

May 2001

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Density and Feeding of *Brachypelma mesomelas* (Araneae: Theraphosidae) in a Costa Rican Cloud Forest

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ABSTRACT

Brachypelma mesomelas is endemic to Costa Rica and found widely distributed from 500m to 2000m in elevation. Their relative densities in any given area may be due to limited prey availability, or lack of sufficient burrows sites. To determine whether or not prey availability was a limiting factor in actual density, prey availability was determined through sampling using pitfall traps. Prey availability was then compared to results of required prey density determined through feeding experiments. Available burrow density was determined and compared to actual *B. mesomelas* density to determine whether or not burrow availability was a limiting factor in density. Neither prey availability nor burrow availability were found to be limiting factors in actual *B. mesomelas* density. Test subjects were fed various prey types to determine if there was a significant trend in feeding rate or percent biomass of prey consumed by *B. mesomelas*. Both feeding rate as well as percent biomass of prey consumed were found to follow a trend based on prey type (although not significantly different). Prey of each type were observed to follow a trend of the rate at which they could be consumed, independent of size, based on high calculated R^2 values of slopes. Softer prey were able to be consumed faster and a greater percent of prey biomass consumed than were harder prey. Based on these results, it is concluded that energy-maximizing feeding occurs in *B. mesomelas* based on consistency of feeding rates of different prey types (i.e. energy is being maximized by limiting the amount of feeding time). Also, it is tentatively concluded based on observations in this study, that the limiting factor of *B. mesomelas* demonstrating optimal foraging traits is an inconsistent optimal prey source.

RESUMEN

Brachypelma mesomelas es endémica de Costa Rica y está distribuido entre 500 y 2,000 metros en elevación. Su densidad en un lugar podría estar asociada a la limitación de presa o a la falta de madrigueras. Para determinar si la presa era un factor limitante se muestreó la disponibilidad de presa usando trampas de fosa y estos resultados fueron comparados con los requerimientos de la araña, obtenidos de experimentos de alimentación. Se determinó la cantidad de madrigueras y se comparó con la densidad actual de *B. mesomelas* para determinar si las madrigueras era un factor limitante en su densidad. Ni la presa ni las madrigueras fueron encontrados como factores limitantes en la densidad de *B. mesomelas*. Además las arañas fueron alimentadas con diferentes tipos de insectos para determinar si había una relación entre el porcentaje de biomasa de presa consumido por *B. mesomelas*. Ambas, el tiempo de alimentación y el porcentaje de presa consumido siguieron

una orientación basado en el tipo de presa (sin embargo no fue significativamente diferente). Presa de diferentes tipos se observó que sigue la tendencia a ser consumido independientemente del tamaño, basado en los cálculos de R^2 de las pendientes. Presas más suaves fueron consumidas más rápido y un porcentaje mayor de biomass fue obtenido comparado con presas duras. Basado en estos resultados se puede concluir que *B. mesomelas* va a maximizar la energía al alimentarse, basado en los diferentes relaciones de alimentación y tipos de presa (por ejemplo, energía se maximizará limitando al tiempo de alimentación). También, es tentativo decir, basado en las observaciones de este estudio, que *B. mesomelas* se encuentra limitada por la inconsistencia en el suministro de presas óptimas.

INTRODUCTION

Brachypelma mesomelas (Theraphosidae) is a large, hairy, earth-dwelling tarantula more commonly referred to as the Orange-kneed Tarantula widely distributed throughout Costa Rica, and is found abundantly on slopes from 500 m to 2,000 m (Valerio 1980). Members of the Theraphosidae family are predominantly nocturnal sit-and wait feeders emerging at night to hunt (Coyle 1986). They have large, paraxial, nearly parallel alignment of chelicerae used in prey capture and feeding, characteristic of tarantulas (Foelix 1996). The chelicerae and pedipalps are used to rotate and push prey into their mouth while feeding.

