Aggregation Behavior and Habitat Selection in *Platydesmus* sp.

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Abstract

Platydesmus sp., a millipede of the neotropics, displays aggregation behavior along the cut ends of logs and other smooth surfaces. This millipede was examined in the southeastern Nicaraguan rainforest to better understand its pattern of movement, its aggregation behavior and its habitat selection. This investigation provides statistically robust results indicating that *Platydesmus* sp. travels little; has a clear habitat preference for dark, woody substrates oriented vertically (i.e. 90 degrees); and tends to aggregate with conspecifics regardless of available habitat. To our knowledge no past behavioral research has been done on this genus of millipede, making our research a foundation for future studies regarding the behavior of this arthropod.

Resumén

Platydesmus sp., un miriópodo de los neotrópicos, agrega en los superficies cortados de los troncos. Este miriópodo fue examinado en la selva en la parte sudeste de Nicaragua para entender sus patrones de movimiento, su preferencia para agregar y su selección de hábitat. Esta investigación provee resultados estadísticos robustos. Estos resultados robustos demuestran que *Platydesmus* sp: es estacionario mayor parte del tiempo, le gustan espacios oscuros, leñosas y verticales (noventa grados), y el miriópodo agregará con otros miriópodos no obstante hábitat disponible. No hay investigaciones disponibles acerca de este miriópodo y por eso nuestra investigación es una fundación para futuras investigaciones con este artrópodo.

Introduction

Aggregation behavior in animals has been known for many years to have a strong effect on the survival and reproduction of a species (Allee 1926). Individuals within aggregations reap benefits such as predator avoidance, increased growth rate, lower mortality rates (Takeda 1984), and a higher number of intraspecific interactions when compared to more scattered populations (Dangerfield and Telford 1993). Many different species are known to benefit from aggregation behavior including terrestrial isopods, which readily form aggregations in conditions of low humidity and high temperatures (Machado 2002), allowing them to lose water less rapidly and thus maintain moisture as a group (Allee 1926). Harvestmen also use aggregations as a way to increase their life expectancy. Aggregations not only allow harvestmen to escape predators more effectively and be less likely to be eaten by a predator via the dilution effect, but also allow their defensive signal to be more potent due to a collective release of secretions (Machado 2002). For isopods and harvestmen, and for many others that employ aggregation behavior, the benefits outweigh the costs, making group living beneficial for survival.

The subject of our study was an unidentified millipede in the genus *Platydesmus*, of which there are approximately twenty-eight known species. To our knowledge no research has been conducted concerning the aggregation behavior of this genus of millipede, however aggregation behavior has been studied in a wide variety of millipede taxa to date. Some tropical species are even known to have dense aggregations containing tens to several hundred individuals (Dangerfield 1993), and many hypotheses have arisen to explain this phenomenon (Wilson 2006). Some studies have suggested that this behavior prevents moisture loss, as with terrestrial isopods, or allows for safety in numbers, as with harvestmen (Koch 1985). Other studies have shown that mating, feeding activity (Dangerfield and Telford 1993), and increased chemical defense may be the cause of aggregation behavior (Fryer 1957; Lewis 1971; Bellairs et al. 1983).

We also examined habitat selection among *Platydesmus* sp. Habitat selection studies usually look at how animals use habitats relative to their availability (Aebischer et al. 1993), however habitat use may not be directly proportional to habitat availability if there are aspects to consider (Pellerin et al. 2010). Factors regarding overall habitat quality with respect to the species or individual may greatly affect whether specific habitat areas are occupied. Habitat quality may be defined by factors such as a particular color substrate (allowing an individual to be camouflaged), by resource availability such as food, or by predator/competitor avoidance (Greyling 2008). To our knowledge, no research has been done regarding habitat preference of

Platydesmus sp.

We first encountered our study species, *Platydesmus* sp. on the flat faces of downed logs cut to allow hikers to pass through more easily. We encountered millipedes at five log faces on three different trails, usually aggregated on the upper half of the log face (see photo 1). We often observed them in an asterisk shaped pattern (see photos 5 and 6) with only anterior ends touching, or lying across one another in no particular configuration, and groups usually contained 20 to 50 individuals. Our initial reason for conducting this study was to explore why these millipedes choose to inhabit the cut faces of logs, and why they exhibit aggregation behavior.

The goals of this study were threefold. First, we studied the habitat preference of millipedes; more specifically, whether they prefer a mossy versus a wooden substrate, a dark versus a light substrate, and whether they preferred to rest on a 0, 45, or 90 degree angle from the ground. Next, looking further into habitat preference, we examined which quadrant of the log face the millipedes most preferred. Lastly, we tested the aggregation behavior of the millipedes by looking at whether or not they would choose to aggregate when taken into a neutral environment.

This study is unique from previous studies because very little is known of the behavior of *Platydesmus* sp., including aggregation behavior and habitat selection. This paper will serve to document the existence of this specific millipede at the Refugio Bartola site in Nicaragua and as an account of its unique aggregation behavior and choice of habitat. Lastly, this paper will provide insight into the possible reasons for the behaviors that we observed.

Methods

Study Site

This study was conducted at Refugio Bartola, a private reserve located in southeastern Nicaragua at the convergence of the Rio San Juan and the Rio Bartola (the geographical coordinates for Refugio Bartola are: 10.79°N latitude and 84.61°W longitude). We studied the aggregation behavior of *Platydesmus* sp. at five sites within Refugio Bartola along three different trails: Yellow Trail marker 3, Red Dot Trial marker 19, and Blue Dot Trail marker 4. Because the Yellow marker 3 site contained three different aggregations of *Platydesmus* sp., this is where we conducted four experiments in addition to movement and aggregation studies, which occurred at all three locations.

