotory activity

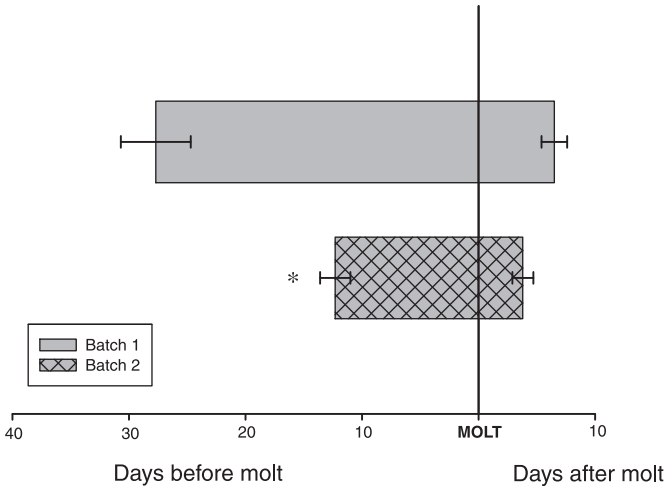
After the cricket was placed into the feeding arena, the distance between predator and prey when the spider made its first movement was measured as the detection distance. For some individuals, this initial movement coincided with a strike response, whereas for others it was merely a small twitch of 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 farther 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 mean detection distance. This was the spider's first movement; however, the movement could not be considered the detection distance because it is likely that detection occurred at a closer distance, but the tarantula did not respond in any way. Data were 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; $F_{[1,36]} = 5.053$, $p = 0.0308$). However, there were no significant differences between the two group means for month 2 ($F_{[1,37]} = 2.425$, $p = 0.128$), month 3 ($F_{[1,34]} = 0.661$, $p = 0.422$), and month 4 ($F_{[1,40]} = 3.774$, $p = 0.591$) (Fig. 4).

Locomotory activity was defined as the number of spiders that left their "home" containers to 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 containers at any point during the feeding trials. During the first 3 months, there was no significant difference in the proportion of each group that left their boxes (month 1: $\chi^2 = 1.78$, $p > 0.05$; month 2: $\chi^2 = 0.55$, $p > 0.05$; month 3: $\chi^2 = 0.61$, $p > 0.05$), but there was a greater proportion of individuals in group 1 (50%) that left their boxes compared with from group 2 (16.7%) in month 4 ($\chi^2 = 4.16$, $p < 0.05$).

Molting

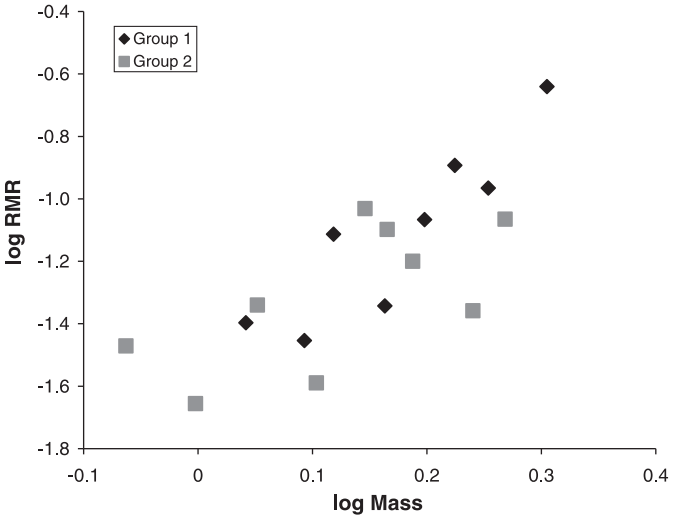
The analysis of premolt and postmolt periods was conducted by dividing group 1 into its respective two batches. Only group 1 was included because group 2 was not fed fre-

Fig. 5. The days before and after molting that individual Hispaniolan giant tarantulas (*Phormictopus cancerides*) from group 1 did not eat. Because of a large mass difference in group 1, it was separated into batch 1 (1.26 ± 0.14 g; mean ± 1 SE) and batch 2 (0.22 ± 0.012 g) for comparison. There was a significant difference between the two batches for time prior to molting during which they did not eat (Student's *t* test, $t = 5.22$, $p < 0.0001$). There was, however, no significant difference between the times after molting until feeding began for the two batches ($t = 1.76$, $p = 0.096$).



quently 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), whereas batch 2 contained much smaller individuals (0.22 ± 0.012 g). All of the individuals but one from batch 2 molted more than once during the study (maximum = 3 molts); 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 their premolt fast; therefore, those spiders were 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; Student's *t* test, $t = 5.22$, $p < 0.0001$) (Fig. 5). There was, however, no significant difference in the postmolt fasting period for the two 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 these data, there were individuals that fasted for periods greater than 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 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 observed, there was a high probability that the tarantulas were unlikely to eat during that trial.