Tarantulas in general and *B. mesomelas* are known to construct relatively permanent tubular retreats, or live in abandoned burrows or natural cavities under logs or rocks (Coyle 1986, Valerio 1980). Investment in retreat construction suggests that tarantulas are adapted to a relatively sedentary life and females may occupy the same burrow for several years (Stradling 1984). Known reasons for relocation include displacement by the same species or other organisms which enter in their absence, or lack of consistent food supply in a given area (Stradling 1994).

Most spiders are not particular about the type of prey on which they feed (Foelix 1996). Insects are by far the largest part of the diet of a spider (Foelix 1996). Previous studies involving tarantulas showed that they fed regularly on a variety of insects, including

katydids, beetles and crickets (Stradling 1994). Energy-maximizers are those animals whose fitness is maximized when net energy is maximized for a given time spent feeding (Schoener 1991). Females of various predatory organisms are commonly found to be energy-maximizers (Schoener 1991).

Although net energy per unit time has rarely been measured, animals have been observed which appear to be feeding optimally, selecting food of greater biomass yield per unit feeding time (Schoener 1991). This selective feeding based on biomass yield is known as Optimal Foraging Theory (Krebs, 1994). Certain insects, such as stinkbugs, ants and wasps are generally avoided by most spiders (Foelix 1996). This is probably due to poor taste resulting from a chemical defense, or difficulty of handling (e.g. wasps with stingers). Prey that are difficult to handle, as well as those that are chemically defended may be undesirable to a spider, due to an increased in handling time caused by such traits. Thus, it is possible that spiders, specifically *B. mesomelas*, are exhibiting optimal foraging traits.

In order to determine whether or not burrow or prey availability are limiting factors in the actual prey density, several experiments were performed and results compared. The number of density of available burrows was compared to actual density found using a Chi-square test, to determine if it was a limiting factor in the actual density of *B. mesomelas*. The available prey density was calculated and compared to the amount of prey consumed in feeding tests to determine if prey availability is a limiting factor in actual *B. mesomelas* density. Feeding tests using various prey types were performed to determine if *B. mesomelas* followed an 'energy-maximizer' feeding pattern, and if there was a relationship between rate of consumption and prey type. It is hypothesized prey hardness will have a direct effect on percent biomass of prey consumed, as well as rate of feeding. The purpose of

this experiment is to determine what effect prey type, prey availability and burrow availability have on *B. mesomelas*.

MATERIALS AND METHODS

Study Site

The experiment was conducted at the Estación Biológica de Monteverde (EBM), Monteverde, Puntarenas, Costa Rica. The EBM is located in lower montane wet and lower montane rain forest (Haber 2000). On the S. Principal and S. Cariblanco trails within the study area, the elevation ranges from 1600 m and 1700 m. From each trail, one section 500 meters in length was used as a transect to study available burrow density, prey availability, and actual density of *B. mesomelas*.

Density

Brachypelma mesomelas burrow and prey availability was examined in order to determine whether or not they were limiting factors in the actual *B. mesomelas* density. To determine both burrow available and actual density, the two pre-determined trail sections were walked, looking on the uphill side of the trail for possible burrows. Burrows that ranged in size from approximately three to ten cm in width, oval in shape and relatively clear of leaves and litter near the entrance were considered available burrows. Silk surrounding the burrow, as well as insect fragments and exuvies (molting remnants) of *B. mesomelas* were also used as signs of a possible burrow based on the findings of Herrero and Bolaños (1982). Once a burrow was determined to be available, the shortest distance from it to the trail edge (perpendicular distance) was measured, and its location marked.

These measurements were taken for each of the 500 m trails. To determine home available density, the mean distance to burrow (d) was multiplied by the total transect distance (1000 m) to determine area sampled. The number of homes available (n_h) was divided by the area sampled to determine home available density ($D_h = n_h/d*1000$).

