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Diversity and morphological variation in Formicidae in three strata of the Monteverde Cloud Forest.

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ABSTRACT

This study examines the arboreal presence of ants. Comparisons of diversity at three forest strata, canopy, mid-level, and forest floor were analyzed. Measurements were also made of leg length to body length and compared across the strata. The hypothesis is that arboreal ants will have a higher leg to body ratio. Finally a representation of each ant species, except three underrepresented species was dropped from the canopy to test for the ability to “glide”. Conclusive results showed that ant diversity is greatest at the mid-stratum ($H' = 1.82$). The remaining two strata, canopy and floor, showed similar diversity values ($H' = 1.04$ and $.86$ respectively). Significance was found between mid-level and forest floor, and mid-level and canopy ($p < 0.05$). Canopy level and mid-level ants showed no difference in body length, leg length, or the ratio between the two ($p > 0.05$). Both, however, showed larger values than the forest floor ants in all three cases ($p < 0.05$). None of the ants glided or showed any signs of being able to. Further study is required to solidify these results but it seems evident that both greater diversity and a necessity for longer legs are consistent in arboreal ants.

RESUMEN

Este estudio examina la presencia arbórea de hormigas. Las comparaciones de la diversidad en tres pisos de los estratos, del dosel, de nivel medio, y del piso del bosque fueron analizadas. Se tomaron medidas de longitud de pierna a la longitud de cuerpo y comparadas a través de los estratos. La hipótesis es que las hormigas arbóreas tendrán una pierna más grande en proporción al cuerpo. Finalmente una representación de cada especie de hormiga, menos tres especies con baja representación fueron tiradas desde el dosel para para probar para que la capacidad “planear”. Los resultados concluyentes demostraron que la diversidad de la hormiga es más grande en el estrato medio ($H = 1.82$). Los dos estratos restantes, dosel y piso, demostraron los valores similares de la diversidad ($H = 1.04$ y $.86$ respectivamente). La significancia fue encontrada entre el piso y nivel medio, y entre el nivel medio y dosel ($< de p; 0.05$). El nivel del dosel y el nivel medio las hormigas no demostraron ninguna diferencia en longitud de cuerpo, longitud de pierna, o un cociente entre los dos ($> de p; 0.05$). Ambos, sin embargo, demostraron valores más grandes que las hormigas del piso del bosque en los tres casos ($< de p; 0.05$). Ningunas de las hormigas planearon o demostraron cualquier muestra de poder hacerlo. Estudios adicionales se requieren para solidificar estos resultados pero parece evidente que la mayor diversidad y una necesidad para piernas más largas son constantes en hormigas arbóreas.

INTRODUCTION

Worldwide ants boast 16 subfamilies, 300 genera, and 8,800 species (Longino and Hanson 1995). In Costa Rica there are seven subfamilies, 81 genera, and 620 species (Longino and Hanson 1995). Such a prolific family is sure to inhabit many of the vertical strata of a tropical rainforest. Tobin (1991) conducted a study in which he fogged two trees in Peru. He counted 28,279 arthropods, 69.7 percent (19,702) consisting of five

subfamilies and 52 species in 28 genera (Tobin 1991). In fact, one tree crown may possess up to 50 species of ants (Longino and Hanson 1995). Tobin's study provides the necessary base information to warrant this study. The environment in the crown of the tree is such that animals inhabiting it probably possess morphological structures that are different than their ground dwelling relatives.

This study is three fold: it examines the diversity of ants at three heights, compares their leg and body lengths across the three levels, and addresses whether or not controlled glide behavior is common in arboreal ants. The study performed by Tobin shows that arboreal ants are numerous and diverse, this study compares their diversity to that of two other stratum. The purpose for testing whether or not arboreal ants are capable of gliding is based on a paper by Yanoviak et al. (2006), who found a species of gliding ant present in the canopy. Leg length and body length may play a significant role in determining where the ant spends the majority of her time foraging and caring for the brood.

I hypothesize that there will be a significant difference in both diversity and in leg length when comparing ants across stratum. I also hypothesize that none of the ants will exhibit the ability to glide, regardless of what level they inhabit. Ants in the canopy or mid-level will be more diverse because they have more resources at their disposal and those resources are at a close proximity to their nest site. Because the crown of a tree displays considerable environmental and biological differences than the forest floor, ants that inhabit the crown will also have longer legs. No ants will display the ability to glide, as that is a large evolutionary step that intuitively appears to be difficult to achieve.