Aggregation Behavior Observations

We began studying aggregation behavior at all three sites by marking each individual millipede with a number using Sharpie markers or paint pens. We marked aggregations that were close to each other with a unique color so that any movement between aggregations could be monitored. We attempted to mark individuals without disruption by marking them while they were still connected to the log, however they occasionally fell off of the log during this process. If this occurred we marked the millipede while gently holding it and placed it back onto the log where we found it. During the first two days of recording aggregation data, we checked the aggregation sites every four hours from 0900-2100 hours (to see whether these were just day roosts). After the initial 48 hours, we focused our attention on the Yellow Trail marker 3 site because it contained three different aggregations. This eliminated extensive travel time to other aggregation sites, however we still checked other aggregation sites (Red Dot and Blue Dot) occasionally. We visited the six sites at Yellow 3 at least once a day for the following ten days (February 2, 2011 through February 11, 2011). During each visit we photographed the six aggregations, documented which individuals were present, and recorded their location on the log face based on four visually established quadrants. During data collection we identified any unmarked millipede with a new number and the color of its corresponding aggregation.

Moss vs. Wood Trials

The first experiment we conducted tested whether *Platydesmus* sp. preferred to attach to a substrate of moss or of wood. We first located a 2cm x 15cm x 3m plank that was mostly covered with moss on one side, then scraped off alternating $15cm^2$ squares of moss until we reached the end of the moss cover on the plank. We then situated the plank so that it was sitting horizontally on the ground with garbage bags below in order to recapture any millipedes that left or fell off of the plank (see photo 2). For each trial, we placed three labeled millipedes on a moss-covered square and three millipedes on a wooden square. The millipedes used in trials were collected from a nearby site that was not being used as an aggregation site so that aggregation data collection was not interrupted. Pilot trials indicated that after transplanting the millipedes to the experimental plank, they became relatively stationary after a period of 30 minutes. We allowed the millipedes to move freely for the half hour period, recording the location of each individual (moss vs. wood) every ten minutes, and any individual that had traveled to the back of the board or escaped from the plank was discounted from the trial. Individual millipedes were only used in one trial per experiment type to avoid individual millipede preference factoring into data analysis. We conducted 15 mossy vs. wood trials, and then used the same method for all four experiments.

Dark vs. Light Trials

The next experiment we conducted tested whether *Platydesmus* sp. preferred a dark or light colored substrate. We obtained another 2cm x 15cm plank and painted alternating $15cm^2$ sections of white paint and dark gray paint around the entire board. We positioned the board in the same orientation as in the previous experiment (see photo 3) and again placed white trash bags underneath the board to account for any millipedes that left the board. For each trial we used the same protocol as in the first experiment, placing three millipedes on white and three on gray, and checking their location every 10 minutes for half an hour until we had conducted 19 trials of this experiment.

Angle Trials

In experiment three we tested whether *Platydesmus* sp. preferred a surface that was level to the ground (0^{o} angle), at a 45^{o} angle from the ground, or perpendicular to the ground (90^{o} angle). To test this we constructed a set up that consisted of surfaces at all three angles (see photo 4) using rectangular sections cut out from cardboard trays that we wrapped in duct tape for support. We placed the unit onto a cardboard tray to catch any millipedes that left the experimental area and used rulers for structural integrity. Initial trials showed that the duct tape proved too slippery for *Platydesmus* sp. so we used the file on a Leatherman tool to roughen the duct tape. For each trial we placed two marked individuals on each of the three angled surfaces, and at the 10, 20, and 30-minute markers recorded the locations of the six individual millipedes as 0 degrees, 45 degrees, or 90 degrees for a total of 15 trials.

Aggregation Trials

For the fourth experiment we tested whether individual millipedes tend to aggregate or to stay isolated from each other when removed from of their natural environment. We placed four marked millipedes in four separate locations in a 15cm diameter Petri dish with a loose lid on top to prevent the millipedes from leaving the dish. We then observed the millipedes for 30 minutes, and every ten minutes we marked whether or not individuals were touching (and if so which individuals were involved) for a total of 29 trials.

Canopy Cover/Directional Readings

To obtain canopy cover readings at each of the three trail locations (Yellow Trail 3, Red Dot Trail 19, and Blue Dot Trail 4) we used a spherical densiometer and measured the canopy cover in three places: at the log face, 5m up the trail from the log face, and 5m down the trail from the log face. For the three logs at Yellow Trail 3 (Blue, Black, and Silver), we used the same readings for up trail and down trail readings due to the close proximity of the logs but measured a unique reading and a compass bearing for each log face.

Data Analysis

To determine whether there was a significant difference in the number of millipedes between quadrants on the faces of each of the five logs we used a Friedman Rank Sum Test with significance based on a p-value of 0.05 or less. We followed this with Wilcoxon Matched Pair Sign Ranks (WMPSR) Tests to determine between which quadrants (UR or UL and LR or LL) the significance existed and to determine which half of the log face (upper or lower) the millipedes chose, based on a significant p-value of 0.0167 or less. We then used WMPSR Tests again to determine whether there was significance in the number of millipedes that moved from moss to wood vs. from wood to moss, from moss vs. from wood, from dark to light vs. from light to dark, and from dark vs. from light. Next, we used a Friedman Rank Sum Test to determine whether there was a significant difference between number of millipedes attached to 0, 45, and 90 degrees after 30 minutes, and followed it with a WMPSR Test to determine between which two angles the difference existed. We then used WMPSR Tests to determine whether significantly more millipedes moved from 45 degrees to 0 degrees or from 45 degrees to 90 degrees. To determine whether there was a significant difference in the number of millipedes that left 0, 45, and 90 degrees after 30 minutes we used a Friedman Rank Sum Test, and followed it with a WMPSR Test to determine between which two angles the difference existed. We then ran a Two-Sample Wilcoxon Test to determine whether there was a significant difference in the percent canopy cover between the locations of the log faces and their surrounding areas. Lastly, we used a Two-Sample Wilcoxon Test to determine if there was a significant difference in the number of millipedes on the left versus the right side of the log face.