At night, the possible home locations were re-visited to check for tarantulas. Those holes that were found to have *B. mesomelas* in them were noted and the tarantula was removed for use in feeding tests. The total number of *B. mesomela* found (n_a) was divided by the area sampled ($d*1000$ m) to determine actual density ($D_a = n_a / d*1000$). Locations other than the two 500 m transects were also used for obtaining tarantulas for testing. However, areas searched and tarantulas found in areas other than the transects were not considered in density calculations.

Prey availability was determined using a series of live pitfall traps along the same transects used for burrow density. One pitfall trap was placed every 100 m along each of the 500 m transects. These traps were checked every three to four days, emptied, and all insects found within were counted and weighed. From this information, an average number of insects per trap per day were determined. Also, the average mass per insect was determined using the total of their individual masses and the total number of insects obtained.

Feeding

First, to test the feeding of *B. mesomelas*, different prey types were offered to determine if there was a difference in rate of feeding and percent biomass of prey consumed. Beetles (Family Scarabeidae), katydids (Family Tettigoniidae), and crickets (Family Gryllidae) were used to test the effect of prey hardness on feeding. Beetles were

classified as 'hard' because of their tough protective elytra, katydids as 'medium hard' because of the presence of an exoskeleton but not as hard as the beetles elytra, and crickets were classified as 'soft'. One species of cockroach was also used to test the effects of chemical odor on feeding.

For each tarantula captured, the second femur on the left side was measured and recorded as an estimation of size. Each spider, as well as the categorized prey, was weighed before the prey was offered. All weighing was done on a Fisher scientific top-loading balance, and weights were recorded to the nearest 0.001 g. Prey were then offered near the anterior of the tarantula to stimulate feeding and the beginning of feeding time was recorded. If prey were not fed upon instantly, they were removed and re-offered later the same day to ensure accurate feeding time calculations. When feeding was completed, both the spider and the prey remnants were weighed and recorded along with the time of completion. Prey presentation and data collection methods were the same for all tarantulas tested and were repeated every two to three days with as many prey and prey types as possible. Prey types were rotated, with the same prey type never being consumed by any one spider two consecutive times.

Using the Gravimetric technique (Southwood 1978), the prey remnants discarded by the tarantula were weighed and this value subtracted from the initial prey weight to determine amount of biomass of each prey consumed. This value was compared to the difference in tarantula pre- and post-weight to ensure accuracy. However, the Gravimetric value was used as the mass of prey consumed in graphs and analysis because of greater accuracy. Lastly, general feeding observed relating to positioning, distance from burrow and activity occurring before, during and after feeding. These observations were noted to

determine if habits had an effect on the rate at which they fed or the amount of biomass consumed for different prey types. Feeding habits have a direct effect on those two areas being tested and could provide an explanation for the results obtained.

RESULTS

Density

Five tarantulas and 84 possible burrows were found in the 1,550 m² area sampled. The D_h was calculated to be 54 burrows available/1000 m², and D_a was determined to be 3.23 tarantulas/1000 m². These values were compared using a Chi-squared (X^2) and were determined to be significantly different between the available burrow density and *B. mesomelas* density ($X^2=47.733$, d.f. =1, $p < 0.001$).

In calculating density of prey available, the area of the opening of the cup on the surface of soil (54.14 cm²) was used as an approximate value for the hunting area of a *B. mesomelas* based on sit and wait techniques used in prey capture. A mean of less than one prey were caught per trap per day. The mean available prey (average mass available per tarantula per day) was determined to be 0.143 grams of prey/tarantula/day. This value was compared, using a Chi-square test, to the average mass of prey consumed during feeding experiments per tarantula per day (0.035 grams of prey/tarantula/day consumed), and was found to be significantly different ($X^2 = 83.08$, d.f.=1, $p<0.001$).

Feeding

A total of nine tarantulas were used in feeding experiments. For each prey type (hard, medium hard, and soft), a regression analysis of percent biomass of prey consumed by the

tarantulas was performed comparing the biomass of prey consumed and the initial prey weight (see Figure 1). An ANOVA test showed there was not a significant difference between the slopes of the three lines produced (p -value=0.2820). However, the graphs showed a relationship between hardness and percent biomass of prey consumed. The softer the prey, the greater percent biomass of prey able to be consumed by the tarantula, and thus more energetically beneficial.