METHODS

Location and Dates

A single fig tree, *Ficus insipida* (Moraceae) was sampled at three heights: the canopy at 30 m from the floor, mid-level at 18-22 m, and the forest floor at zero m. The research site was located in the Monteverde Cloud Forest Reserve, a lower montane wet forest, and the study tree was located at 1550 meters above sea level. Each site was sampled for eight hours at various times ranging from 9:30 a.m. to 3:00 p.m. Collection and observation were performed on the days of July 22nd, 23rd, 27th, 29th, and 30th. The weather for all days was clear with no precipitation except for the occasional short-lived mist shower. Each site was sampled on at least two separate days.

Sampling and Collection Methods

Two methods of sampling were utilized, baiting and direct collection (Bestelmeyer et al. 2000). Bait sampling was used to attract out-of-reach ants and also because dietary generalists represent a significant portion of ant faunas worldwide and these generalists can be used to examine patterns in ant communities (Bestelmeyer et al. 2000) (Longino and Hanson 1995). Tuna and honey were used as baits as they attract both carnivorous and non-carnivorous predators. During each sampling period two honey and two tuna baits were set. Because baiting the same area often attracts the same ants (Bestelmeyer et al. 2000) all four baits were placed at different spots during each sampling period.

Direct sampling was performed with the aid of collecting forceps and an aspirator. Epiphytes within reach were searched as well as any vines or lianas. Hollow twigs and other hollow structures were broken apart and searched as well. All collected ants, including those from the bait traps, were placed in plastic vials and kept alive. Ants from each morpho species, with the exception of morpho species 2, 7, and 11 were dropped from the crown using the techniques of Yanoviak et al. (2006). Note was taken of whether or not the animal performed a J-shape arc back to the tree, or showed any signs of controlling their descent. Once in the laboratory, an alcohol soaked rag (>75% EtOH) was placed in the vials to kill the ants.

Laboratory Methods

All ants were separated based on morphology and categorized into morpho species using an Olympus SZ51 dissecting microscope. Separation by morpho species was permissible because I was sampling a small geographic area (one tree), which means there would be little morphological variation among any given species (Agosti et al. 2000). As suggested by Agosti et al. (2000) I preliminarily separated ants based on color, general shape, and size of each individual. Coloration in the class Insecta is very plastic at the specific level so further examination was needed. Colonies of ants are widely known to exhibit caste behavior in which each caste may represent many different size variations. However, the majority of worker castes are monomorphic (Hölldobler and Wilson 1990). This legitimizes separation by size. Further observations were necessary to make sure all ants were categorized correctly as some species displayed polymorphism. Ants collected at each level were kept separate.

Characters suggested by Agosti et al. (2000) were used for morpho species identification. Three major characters had to be consistent across the specimens if they were to be considered the same species. Major characters include: the head, general shape, eyes, mandible and mouth parts, and antennal length versus body length; the petiole, shape and presence or absence of a peduncle; the gaster, examined laterally to count number of tergites and their separation; and the alitrunk, presence or absence of spikes or other notable nodules or protrusions. Figures 2-1 and 2-3 and accompanying descriptions by Hölldobler and Wilson (1990) were used to aid in morphological clarification.

Statistical Tests

Shannon-Wiener index was used to quantify diversity, modified student t-tests were run to determine if the values differed, and an ANOVA was run to test for differences among leg to body length with respect to collection site. Ants that were collected at more than one site (only three individuals) were placed into the mid-level for calculations.

RESULTS

No ants glided, exhibited “controlled aerial descent”, or otherwise showed any indication of free falling aerial control. Of all ants collected, only one (Morpho 6) showed any

morphological traits, enlarged or flanged tarsi and high gaster mobility (Yanoviak et al 2006), which would suggest the ability to glide.

The canopy had the smallest population ($N = 16$) (Fig. 1). In contrast, the middle level had the greatest number of specimens collected ($N = 48$) (Fig. 1). Similarly the forest floor was represented by a high number of individuals ($N = 36$) (Fig.1). The middle level was also defined by the highest species diversity compared to the other two levels ($H' = 1.82$). Both the canopy and the forest floor expressed similar Shannon-Weiner values ($H' = 1.04$ and $H' = .86$ respectively). When comparing diversity across levels the mid-level shows more diversity than the canopy and more diversity than the forest floor ($p < 0.001$ for both analyses). There was no significant difference in diversity between the canopy and the forest floor ($p = 0.5$).