Results

Aggregation Behavior Observations

The Friedman's Rank Sum Tests conducted for each of five logs determined that there was a significant difference in the number of millipedes between log quadrants for all except the Yellow Trial Black Log (Log 2). This includes Yellow Trail Blue Log (Log 1), Yellow Trail Silver Log (Log 3), Red Dot Log (Log 4), and Blue Dot Log (Log 5). The WMPSR Tests then determined that Logs 1, 3, and 5 had significantly more millipedes on the upper half of the log versus the lower half. Of these logs, Logs 3 and 5 had significantly more millipedes on the UR and LR quadrants versus the UL and LL quadrants respectively, and Log 1 had significantly more millipedes on the UL and LL quadrants versus the UR and LR quadrants respectively. Log 4 did not show significant differences in the number of millipedes between upper versus lower, UR versus UL, or LR versus LL. (Statistical data for this information is summarized in Figure 4.) When all five logs were analyzed together to determine whether millipedes preferred the upper or lower log face in general, the results showed that there was no significant preference ($V = 0$, p-value = 0.0625).

Moss vs. Wood Trials

The millipedes preferred panels of bare wood over panels covered with moss. Using WMPSR Tests we determined that significantly more millipedes ($V = 119$, p-value = 0.000661) moved from mossy to wood (38 millipedes, 52.8% of total that started on mossy) than from wood to mossy (6 millipedes, 8.3% of total that started on wood) and that significantly more millipedes (V = 90, p-value = 0.001572) moved away from a mossy substrate (66 millipedes, 91.7% of total that started on mossy) than moved away from a wooden substrate (31 millipedes or 43.1% of total that started on wood) based on a sample size of 15. Figure 1 shows that the proportion of millipedes on bare wood tended to increase after the first ten minutes and then remain higher than the starting position of 0.5 for the remainder of the trial.

Dark vs. Light Trials

The millipedes preferred a dark colored substrate to a light colored substrate. Using WMPSR Tests we determined that significantly more millipedes (V = 0, p-value = 0.0003503) chose to move from light to dark (34 millipedes or 59.6% of total that started on light) than from dark to light (11 millipedes or 19.3% of total that started on dark), and that significantly more millipedes (V = 9.5, p-value = 0.006161) moved away from a light substrate (44 millipedes or 77.2% of total that started on light) than moved away from a dark substrate (19 millipedes or 33.3% of total that started on dark) based on a sample size of 19. Figure 2 shows that the proportion of millipedes on the dark substrate tended to increase after the first ten minutes and then remain higher than the starting position of 0.5 for the remainder of the trial.

Angle Trials

The millipedes preferred a vertical (90 degree) surface as opposed to a 0 or 45 degree surface. A Friedman Rank Sum Test showed that there was a significant difference in the number of millipedes between the three locations after 30 minutes (Friedman chi-squared = 21.9636, df = 2, p-value = 1.701e-05), and a WMPSR Tests showed that, after 30 minutes, there were significantly more millipedes at 90 degrees (58 millipedes or 64%) than at 0 degrees (14 millipedes or 15.6%) (V = 0, p-value = 0.00103) or at 45 degrees (12 millipedes or 13.3%) (V = 105, p-value = 0.0009685). However, the test showed that there was no significant difference in the number of millipedes at 0 degrees versus 45 degrees (V = 44, p-value = 0.7055) based on a sample size of 15. WMPSR Tests also showed that significantly more millipedes (V = 66, p-value = 0.003116) moved from 45 to 90 degrees (18 millipedes or 60.0% of total that started on 45 degrees) than from 45 to 0 degrees (7 millipedes or 23.3% of total that started on 45 degrees). Lastly, a Friedman Rank Sum Test showed that there was a significant difference in the number of millipedes that moved away from 0 degrees, 45 degrees, and 90 degrees (Friedman chi-squared = 13.4419, df = 2, p-value = 0.001205) over the course of 30 minutes. WMPSR Tests then showed that significantly more millipedes (V = 0, p-value = 0.001761) left 45 degrees (27 millipedes or 90.0% of total that started on 45 degrees) than left 90 degrees (10 millipedes or 33.3% of total that started on 90 degrees) but the number of millipedes that left 0 degrees (24 millipedes or 80% of total that started on 0 degrees) is not significantly different than the number that left 90 degrees (V = 4.5, p-value = 0.1206). Figure 3 shows that the millipedes significantly chose the 90 degree substrate over the 0 or 45 degree substrates.

Canopy Cover/Directional Readings

A Two-Sample Wilcoxon Test showed that the percent canopy cover at the log faces was significantly lower than the percent canopy cover in the surrounding areas (W = 2.5, p-value = 0.0066). The average percentage of canopy cover at the log faces was 84.45%, whereas the average canopy cover in the surrounding areas was 94.31%. Figure 5 shows percent canopy cover readings at the five log faces and 5m up and down trail from each face.