For comparison of feeding rates between different prey types, the possibility of different feeding rates for tarantulas of different sizes had to be considered. To do this, weight gain (g), tarantula weight in grams (T) and feeding time in hours (f) were used to determine a relative consumption rate ($RCR = g / (f * T)$). A regression of the RCR was compared to one over the tarantula weight in grams for each prey type (see Figure 2). The value $1/T$ was used rather than T so as to avoid a tarantula being affected negatively simply on the basis of a slower feeding rate do to smaller size. From the regression plots produced, an ANOVA test showed there was not a significant difference in the slopes of different prey types (p -value=0.1290). The medium hard and soft prey was found to be consumed at faster rates than the hard prey, with the medium prey being consumed at the greatest rate. Comparing prey type and feeding rates was necessary for the testing of *B. mesomelas* as an energy-maximizer in feeding.

Based on data collected from all attempted the tarantulas fed 75% of the time prey was offered. Out of those successful feedings, 50% took place in the morning (between 07:00 and 12:00), and 50% took place at night (between 16:00 and 24:00). Also, out of those successful feedings, 50% took place after the tarantula was woken up before prey

was offered, and 50% took place during time when the tarantula was already awake prior to prey offering.

There were several feeding behaviors that were consistent throughout feedings, despite tarantula size (a measured femur length ranging from 1.066 cm to 1.945 cm) and varying types of prey. When a prey item was captured, the following general sequence was observed: 1) the prey was attacked rapidly, grabbed and pierced with the chelicerae only after movement of prey was detected, 2) upon capturing prey, the tarantula lifted itself off of ground by extending legs, and then 3) began to knead a layer of silk into dirt or on top of litter and surrounding substrate underneath itself while rotating in a circle, and finally 4) pushing the prey into the silk to attach silk lines from itself to both the and the prey. After prey was captured and pierced with chelicerae, digestive enzymes were secreted from glands above the chelicerae, allowing the fluids to drip down the fangs onto prey, beginning the digestive process. While actual feeding was occurring, the prey was periodically rotated and folded in its mouth using the chelicerae and pedipalps to control movement. This behavior continued until feeding was complete, at which time the prey was then dropped to the ground and, in some cases, pushed away from the tarantula using pedipalps and front pair of legs. After feeding had occurred, five times tarantulas were observed cleaning chelicerae by wiping them with pedipalps for up to an hour (mean time=56 min). After cleaning, the tarantula's movement would be minimal for up to a day, and in a few cases several days, during which time it would digest prey. When a tarantula did move after feeding, often they retreated to the artificial burrow where they would stay for a length of time similar to that if they did not enter the burrow (approximately one day).

The tarantulas tested fed regularly on beetles, katydids, and crickets. However, two of three times a cockroach was offered, the tarantula being tested did not feed. One of the two observed times a tarantula chose not to feed on a cockroach, it later found a beetle in the ground by foraging by feel. Also, special feeding behavior was noticed for beetles. In the cases where beetles were consumed, the head, elytra and wings were removed by the larger tarantulas early in the feeding process.

DISCUSSION

The number of possible burrows available was determined to not be a limiting factor in the actual density of tarantulas in the test area. However, it was noted that the three largest tarantulas obtained were found in burrows either underneath a log, or surrounded by roots, and thus possibly optimal burrow sites. A large individual can be considered successful (i.e. having high fitness) because of the difficulty of survival based on successful foraging process and predator avoidance. The burrow locations of large tarantulas found are similar to each other and consistent with the burrow description of Coyle (1984). This suggests that quality burrow availability, rather than simply number of burrows available, could be a limiting factor. Considering this, quality burrow availability could have a considerable effect on the actual density of *B. mesomelas*. This is due to the fact that they are at a much greater risk of predation when they are out searching for a quality burrow, especially during the day.