Body length, leg length, or the ratio of the two was not significantly different between the canopy and the mid elevation (Fig. 2, 3, 4). Both the canopy and mid-level species are larger than the floor species ($p = 0.03$, df effect = 2, $F = 6.56$, df error = 94) (Fig. 3). Leg length and leg to body length ratio produced identical results with even greater p -value correlations, ($p = .002$, df effect = 2, $F = 3.52$, df error = 94 and $p < .0001$, df effect = 2, $F = 40.99$, df error = 94 respectively) (Fig. 2 and Fig.4 respectively).

DISCUSSION

Formicidae Diversity

There is evidence for a greater diversity of ants at the mid-level strata compared to the forest floor. The results comparing diversity between the canopy and the floor did not prove to be significantly different, however they appear to be inconclusive and more testing is necessary. The canopy does show a higher degree of diversity than the floor (as shown in the results) but only three species were collected at each of those two levels (Table 1). I feel that not enough species were collected at either level to accurately depict the true diversity. The reasons for a greater diversity of ants in the upper strata are many but only two will be discussed at any length.

The strongest evidence of ant-plant mutualism is domatia, plant constructed shelters to house ant colonies (Hölldobler and Wilson 1990). Similarly many epiphytic plants are known to harbor ant colonies including but not limited to the bromeliads (Bromeliaceae) and the orchids (Orchidaceae) (Hölldobler and Wilson 1990). I observed many such domatia including epiphytes and counted no fewer than what appeared to be 15 different species growing on this single tree. Each plant is a potential host to a different species of ant. Ant gardens were also a common sight. Ants that live in carton nests place seeds of epiphytic plants inside their nest. The roots become integrated with the nest and the ants feed off of the roots; bromeliads are a common choice (Hölldobler and Wilson 1990). A study performed by Nieder et al. (2000) noted that the majority of epiphytes examined (51 percent) were ant garden epiphytes. A high number of epiphytes support a high number of ant gardens of diverse ant species.

One possible reason the high ant community diversity in the canopy is the concentration of food. Tobin (1991) claims that ants probably attain more nutrients from plant matter than previously thought. It is possible that ant species specialize on different epiphytes for sustenance. Those ants that are carnivorous or generalists have a wealth of insect larvae, insects and other sources of protein at their disposal (pers. obs.).

Further studies assessing biodiversity should be concerned primarily with only two strata, the canopy and the forest floor. In my opinion the middle level and the canopy level are not far enough apart and both should be grouped collectively as canopy. The crown as a whole should be assessed and then compared to the forest floor. Or a greater separation between the crown and the mid-level could be made.

Examination of Leg and Body length and the ratio between the two

The results of this study suggest that there is indeed a difference in absolute leg length (Fig. 2). Morpho species 14 exhibits significantly longer legs than the other two terrestrial species, species 14 was identified as a leaf cutter ant, *Atta spp*, in which having long legs to climb trees would be beneficial. Explanations for the evolution of long legs in arboreal ants have not been studied.

Though no ants displayed the ability to glide, long legs may serve a similar purpose. Arboreal ants can easily become displaced from their host tree by harsh weather conditions, predators or a misstep (Yanoviak et al. 2006). Increased leg length may offer an opportunity for a greater chance at regaining contact with the host tree after the animal has become dislodged. Longer legs could reach out to leaves, branches or any other substrate within the ants reach. Terrestrial ants have no such use for longer legs.

Previously, a common assumption was that as animal body size gets smaller the ratio of leg length to body length diminishes. The size-grain hypothesis presented by Kaspari and Weisner (1999) suggest that not only are the legs of ants unnaturally long for their body length, but that as the ant grows their legs not only keep up with their growth but increase at a rate that further raises the ratio of leg length to body length. They discuss that small animals must walk through their environment, not around it or on top of it; this reinforces the previously held thought that as animals get smaller larger legs are too costly (Kaspari and Weisner 1999). In the case of ants, having larger legs prevented them from accessing their interstitial world, however, having a larger body size and consequently possessing longer legs meant an increased resistance to desiccation, access to a larger food niche, and increased speed at a comparatively lower cost (Kaspari and Weisner 1999).