WMPSR Tests determined (as Figure 6 shows) that only Logs 1, 3, and 5 had a significant difference between the number of millipedes on the left versus the right side of the log face. Log 1 had significantly more millipedes on the left side whereas Logs 3 and 5 had significantly more on the right side. When taking into account the orientation of each log (shown in Figure 6), the areas of highest millipede abundance correspond to the West side of log faces 1 and 3 but the East side of Log face 5.

Discussion

Aggregation Behavior Observations

Logs 1, 3, 4 and 5 showed a difference in the number of millipedes between log face quadrants, but only Logs 1, 3, and 5 showed a difference in millipede abundance when comparing UL vs. UR and LL vs. LR. For these three logs the millipede abundance was higher on the upper half of the log face than the lower half. Thus, millipedes may prefer the top half of the log to avoid potential ground dwelling predators. This sort of behavior is already known to exist in *Isthmohyla picadoi,* a frog also found in Nicaragua, which rests on bromeliads and trees to stay off the ground where potential predators live (Stuckert et al. 2009). Millipedes may also choose the upper log face to avoid splashing water and mud during hard rains. Because the millipedes tend to aggregate, choosing the upper half of the log may be a result of conspecifics already present on the upper log face due to factors like food resources or other indications of a suitable habitat. Conspecific attraction has been witnessed in the praying mantid, *Ciulfina biseriata*, in which males prefer to select tree trunks where another praying mantid is already present (O'Hanlon 2011).

During the two-day observational period when we documented the millipede aggregations every four hours from 0900-2100 hours, we found there to be little to no movement amongst the millipedes. This leads us to believe that these aggregations are not just day roosts but are present at all hours of the day.

Moss vs. Wood Trials

More millipedes moved from mossy to wood than wood to mossy substrates and more moved away from mossy than moved away from wood. This demonsrates that millipedes prefer a wooden substrate to a mossy substrate. During our observations of *Platydesmus* sp., we encountered small, fluffy, white clumps on the log faces near the millipedes that we believe to be a fungus (see photo 6). We often saw the fungus on the wood of the log face but never on the mossy cover, and we suspect that the fungus is a source of food for the millipedes. At times we saw the millipedes with their anterior ends touching (like an asterisk shape) with a small clump of the possible fungus in the middle. If this fungus is a source of food then it may help explain why the millipedes were found on the wood where the fungus was found, but not on the moss where the fungus was absent. It has been documented that the sporangia of fungi are high in carbohydrates making a good source of energy for millipedes (Dangerfield 1993), and that the leaf litter in tropical environments often contains phenols and tannins that is difficult to digest for detritivores like millipedes (Dangerfield 1993). This being the case, it may be beneficial for *Platydesmus* sp. to find an alternate habitat than leaf litter (such as a log), as well as an alternate source of food (such as fungus).

One day in the forest we observed a downed log with fungus shelves protruding from it, each shelf approximately 3 to 8 cm in diameter, orange color with a white rim, and no more than 30cm off of the ground (see photos 7 and 8). Of approximately twenty shelves, about eight of them carried anywhere from one to eight millipedes and we theorize that these shelves may be a high carbohydrate food source for the millipedes. It has been found that millipedes can use both their tactile and olfactory responses for resource location (Haacker 1974; Bellairs et al. 1983), which may have originally allowed *Platydesmus* sp. to find an alternate resource site and habitat such as a downed tree. Millipedes may also prefer wood to moss as a substrate because moss may be more difficult for the millipedes to traverse with legs only a few millimeters in length.

Dark vs. Light Trials

More millipedes moved from dark to light than from light to dark and significantly more millipedes moved away from a light substrate than moved away from a dark substrate. Millipedes may be able to camouflage themselves better on a darker background, making them harder for predators to locate. As Stevens (2006) describes, many animals utilize camouflage to decrease the chances of being detected or recognized by predators, with the majority of cases involving visual camouflage having to do with body coloration. Creatures like moths often have certain markings or patterns that allow them to blend into the background (Kettlewell 1955), as do some marine isopods that make their body shape less recognizable to predators (Merilaita 1998). Some insects have even gone so far as to resemble bird droppings to look as unappetizing as possible (Herbert 1974). Because the body color of *Platydesmus* sp. is very similar to that of the log face it is likely that this millipede chooses to reside on a darker substrate so that it is less obvious to passing predators.

Angle Trials

More millipedes chose the 90 degree surface than the 0 or 45 degree surfaces and more millipedes moved from 45 degrees to 90 degrees than moved from 45 degrees to 0 degrees. Furthermore, more millipedes left the 45 degree surface than left the 90 degree surface, but there was no significant difference between the number that left the 0 degree surface and the number that left the 90 degree surface. Vertical surfaces may make millipedes less visible to aerial predators. Similar behavior has been seen in the lizard *Lacerta perspicillata*, which is more often found on vertical rock surfaces to avoid being spotted and attacked by birds overhead (Vitt

2002).

Millipedes may also prefer a vertical surface to avoid direct sunlight. If the millipedes were to attach to a horizontal surface they would experience higher temperatures and be at a much greater risk of desiccation. This is especially important since moisture loss is a major concern for millipedes. Dangerfield and Chipfunde (1995) found that among the African millipede *Alloporus uncinatus,* increased temperatures cause a rapid decrease in water loss. Attaching to a vertical surface would make millipedes less likely to be washed away by rain showers, which are extremely common in the tropics. (It rained fifteen out of the last seventeen days of our stay at Refugio Bartola.) With such a high frequency of rain it is likely that the millipedes tolerate such weather conditions by positioning themselves on vertical surfaces to avoid direct impact from the rain as much as possible. Lastly, the millipedes may choose a vertical surface to avoid being trampled by large vertebrates. By attaching to a 90 degree surface an animal is much less likely to be stepped unintentionally than if they were on a horizontal surface like the ground or the top of a log.