Fig. 6. The resting metabolic rate (RMR) increases with mass in Hispaniolan giant tarantulas (*Phormictopus cancerides*). These are the unadjusted RMRs at month 0. This figure serves as a representative of the data, as all months showed a similar trend.



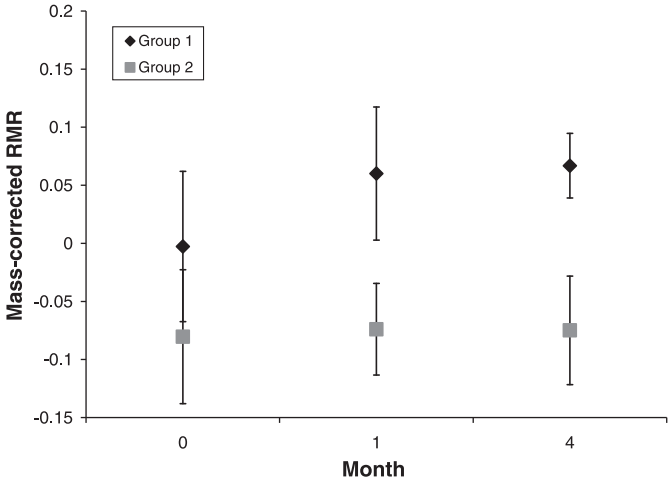
Metabolic trials

Metabolic measurements were only completed for batch 1 throughout the experiment. As expected RMRs increased with body mass (Fig. 6) 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. Month ($F_{[2,48]} = 0.49$, $p = 0.62$) and group × month interaction ($F_{[1,16]} = 0.33$, $p = 0.72$) did not significantly affect RMR. In addition, although group did not have a significant effect on RMR ($F_{[1,48]} = 4.19$, $p = 0.061$), there was an increase in RMRs for the well-fed group after the initial baseline recordings (Fig. 7) that remained consistent for both month 1 and month 4, whereas RMRs for group 2 show little variation across all months. RMRs were compared within groups across all months. Despite the increase in RMR for group 1 after month 0, these differences were not significant. RMRs for group 2 were very similar across all months (Fig. 7).

Discussion

We predicted that there would be changes in the foraging strategies between these two groups; however, we found no differences in prey detection or activity between the two feeding regimes using our experimental setup. There was also no obvious pattern to differences in prey detection using our method of measurement and prey capture times only showed a significant difference after 4 months. However, between the two groups there was a significant difference in the number of animals that ate at each feeding trial. In addition, the food-limited tarantulas maintained a constant RMR across the study period, whereas there was an increase in MRs (after correcting for mass) in the well-fed group, suggesting that they were not yet postabsorptive.

Fig. 7. Mass-corrected resting metabolic rates (RMRs; residuals of log mass × log RMR) of Hispaniolan giant tarantulas (*Phormictopus cancerides*) from batch 1. There was no difference between group 1 and group 2 at month 0 (Student's *t* test, $t = 1.05$, $p = 0.30$), month 1 ($t = 1.81$, $p = 0.081$), or month 4 ($t = 1.92$, $p = 0.066$). There were no significant intergroup differences between any months.



Feeding trials

The result of the feeding trials indicated that a 5-day feeding regime was more than adequate for survival and growth in *P. cancerides*. Before the experiment began, all individuals used in this experiment were fed on a weekly basis. The first month feeding trial was the only time both the 5- and 30-day feeding groups captured prey with the same frequency. By the second feeding trial, there was a significant difference ($p < 0.01$) in the proportion of spiders that ate in the two groups. 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 with 66% of group 2. This trend in the proportions of individuals that ate within the two groups continued for the next 2 months of the trial, with an increasing divergence over time.