All prey caught in the traps were insects, and the amount of prey available suggests that it is not a limiting factor in female *B. mesomelas* density ($p < 0.001$). The majority of those prey caught in traps represented one species of beetle, of the family Carabidae that

was relatively small in size (approximately 1 to 1.5 cm long and .150 g in weight). Thus, it was considered an unlikely prey choice for *B. mesomelas*, because of its size (less than 1/4 of the 0.64g/prey average of feeding tests). Food records of tarantulas comprise katydids, cockroaches, and large beetles (Stradling 1994). However, such insects, although observed in the leaf litter, were not collected in traps. Thus, the choice prey available would be predicted to have a larger density than was collected. Smythe (1982) showed that abundance of night-flying insects varies throughout the year relative to the wet and dry seasons. These data were collected during April and May; the end of the dry season in Monteverde, and thus the prey availability is probably underestimated.

The density of *B. mesomelas* calculated appeared to be low for the area tested (data from this study). However, the density was still not limited by either prey or burrow availability (data from this study). Arboreal spider densities have been observed to fluctuate throughout the year, based on mating season, with the lowest density found in May and June (Pfeiffer 1996). Based on this pattern in density fluctuation, we can assume *B. mesomelas* to be similar due to their large mating season relative to seasonal changes, explaining the low densities found during the testing period. The low calculated density could also be due to search procedure used. As mentioned previously, it was observed that a female *B. mesomelas* which had consumed a relatively large volume of prey in a short period of time, may not be highly active for up to two days because it is either unable to feed more (i.e. 'full') or digesting additional prey. The possible burrow locations were checked for individuals thoroughly, but only for one night for each transect due to limited time. If a female were deep within its burrow due to a recent feeding, it would not be observed and counted. Thus, the density calculated may be lower than the actual density of

female *B. mesomelas* in the test area. An area would need to be searched extensively for several consecutive nights in order to exhaustively sample an area.

The low density could also be explained by predation on *B. mesomelas* in the test area. The two main predators of *B. mesomelas* found in the test area are coatis, and Pompilidae wasps. Parts of spiders appeared in half the scats of coatis (*Nasua narica*) tested in Barro Colorado Island, Panama (Russell 1985). Coatis are relatively dense in Monteverde, and seen regularly foraging near the test area. Coatis were often observed eating soft-bodied animals excavated from rotten wood (Russell 1985). Thus, it is likely that those spiders with more solid surroundings can more easily avoid predation. The second possible predators, Pompilidae wasps, are a family of large wasps that are known as tarantula hawks or tarantula wasps. *Pepsi thisbe*, a species which occurs in Costa Rica, preys on mygalomorph spiders (Hanson and Guald 1995). These wasps are regularly seen flying throughout the test area, and thus could have had a substantial effect on population density.

Tarantulas feed regularly on various prey types, but tend to avoid bad smelling, small, or difficult-to-handle prey as found in previous studies (Baerg 1958, Stradling 1994, Foelix 1996). As predicted, dropping insects to the anterior of the tarantula proved to produce the most rapid response. The tarantulas fed regularly on prey offered with the exception of the cockroaches. Based on its strong odor, it is believed that the species of cockroach is possibly unpalatable, and thus undesirable as a prey item. Although the slopes of percent biomass consumed for different prey types were not significantly different, the slopes did follow an observable trend (see Figure 1). The slopes of each line fit well ($R^2=0.747, 0.987, \text{ and } 0.965$), implying that the approximate maximum percent of biomass

consumable from each prey type was consumed, independent of prey size. The harder the prey, the lower percent of biomass was able to be obtained from the prey, agreeing with the hypothesized trend.