Aggregation Trials

Millipedes seem to prefer to be aggregated even when they are removed from their natural habitat. Out of 29 trials, some aggregation (at least two millipedes aggregated at one of the three time points) behavior occurred in all 29, and in 14 trials at least three millipedes were aggregated during at least one time point during the trial. This suggests that resource abundance alone does not explain aggregating behavior in millipedes. If resource availability was the only reason for aggregation behavior then we would not expect to find aggregation when the millipedes are placed in an environment without any food resources.

Canopy Cover /Directional Readings

The canopy cover density readings were significantly lower than the densities of the surrounding areas. It does not appear that millipedes choose a habitat with less canopy cover (i.e. more sunlight) because millipedes face desiccation as a result of their thin cuticle (Baker 1978). Thus, the fact that millipedes are found where there is less canopy cover could simply be a consequence of their preference for residing on cut logs (as where there are cut logs there will be lower canopy cover). This implies that the benefit of aggregating on a cut log face outweighs any detrimental effects of lower canopy cover.

Logs 1 and 3 had significantly more millipedes on the West side of the log face and Log 5 had significantly more millipedes on the East side of the log face. With such a small sample size it would be difficult to determine whether millipedes in general prefer the East or West side of the log face. Because there was variation in the results (not all logs had aggregations the same side of the log face) it seems that direction is not a determining factor in habitat selection, however more data would need to be collected to know for certain.

Further Observations and Explanations

When the millipedes were moderately disturbed (i.e. we attempted to mark them with a Sharpie pen) individuals would begin to crawl away on the log face. When they reached another individual or if they were already touching other individuals in their aggregation when disturbed, those new individuals would also begin crawling away. This shows that aggregations may be useful in predator avoidance (Turchin 1989). If sudden crawling behavior indicates to other millipedes in the area that a predator is near, they have a chance to escape before they are eaten by the predator. This would also support Takeda's (1984) hypothesis that some aggregations may reduce the mortality rates of individuals involved by alerting each other to potential danger.

When individuals were severely disturbed (i.e. we continued to try to mark them once they began crawling away) they would conglobate and fall off of the log face down to the leaf litter. This shows that effective predator response could be one of the reasons why millipedes prefer logs, which are up off of the ground. By conglobating and falling a significant distance down to the leaf litter, the millipede is quickly lost in the grayish leaf litter beneath and (as we know from personal experience) is very hard to locate.

At one of the aggregation sites we noted the presence of small white juvenile millipedes intermixed with the adults (see photo 5). Past studies have hypothesized that mating is the main cause of aggregation in millipedes, as some groups have been found containing a sex ratio near one male per two females (Lawrence 1952). Furthermore, Bhakat (1987) described how aggregations could be used for mating since aggregations of only one sex were never located. However, the presence of aggregations after eggs have been laid and hatched suggests that while mating may occur in these aggregations, it is not the sole reason for them. Perhaps the presence of a mixed group of juveniles and adults suggests the existence of parental investment in this millipede species. Parental care has been documented in some millipede taxa (Kudo 2011), with the family Androgn athidae exhibiting both maternal and paternal care. In the millipede *Brachycybe nodulosa* males are thought to play an important role in defending eggs against fungal infections by curling their bodies around eggs beneath decaying logs (Kudo 2011).

Platydesmus sp. may be present on logs but not in the leaf litter due to niche partitioning. Millipedes are considered primary decomposers and are capable of consuming a large variety of foods (Wallwork 1970), and show little discretion when it comes to the foods that they consume. However, if there are sympatric species present, instead of partitioning certain food resources it has been suggested that each species should specialize in a particular *area* in which to search for food (MacArthur and Pianka 1966). If this is the case with *Platydesmus* sp., perhaps the face of downed logs is the area it has chosen in order to not have to compete with fellow macrodecomposers, which are common in soil and leaf litter (Dangerfield 1993). On the other hand, if there is a specific food niche available on the log face that is nutritious to *Platydesmus* sp. and prevents it from having to compete with other decomposers then this dietary specialization could be a result of competitor avoidance (Dangerfield and Telford 1993). (Although, if aggregation is due to resource availability alone, then individuals would not have tended to aggregate in our dish experiments.) Additionally, because their environment is so humid, perhaps *Platydesmus* sp. does not need to remain in the leaf litter or soil to retain moisture like many other species of millipede in drier geographic locations.

On one occasion we observed a group of approximately 10 millipedes nearly touching each other in various states of molting. Some were curled up presumably preparing to molt while others were attached normally to the log in a straight fashion (see photo 9). Interspersed among the millipedes were already-shed exoskeletons. Molting is a common behavior among millipedes, so it is not surprising to observe, yet molting does not always occur in aggregations as we observed in *Platydesmus* sp. As Ewer (2005) describes, when an animal molts, replacing its exoskeleton, it must do so while it is essentially unsheltered, as the exoskeleton is important not only for movement and feeding but for desiccation prevention as well. Perhaps remaining close to fellow millipedes while molting helps the group maintain moisture during this vulnerable time.