Arboreal ants generally forage at the tips of branches (Yanoviak and Dudley 2006). Their nests are usually concentrated towards the center of the tree at the interface of epiphytic roots and thicker branches (Longino 1991). Traveling from the nest to foraging territory and back often forces the ant to expose herself to predators. Longer legs would allow the workers to cover ground more quickly as branches offer few places to hide from predators. Again referring to the Kaspari and Wiesner (1999) study, contact with intense tropical sunlight is greater in the canopy than on the forest floor. Thus, it is necessary to have a larger body size to aid in the avoidance of desiccation.

Weaver ants inhabit only the Old-World tropics and are large, long-legged and solely arboreal (Hölldobler and Wilson (1990). The weaver ants use these long legs in their nest construction. They link with one another; forming large bridges to pull leaves together, then utilize the silk produced by their larvae to “glue” the nest together (Hölldobler and Wilson 1990). Exceptionally long legged ants in the Neotropics may be an evolutionary step towards this kind of nest weaving behavior. A more likely explanation though is that the arboreal ants use their long legs to link together in a similar

fashion creating “bridges” to access food or new foraging sites instead of for nest construction. Personal observations of solitary ants in the canopy “reaching” for a branch or leaf led me to the belief that it was entirely possible for ants to link with one another to access otherwise unreachable areas.

More experiments and tests are needed. A larger data set is most certainly necessary and more trees and different species of trees need to be sampled. This is a start however and the preliminary results are promising in explaining not only those arboreal ants possess longer legs, but also why those long legs are necessary and much more pronounced in arboreal ants.

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Table 1. Abundance of ant morphospecies at each forest stratum in *Ficus insipida*. The corresponding heights are canopy (30 m), middle (18-22 m), forest floor (0 m).

	Canopy	Middle	Forest Floor
Morpho 1	13		
Morpho 2	1		
Morpho 3	2		
Morpho 4		10	
Morpho 5		4	
Morpho 6		6	
Morpho 7		1	
Morpho 8		1	
Morpho 9		9	
Morpho 10		12	
Morpho 11		5	
Morpho 12			26
Morpho 13			2
Morpho 14			6

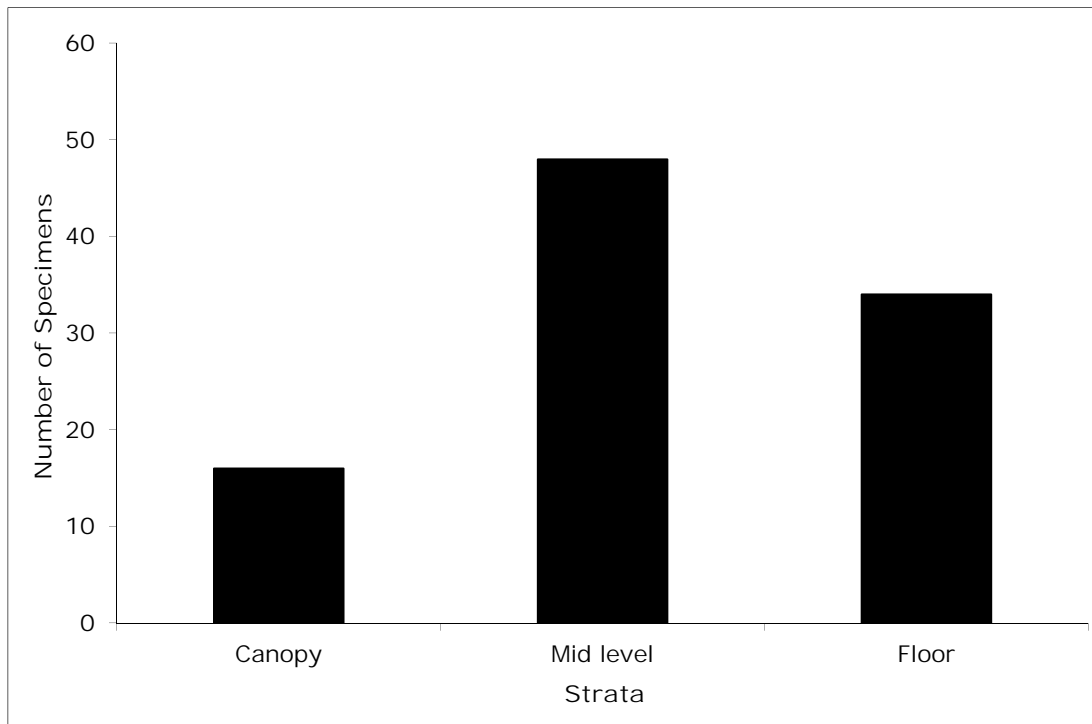


Figure 1. Depicts values of ants collected at each collection site.

