

Original paper

Use of fluorescent powder as a method for marking millipedes

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Summary. Millipedes (class Diplopoda) are a diverse group of detritivores that are crucial for nutrient cycling and decomposition. Despite this, there are gaps in our knowledge of their ecology, such as home range, movement patterns, population size, and sociality. This is partly due to the fact that there has been no effective method for marking millipedes, because of their small size, elongate shape, and fossorial behavior. There has been previous research on the usage of fluorescent powder for mark-recapture and movement studies on insects. We tested the effectiveness of fluorescent powder as a marking method using members of the North American families Parajulidae (Julida) and Xystodesmidae (Polydesmida). Initial lab studies assessed the longevity of fluorescent powder and impact on mortality using twenty individuals: ten marked with powder and ten unmarked. For both species, the use of fluorescent powder had no apparent impact on individual mortality. Areas on the millipede where powder was retained varied, with *Ptyoiulus impressus* (Say, 1821) retaining powder on the sterna and *Dicellarius paynei* (Shelley, 2002) retaining powder under the paranota. Immediately after the mortality study, the powder was assessed for longevity when exposed to water, by submerging each remaining marked individual into water, then assessing changes in the markings. Exposure to water had no apparent impact on the fluorescent powder markings. A field experiment was conducted to assess longevity in natural conditions, possible transfer between individuals, and survival of marked individuals in the wild. Marked and unmarked individuals were placed into mesocosms for approximately two weeks. All marked individuals retained markings and were easily differentiated from unmarked individuals. Overall, fluorescent powder shows promise as an effective method for marking individual millipedes, even in field conditions, and could prove useful for future studies.

Keywords: arthropod, Diplopoda, ecology, mark-recapture, millipede, Myriapoda, Parajulidae, Xystodesmidae.

INTRODUCTION

Millipedes, class Diplopoda, represent a diverse group of arthropods which are present on every continent except Antarctica. There are over 13,000 described species worldwide (Sierwald et al. 2025). However, there are estimated to be 80,000 species, as many species are still being discovered. Millipedes are divided into 16 orders and occupy a variety of habitats, including tropical and temperate forests, deserts, mountains, caves, marshlands, under tree bark, and more (Golovatch and Kime 2009).

Millipedes are detritivores, making them crucial for processes such as decomposition, nutrient cycling, and soil formation (Hopkin and Read 1992). In temperate environments, millipedes are estimated to consume approximately 10–15% of autumn leaf litter (Golovatch and Kime 2009). This breakdown of leaf litter is even shown to increase microbial activity, increasing the speed of decomposition (Cárcamo et al. 2000). Millipedes are typically fossorial, meaning they spend majority of their lives digging underground. Their movement across soil strata provides soil aeration and movement of nutrients (Stašiov et al. 2021). Along with being fossorial, many,

but not all, millipedes are also very secretive. Even when aboveground, they will often seek cover under logs, rocks, and leaf litter. Along with being secretive, many millipedes are small in size or cryptic in order to be better concealed (Shear 2015).

Despite their importance in various ecosystems, millipedes' ecology makes them difficult to study. Being secretive, small, and cryptic, it can be challenging to locate these organisms within soil and organic horizons. Without being able to locate and observe them in the environment, we know little about their behavior (Coleman et al. 2018). We consider most millipedes to be solitary; however, some are seen to exhibit social behavior such as swarming, brood care, and mate guarding (Nijima et al. 2020; Wong et al. 2020). Nonetheless, these behaviors are only studied among a few species, generally only aboveground or anecdotally.

Along with behavioral ecology, we know relatively little about millipede population and community ecology, including how they are impacted by human encroachment. Some studies have reported density of millipede species (e.g., Dangerfield 1990) or communities (e.g., Suriel et al. 2025). However, for the same reasons listed above, we lack estimates of population size. One exception is Shaw (1968) who used two-stage sampling and statistical techniques to estimate the population size of the *Narceus americanus/annularis* complex in a topographically unique site in New Brunswick. Estimates for this unusually dense population over the course of four months varied wildly from 24,770 to 233,247 with overlapping confidence intervals, raising questions about the precision of this estimate.