We often observed a number of the millipedes form an aggregation (usually three to six individuals) with their anterior ends all touching, and with posterior ends of their bodies pointing outward in the shape of an asterisk. We encountered this on all five logs we observed. It has been found that millipedes have many sensory structures on their antennae including mechanical and chemical receptors (Hopkins and Read 1992). Furthermore, Carey and Bull (1986) determined that if a male's antennae are removed, he will not be able to successfully mate with females. They hypothesize that when the antennae are removed it prevents the male from detecting pheromones produced by the female, making the mating process nearly impossible (Carey and Bull 1986). Perhaps *Platydesmus* sp. establishes these asterisk-shaped conglomerations as a way of communication through the receptors on their antennae.

We would also like to document the presence of a second millipede species that is the same general size and body shape as the *Platydesmus* sp. but has a striped pattern on the dorsal side instead of solid gray (see photo 10). We only saw this particular striped species a few times, always near *Platydesmus* sp. but not in contact with any other individuals, and always encountered only one individual at a time. We believe that these striped millipedes are also from the Genus *Platydesmus* but, like the gray morph, we are unsure of the species.

Improvements and Future Experiments

In future experiments, a number of factors should be considered or revised. First, a more complete measurement of weather conditions including humidity and temperature at the five log sites should be documented to determine whether these two factors affect aggregation behavior. Secondly, sex and general age demographics of millipedes present in aggregations should be collected to determine if breeding is a reason for aggregation behavior. Thirdly, if time permits, aggregations should be observed over the course of the year and with a larger number of millipede groups to see if there is seasonal variation in aggregation patterns as has been noted for other millipede species (Banerjee 1967).

If we were to repeat our aggregation experiment we would collect data on the location of all four individuals at all three time markers (not just those that aggregated) to allow for statistical data analysis. If we were to repeat our angle experiments, we would reconstruct our contraption so that the millipedes had equal opportunity to move to each of the other two angled surfaces from where they were first placed. In our documented set-up, millipedes placed on 0 or 90 degrees had move through the 45 degree surface to reach the 0 or 90 degree surface, while those that started on the 45 degree surface had equal opportunity to move to 0 or 90 degrees.

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Figures

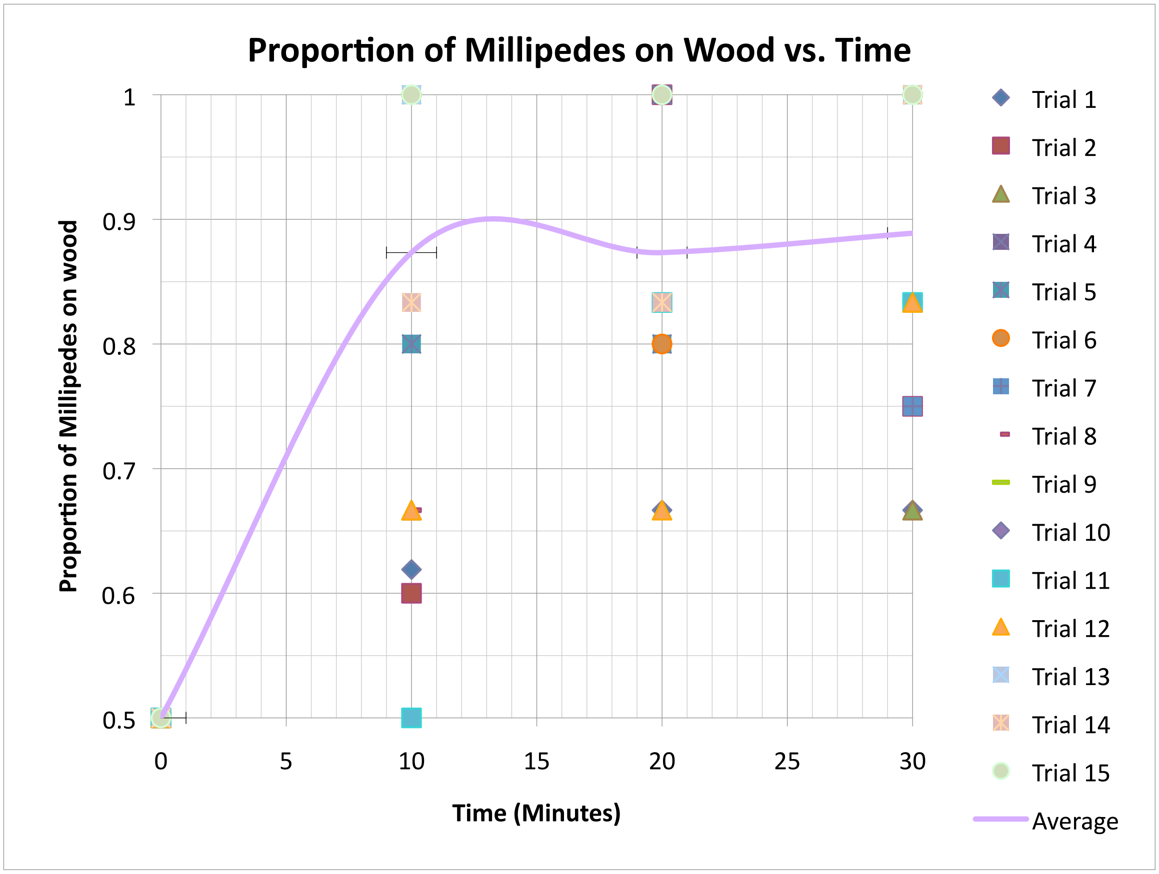

FIGURE 1. Millipedes made a clear choice for the wood substrate early in the trials and once there tended not to leave.