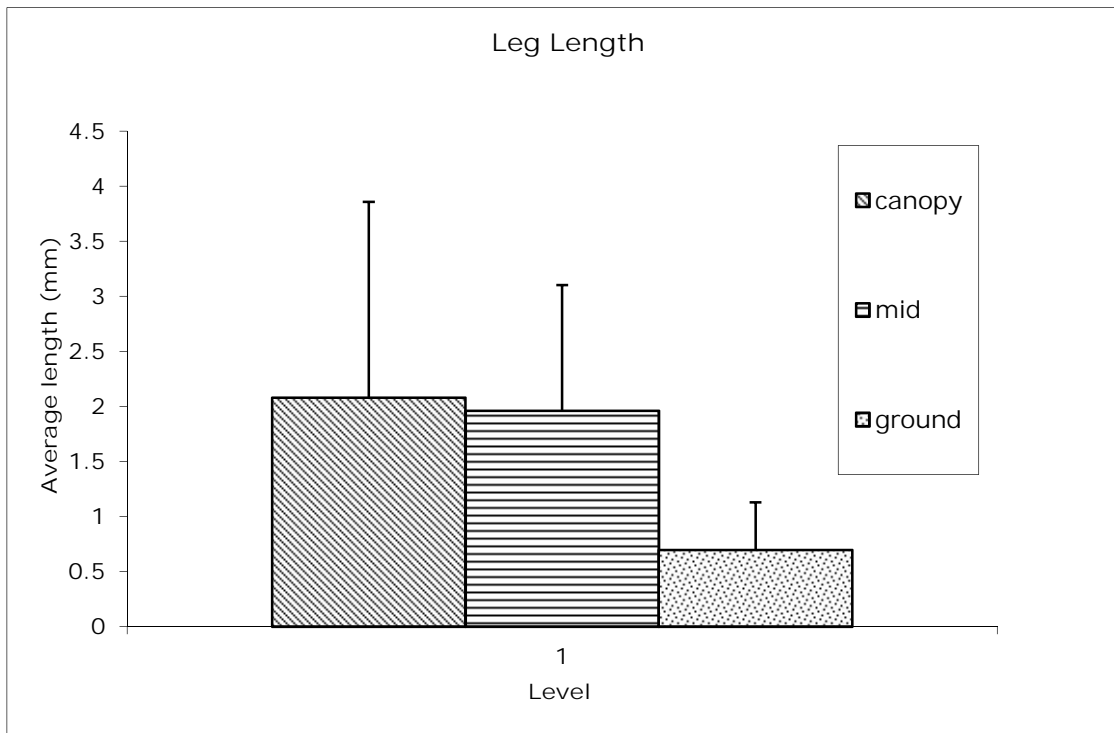


Figure 2. The average leg length of ants at each level. (df effect = 2, F = 3.52, df error = 94)