Keeping millipedes under close observation in lab environments has allowed us to learn more about their behavior and ecology. We are still extremely limited in the ways we can study them, as lab studies are simplifications of natural systems and can alter natural millipede behaviors. Lab studies also do not give us information on population size or diversity. In captivity and in the field, we have no way to distinguish individuals from each other because size and color patterns tend to be consistent within populations (Marek and Bond 2009). A lack of individual identification prevents us from studying individual variability in group settings, which is important for captive breeding programs, mate selection studies, and sociality studies.

There are many methods used on other animals for the purpose of marking and tracking individuals to collect information on movement patterns, home range, and population estimates. Although accelerometers are becoming small enough to attach to some insects, millipedes are still too small, and too fossorial, for biologging (Iyer et al. 2020). Color markers, including specialized bee markers, have also been noted to impact behavior when used on millipedes

(Drahokoupilová and Tuf 2011). Some inks and paints are also highly toxic and potentially deadly when applied to millipedes. Even if paints and inks are nontoxic and do not impact the millipedes' behavior, many will rub off when burrowing through the soil.

Fluorescent powder has been used as a marking method for grasshoppers (Narisu and Schell 1999; Perry et al. 2017). Fluorescent powder is a fine, synthetic powder made of pigments that emit visible light when exposed to ultraviolet light. This makes them excellent marking agents, as their high surface area allows them to adhere tightly to surfaces, and their fluorescence makes them extremely visible, especially at night. On grasshoppers, fluorescent powder markings allowed for a higher rate of recapture of marked grasshoppers using a UV flashlight at night as compared to other methods, such as daytime recapture or sweep netting (Narisu and Schell 1999).

Fluorescent powder has not been studied as a method for marking millipedes. We tested the use of fluorescent powder as a marking method for the purpose of mark-recapture studies, movement studies, and individual identification. We assessed the powder's impact on millipede mortality, general wear over time, and possible transfer to other individuals. With an effective marking method for millipedes, we would be able to run true mark-recapture studies, dispersal studies, and distinguish individuals in captivity for the purpose of captive breeding and mate choice studies. Due to its effectiveness on other arthropods, we believe fluorescent powder could be an effective method for marking millipedes.

MATERIALS AND METHODS

Millipede Species

A total of three species across two different millipede families were used. The first was *Ptyoiulus impressus* (Say, 1821) (Julida: Parajulidae), a cylindrical and moderately long (28–58 mm) millipede with many setae, especially on the posterior end (Shelley and Smith 2016). These millipedes have a late fall and early spring activity period. The second was *Uroblaniulus* sp. (Julida: Parajulidae), a similarly-sized species which is much more glabrous (Chamberlin 1951). *Uroblaniulus* sp. also have a fall activity period, but were more readily available during collections than *P. impressus*. All Parajulidae were hand collected from Lake Laurel Biological Field Station, owned and maintained by Georgia College & State University in Milledgeville, GA, USA (33.118° N, 83.184° W). Lake Laurel is comprised of a mixed forest, with various coniferous and broadleaf trees, surrounding a small freshwater lake. Individuals of the species *P. impressus* were adults, all collected in the fall of 2023. Individuals of *Uroblaniulus* sp. were juveniles, all collected in the fall of 2024.

The second family we examined was Xystodesmidae (Polydesmida), one of the most diverse families in the south-eastern United States (Means et al. 2021; Andrew 2025). The species used was *Dicellarius paynei* (Shelley, 2002). Members of this species are small (21-25 mm in length), naturally fluorescent under UV light, and are most active in the spring and summer (Shelley 1984, 2002). All individuals were hand collected in the spring of 2024 from a residential front lawn in Milledgeville, GA.

Fluorescent Powder

For all experiments, we used Magenta Fluorescent UV Powder (Techno Glow, Inc., Ennis, TX). This 4.5-micron powder is UV active, emitting visible light when exposed to UV light. The powder itself is considered “eco-friendly” and is free of materials such as formaldehyde, heavy metals, bisphenol A, and other harmful and/or toxic materials (Techno Glow 2025).