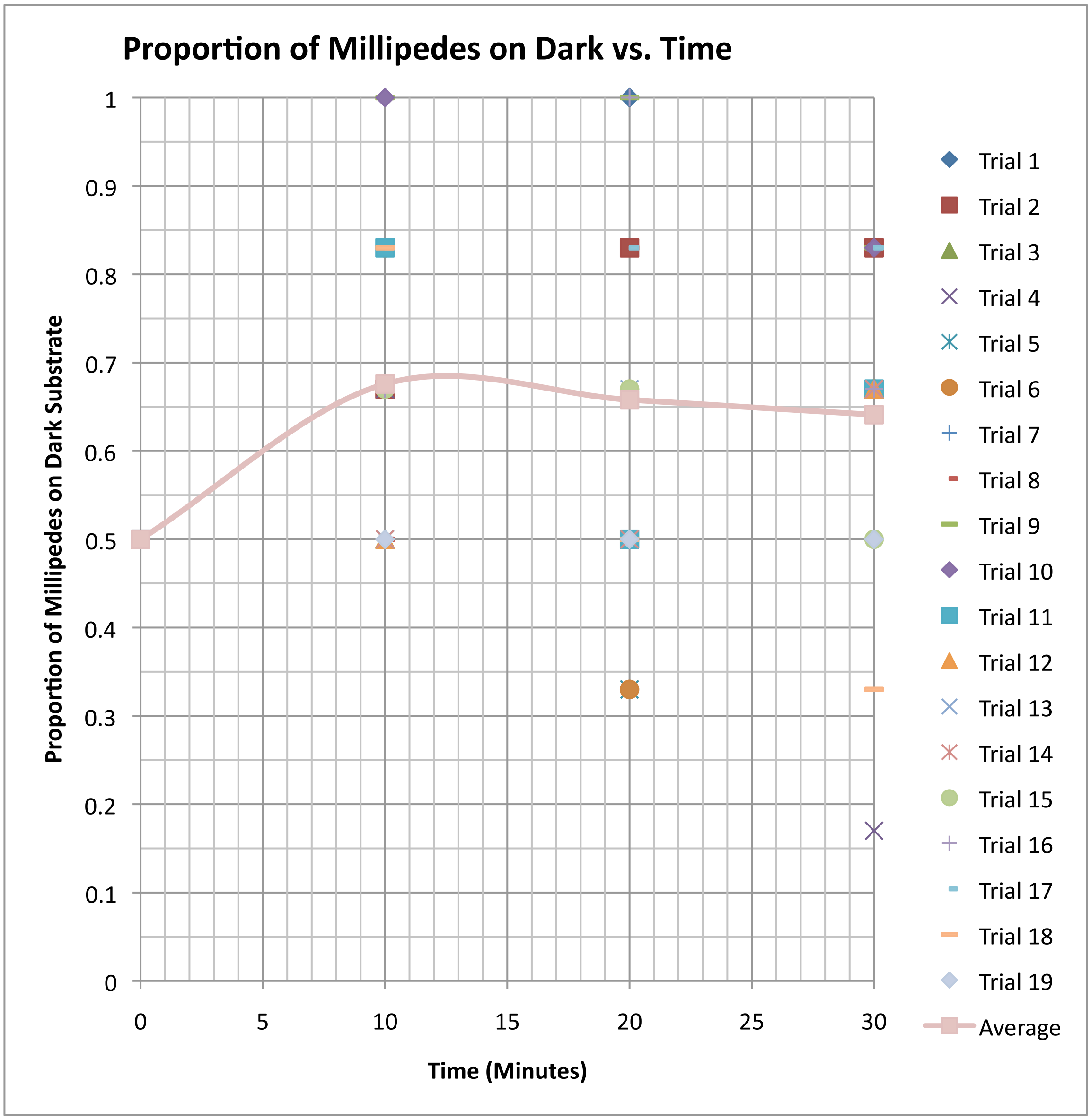

FIGURE 2. Millipedes made a clear choice for the dark substrate early in the trials and once there tended not to leave.

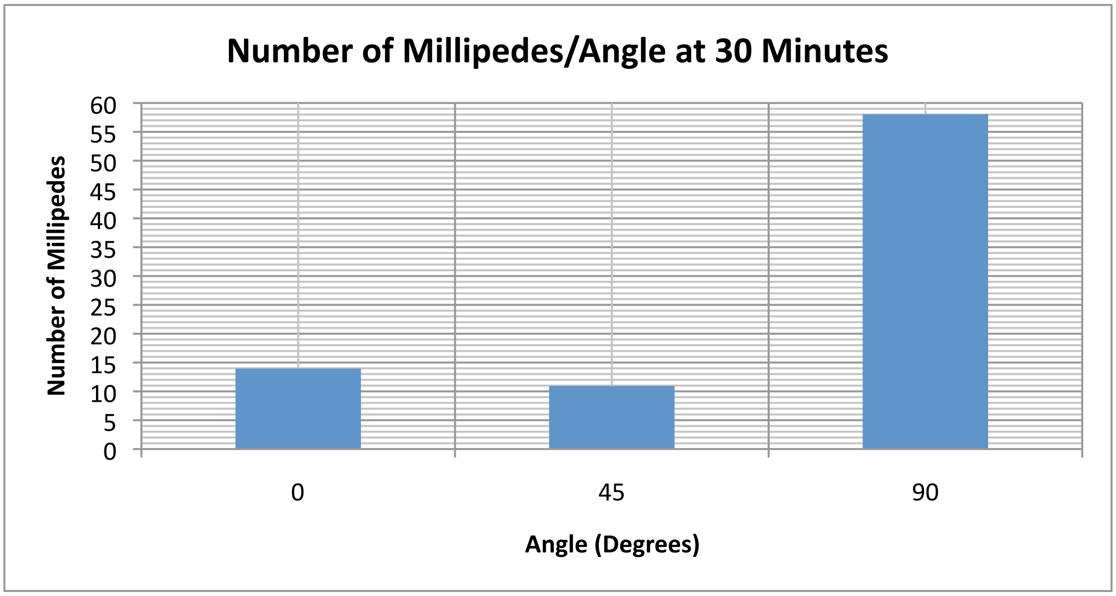

FIGURE 3. The millipedes significantly chose the vertical substrate after each thirty-minute trial period.