Before acquiring batch 2, all spiders were being fed 25% ± 5% of their body mass during feedings. After adding batch 2 to the trials, it became very difficult to find crickets that measured 25% ± 5% of their mass. Therefore, all individuals were fed based on their batch; batch 1 continued to receive 25% of their mass, whereas batch 2 received 50% of their mass. There were differences in mass gain between the two batches, but these differences were consistent between the groups. The difference in the percent mass 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. However, 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 mass 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 Sydney brown trapdoor spiders (*Misgolas rapax* Karsch, 1878) needed ~4 meals in the period of 1 year to maintain a constant mass and 20 meals to double its mass. With 4 meals in 4 months, group 2 increased their mass by 25%. Thus, to double their mass over a year, tarantulas in this experiment would need ~16 feedings, similar to the 20 expected by Bradley (1996). Because tarantulas can survive >2 years without food (Baerg 1958), feeding once a month provides them with enough energy to continue to grow and gain mass.

No individuals in group 1 ate at every feeding opportunity, whereas all individuals in group 2 ate in 21% of the feeding trials. Bradley (1996) also found that when trapdoor spiders were fed every other day, after four meals, they ceased eating and responding to prey stimulus for days to weeks. We also observed specific behaviors in individuals that did not eat during the feeding trial; they would often move away from the prey or raise their front legs when prey approached, sometimes even striking at the prey but not capturing. Surprisingly it was only after 4 months that significant differences were seen in prey capture times, and this was due to an increase in time to capture prey in group 1. For group 2, prey capture times did not differ significantly over the four feeding trials. This again suggests that group 1 was satiated.

Although we expected satiated spiders to reduce their activity levels, individuals in group 1 left their "home" containers during feeding trials more often than did individuals in group 2. Most spiders that ate did not leave their "home" container (90%). The majority of individuals that left the boxes were those that 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 container during the 5 min trial. Tarantulas will often explore unfamiliar areas given the opportunity (B.N. Philip and C. Shillington, personal observations). Thus, differences in frequency of locomotory activity that we observed 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, we predicted that individuals in group 2 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 with individuals in group 1, month 1 was the only month in which group 2 had a significantly higher detection distance than group 1 (Fig. 4).

We predicted that if spiders were food-deprived for a 1-month period, they would increase their detection distance. Although we found no significant change in detection distance during the trials, we suggest that 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 may not have been in a position conducive for striking, while others may simply have been aware of the prey but were waiting for it to come closer before attacking. According to Punzo (1989), tarantulas deprived of food for 72 h 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 h. 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 at the beginning of the study; therefore, the differences in detection distance for the two studies may be due to differences in feeding histories. Our observations suggest that a different method is required to more accurately assess prey detection by tarantulas.

One major confounding factor in the experiment was molting. It was difficult to separate an individual's response (feed vs. not feed) from the premolt and postmolt fasting periods. The feeding schedule of group 1 enabled measurement of the premolt 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, not age. Although the spiders in batch 1 and batch 2 were from the same egg sac and were thus the same age, there was a significant difference in the nonfeeding premolt period. Although our mean premolt fasting time in group 1 was similar to the 30 days stated by Deevey (1949), we found individuals that fasted for much longer than this 1-month period. The mean length of premolt fasting, which ranged 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

We expected that by reducing the amount of food given to tarantulas, their RMRs would be lower than those of well-fed individuals (see Anderson 1974). Although we found differences in MRs between the two feeding groups, the magnitude of the change was different from what we had predicted: RMRs for food-deprived individuals remained constant, whereas RMRs for well-fed individuals increased. RMRs for the well-fed group increased after 1 month and remained consistently higher than those for group 2 in the last month (Fig. 7). Although wolf spiders show a decrease in RMRs after 1 month of starvation (Anderson 1974), a longer food-deprivation time may be required to see similar responses in tarantulas because of their ability to survive long periods without food (Baerg 1958). The increase in MRs in group 1 suggests that animals were not postabsorptive and this elevated MR might be part of the specific dynamic action (SDA) or physiological response associated with feeding (reviews by McCue 2006; Secor 2009). The duration of SDAs is very variable, but for most invertebrates, MRs return to RMR levels in under 5 days (see Secor 2009). However, there are no studies of SDAs in tarantulas or other spiders. In comparison with other spiders, it is suggested that tarantulas have lower than expected RMRs (Anderson 1970), and it is possible that there is a correlation between low RMR and duration of SDA. Further studies are needed in this area.

In conclusion, feeding once a month did not appear to negatively affect tarantulas. Individuals continued to gain mass; there were no significant changes in their behaviors; and RMRs remained constant throughout the 4-month study period. In contrast, individuals fed every 5 days reached satiation after 1 month and prey capture rates significantly decreased, while the MRs increased. It is likely that the feeding parameters must be greatly exaggerated (i.e., increased food-deprivation period) before significant changes in foraging activities and metabolic rates are observed.

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