Experimental Design

Initial Powder Retention Experiment

The Initial Powder Retention (IPR) Experiment tested the powder’s impact on mortality in controlled lab conditions. First, twenty polypropylene specimen cups (148 mL, Fisher Scientific 14-955-114B) with lids were prepared to be microcosms. To do so, each microcosm was filled with 1 cm of soil (sieved to 2 mm, collected from Lake Laurel). On top of the soil, we cut leaf litter of *Quercus falcata* Michx. into approximately 4 cm² pieces with shears. The lids were perforated with 4 pin holes using a dissection probe. The contents of the containers were sprayed with tap water, sealed with the lid, and left for 24 hours before adding millipedes. Specimen cups were labelled 1–20 using a marker. The cups were

randomly assigned to one of two treatment groups using a random number generator. Half were assigned “marked” to contain millipedes marked with fluorescent powder while the other half were the control, or “unmarked.”

Twenty *P. impressus* were collected. The unmarked group was treated first to avoid risk of cross contamination. Ten individuals were placed into a 22.86 cm by 30.48 cm plastic zip top bag. The bag was then very gently shaken for approximately 5 seconds, and the millipedes were then placed into their respectively assigned specimen cups. The remaining ten individuals were placed into the same bag to be marked. Then, 0.1 g of fluorescent powder was added on top of the millipedes. The bag was again very gently shaken for approximately 5 seconds to evenly coat the millipedes in powder, and then the millipedes were transferred to their respective specimen cups, with special care to clean up any spilled powder (Fig. 1). A UV flashlight (Convoy S2+ 365 nm) was used to locate the powder and check on the marked millipedes (Fig. 2).

Millipedes were checked every other day for 20 days, checking the unmarked millipedes first by opening the container and using a dissection probe to gently move leaf litter to locate each individual and check for mortality. The marked millipedes were checked after the unmarked millipedes using a probe and the UV flashlight, with careful consideration in washing the dissection probe when finished.

The same process was repeated for the *D. paynei* group (Fig. 3). However, *D. paynei* coiled tightly when shaken in the bag. They were left in the bag longer and allowed to uncoil inside of the bag, facilitating powder contact with the ventral side of their body. After thorough coating they were placed into their respective cups.

After twenty days, millipedes were removed and placed under a microscope to sex individuals and take photographs with and without a fluorescent light. Photos were taken with



Fig. 1. *Ptyoiulus impressus* being marked with powder.



Fig. 2. Marked *Ptyoiulus impressus*, in specimen container, being exposed to UV light, showing illumination from marking.

a Canon EOS T6i DSLR camera mounted on a Leica M80 stereomicroscope via a MDCLR-LM 1.38x Widefield Adapter (Martin Microscope Company, Easley, SC). To facilitate ventral views of live specimens, a press was created by nesting a Petri dish and cover such that the openings both faced up (Fig. 4). A flat, ring-shaped spacer was placed inside the larger dish cover, a millipede placed inside the spacer, and

the dish placed on top. The entire device was then flipped upside down to view the ventral side. A spacer of the correct thickness allows the millipede to be restricted to a space not much larger than the dorsal-ventral axis. For 'flat-backed' millipedes (Polydesmida) whose paranota make them wider than tall this is sufficient to prevent curling, coiling, or rolling over, and does not cause damage. The spacers used were cut from neoprene rubber sheets of 3 mm thickness. The spacer inner diameter was 63 mm and outer diameter was 96 mm, which allowed a close fit between the spacer and the edge of the Petri dish cover.

Cylindrical millipedes, such as parajuilds, posed an additional challenge, as the spacer alone was insufficient to prevent rolling. The press was modified by affixing a cushion of paper towel and polyester fiber fill to the outside (bottom) of the dish, which contacts the millipede inside the press (Fig. 5). The spacer could be used but was not needed in this arrangement, but constant gentle pressure was needed to keep individuals in the correct orientation during press flipping and during observations. After viewing the ventral side, pressure could be lessened to allow the millipede to roll over and increased again to hold in position to view the dorsal side with minimal movement.