A general trend was also observed in the graph comparing rate of feeding on different prey types and tarantula weight, although the slopes were determined to not be significantly different (see Figure 2). Both medium and soft preys were consumed at faster rates than the hard prey, with medium prey being consumed the most rapidly. The slopes of lines produced comparing Relative Consumption Rate to tarantula weight support the claim that *B. mesomelas* is also an energy-maximizer (i.e. net energy maximized for given time spent feeding). This is based on the fact that the percent of prey consumed followed a steady slope for each prey type, meaning that they are probably being consumed at the most efficient rate possible, independent of tarantula or prey size. This graph partly agrees with the rate of feeding trend hypothesized, and may not completely agree with the hypothesis based only on limited sampling. It is predicted that with greater sampling size, softer prey would in fact be found to be consumed at faster rates than medium hard prey.

General feeding behavior was consistent with previously known feeding behavior in tarantulas. As was observed by Coyle (1986) and Stradling (1994), tarantulas tested reacting quickly and directly to anterior prey after movement of prey was detected. Piercing of prey with chelicerae and digestive enzyme secretion following piercing occurred in the same manner as noted by Herrero (1984) and Herrero and Odell (1988).

On several occasions, tarantulas were observed feeding near to and facing the burrow. Predator avoidance was proposed as an explanation for this behavior. Rapid retreat into the burrow is easily accomplished upon sensing a predator by this positioning.

Secondly, there are small bristles (urticating hairs) on the abdomen and legs which can break off easily on contact or be 'thrown' by the tarantula by scratching its abdomen with hind legs in response to a close threat of a possible predator (Cooke, Marshall 1996). These hairs can be inhaled by small rodents or stick into skin, causing irritation, and thus limiting the possibility of being preyed upon by rodents and small mammals. By facing the burrow, its abdomen is facing outward toward the direction of a predator approach, allowing the tarantula to defend itself with these urticating hairs.

The observed behavior of silk kneaded into the dirt underneath the tarantula where prey was found before feeding is one of particular interest. This particular behavior had not been observed during post-capture feeding in previous studies. It has, however, been noted that silk surrounding the burrow entrance is characteristic of several species of ground-dwelling spiders, presumably used to increase prey-capture effectiveness by trapping or temporarily slowing prey, or as sensory lines for detecting passing prey (Coyle 1986). However, in my study of the silk, it was not related to the entrance, but rather to where preys were captured. I proposed that it is used to mark a successful hunting location, and used in the capture or immobilization uses mentioned. On one occasion when I blew on the tarantula when it was eating, it quickly dropped the katydid and moved toward its burrow, agreeing with the proposed reasoning for the silk. First, it is odd that they often choose to do this behavior in the location where prey are captured, directly being followed by feeding. This is because preys are most often captured outside the nest, simply based on amount of area available to hunt. Since most preys are found outside of the burrow, most prey captured is also eaten outside of the burrow, based on observed behavior. Eating outside the burrow increases chance of predation, thus being an undesirable and even fatal trait in some cases. I

propose that the previously mentioned silk kneading habit is directly related and necessary to compensate for an increase in vulnerability due to feeding outside the burrow. I believe that the silk kneaded into the ground before feeding and attached to the spider and prey may be used as a sensory tool for predators. This sensory tool is needed to protect *B. mesomelas* from predation due to feeding often occurring outside the burrow for extended periods of time. Successful predatory avoidance would be increased using this technique along with the positioning of the tarantula in comparison to its burrow previously mentioned.

The behavior of the removal of the elytra, wings and head of beetles prior to feeding by large tarantulas may be an example of energy-maximizing feeding. I propose that this is a learned behavior based on an inability to digest these items. Therefore, they are determined to be non-beneficial based on experience, and thus removed by those older *B. mesomelas* (since only three largest tarantulas were found to do this behavior). This could be a possible behavioral adaption relating to energy-maximizing feeding. By removing the unusable parts of the prey, the amount of prey consumed in a given amount of time is maximized. Based on the findings of this study, it is believed that *B. mesomelas* are a strong example of an organism that exhibits energy-maximizing feeding. The adaption to feeding on beetles seen (removing elytra, wings and head), is a result of an inconsistently available optimal prey supply because of variation in both seasonal and annual insect species densities. Thus, I propose that the only factor restricting *B. mesomelas* from optimal foraging, rather than generalistic feeding, is a lack of a constant supply of the most optimal prey.