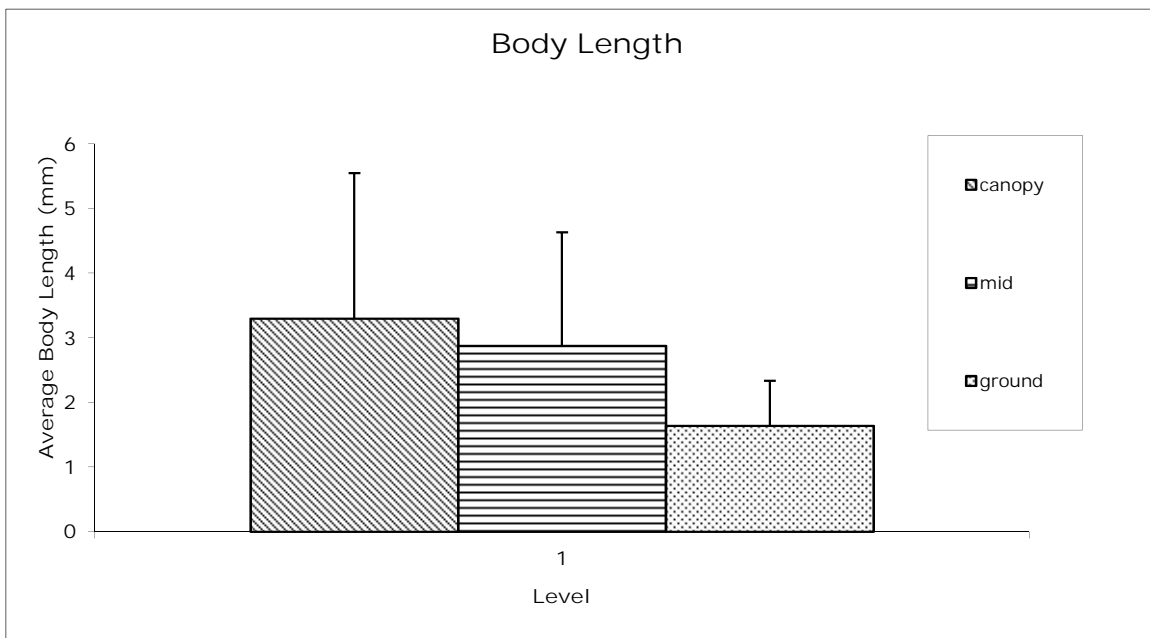


Figure 3. The average body length of ants at each level. (df effect = 2, F = 6.56, df error = 94)

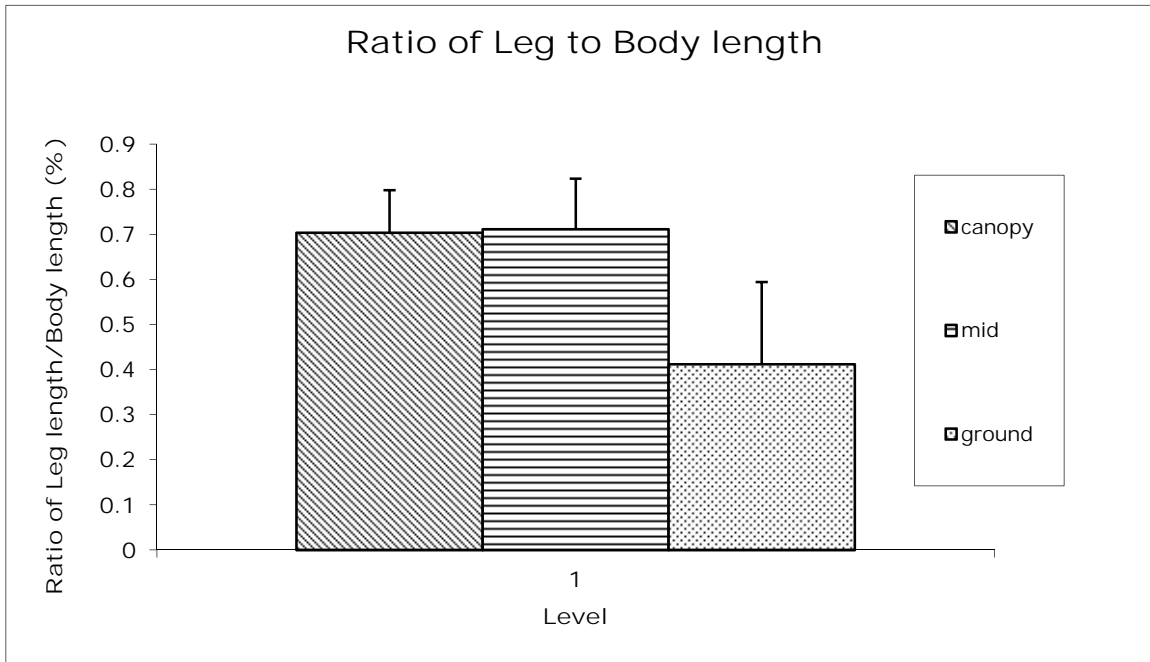


Figure 4. The ratio of leg length compared to body length of ants at each level. (df effect = 2, F = 40.99, df error = 94)