Log	Friedmans Rank Sum Test-Millipede Abundance-Between Quadrants	WMPSR Test-Millipede Abundance-UR vs. UL	WMPSR Test-Millipede Abundance-LR vs. LL	WMPSR Test-Millipede Abundance-Upper vs. Lower
1	Friedman chi-squared = 26.2034, df = 3, p-value = 8.646e-06 n=20	V = 12.5, p-value = 0.0005824 (Preferred UL)	V = 6, p-value = 0.001430 (Preferred LL)	V = 169, p-value = 0.003024 (Preferred upper)
2	Friedman chi-squared = 5.0345, df = 3, p-value = 0.1693 n=21 NOT SIGNIFICANT	NOT SIGNIFICANT	NOT SIGNIFICANT	NOT SIGNIFICANT
3	Friedman chi-squared = 48.7358, df = 3, p-value = 1.485e-10 n=20	V = 210, p-value = 9.264e-05 (Preferred UR)	V = 45, p-value = 0.006058 (Preferred LR)	V = 210, p-value = 9.343e-05 (Preferred upper)
4	Friedman chi-squared = 9.8824, df = 3, p-value = 0.01959 n=4	NOT SIGNIFICANT	NOT SIGNIFICANT	NOT SIGNIFICANT
5	Friedman chi-squared = 20.1, df = 3, p-value = 0.0001618 n=8	V = 28, p-value = 0.02249 (Preferred UR)	V = 21, p-value = 0.03552 (Preferred LR)	V = 28, p-value = 0.02225 (Preferred upper)

FIGURE 4. Millipedes varied significantly between quadrants on all logs except Log 2.

Millipedes significantly preferred the UL quadrant to the UR quadrant on Log 1, but preferred the UR quadrant to the UL quadrant on Logs 3 and 5. Preference was shown to be significant for the LL over the LR quadrant on log 1 but for the LR over the LL quadrant for Logs 3 and 5. Millipedes on Logs 1, 3, and 5 preferred the upper half of the log face to the lower half. The data showed no significant preference for UR vs. LR, LR vs. LL, or Upper vs. Lower for Logs 2 and 4.

Log	% Canopy Cover at log face	% Canopy Cover 5m up trail	% Canopy Cover 5m down trail
1	79.20%	95.32%	95.84%
2	94.28%	95.32%	95.84%
3	87.52%	95.32%	95.84%
4	76.60%	91.68%	88.82%
5	84.66%	94.8%	94.28%

FIGURE 5. The percent canopy cover at the five log faces is significantly lower than the percent canopy cover in the surrounding areas.

Log	Direction of Log Face	WMPSR Test-Millipede Abundance-Left versus Right
1	170^{o} SSE	V = 210, p-value = 9.516e-05
2	240^{o} WSW	V = 84.5, p-value = 0.6852
3	340^{o} NNW	V = 0, p-value = 9.409e-05
4	290^{o} WNW	V = 0, p-value = 0.125
5	210^{o} SSW	V = 0, p-value = 0.02225

FIGURE 6. Only Logs 1, 3, and 5 showed a significant difference between the number of millipedes on the left versus the right side of the log face. All logs face in a slightly different direction.

Photos

PHOTO 1. Aggregation behavior of millipedes.

PHOTO 2. Mossy vs. wood experimental design.

PHOTO 3. Dark vs. light experimental design.

PHOTO 4. Angles experimental design.

PHOTO 5. Adult millipedes aggregated with small, white, juvenile millipedes. Also displaying star aggregation behavior.

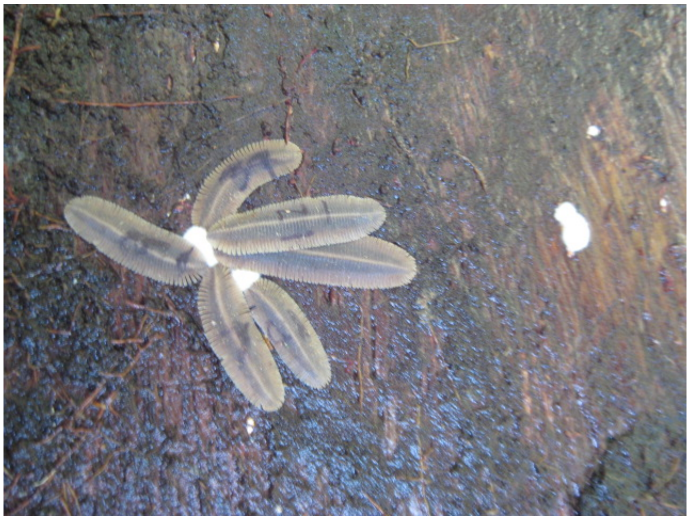

PHOTO 6. Millipedes facing one another anteriorly, while possibly feeding on what may be white fungus.

PHOTO 7. Millipedes found on fungal shelves. Fungus is highly nutritious.

PHOTO 8. Millipedes found on fungal shelves.

PHOTO 9. Millipedes molting on the branch of a downed log.

PHOTO 10. Two different species of *Platydesmus* found in Nicaragua.