ACKNOWLEDGEMENTS

I would like to thank both Mauricio for his assistance in planning, statistical analysis, and dealing with constant questions regarding this study. Also, I would like to thank Andrew for his willingness to open up a hostel for myself and others from “The Valley” who spent large amounts of time going back and forth to and from the station, and thus often needed a place to stay. I would like to thank both Mauricio and Andrew for spending several different nights in the forest, searching for difficult to find test subjects. Lastly, I would like to thank those two test subjects who gave their lives so that I could have data. May they rest in peace with all the creatures of the forest at the EBM.

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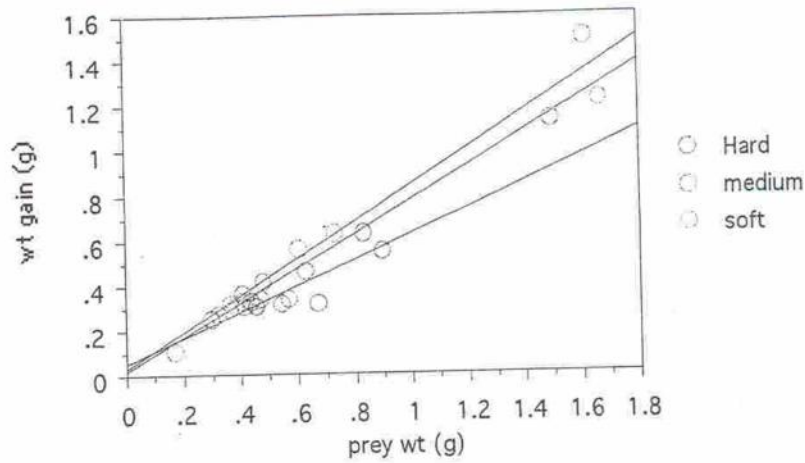


FIGURE 1. Regression of the prey weight versus the weight gained (amount of prey biomass consumed) for each of the three prey types sampled. Slopes were determined to be $m_{\text{hard}} = 0.575 (R^2 = 0.747)$, $m_{\text{medium}} = 0.756 (R^2 = 0.987)$, $m_{\text{soft}} = 0.811 (R^2 = 0.965)$.

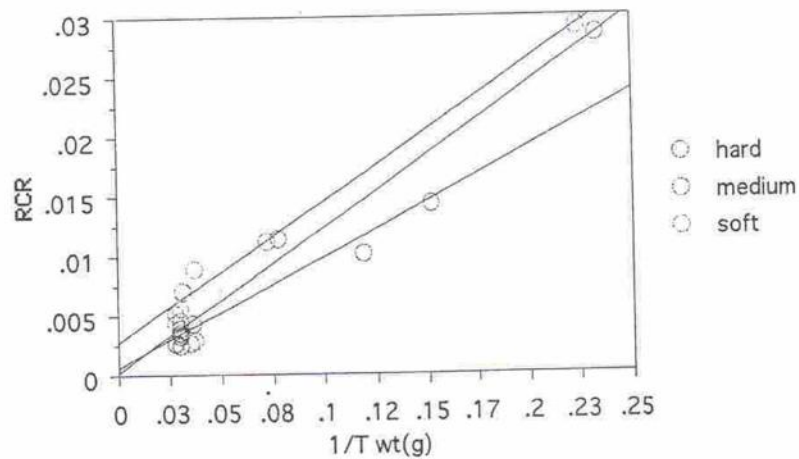


FIGURE 2. Regression analysis of Relative Rate of Consumption versus the inverse of tarantula weight(g) for each prey type tested. Slopes were determined to be $m_{\text{hard}} = 0.093 (R^2 = 0.890)$, $m_{\text{medium}} = 0.122 (R^2 = 0.981)$, and $m_{\text{soft}} = 0.118 (R^2 = 0.983)$.