Puddle Test

Following the IPR Experiment, marked millipedes were put through an experiment to qualitatively assess the impact that water exposure has on powder retention. The intent was to mimic what millipedes may experience in their natural environment, including rain events and flooding.



Fig. 3. *Dicellarius paynei* being marked with powder, being allowed to unroll to coat ventral side with powder.

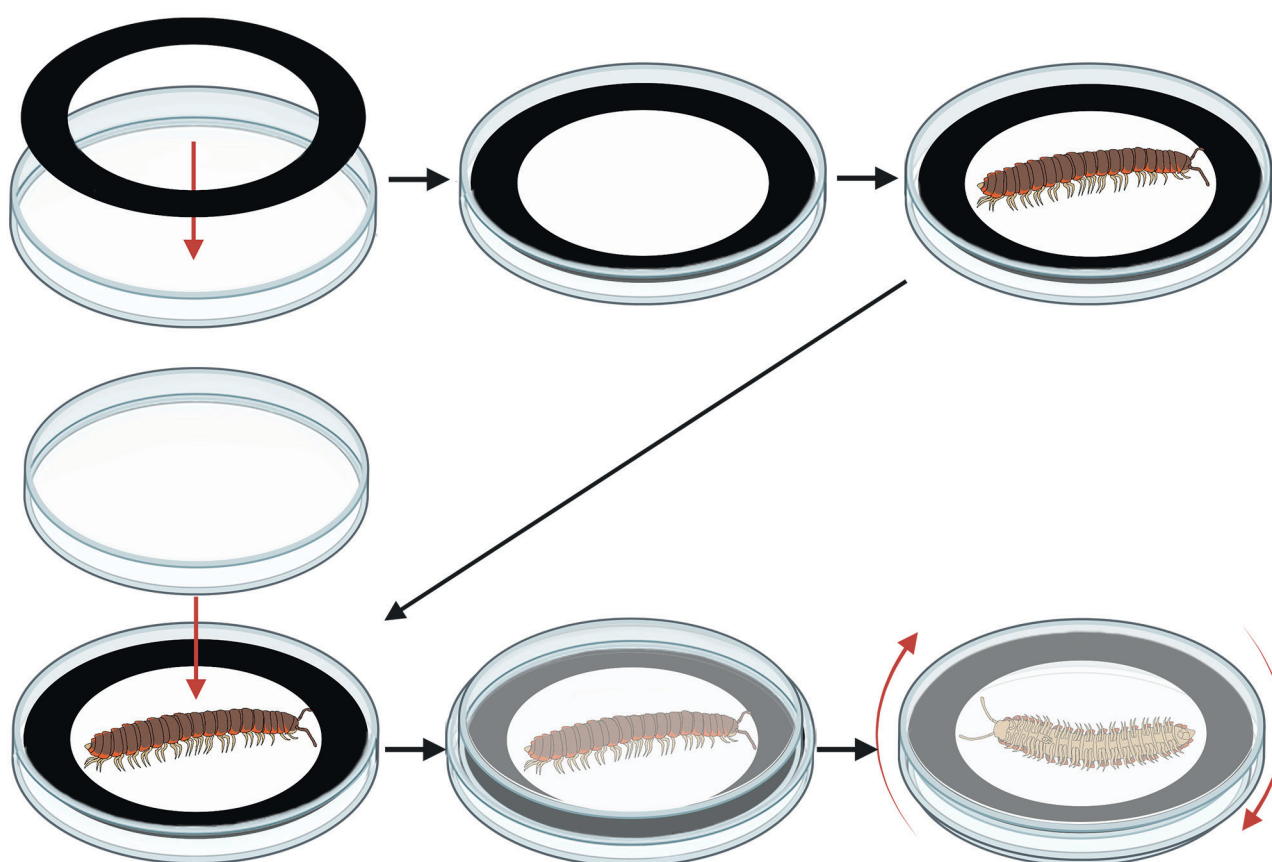


Fig. 4. Diagram showing method for facilitating ventral views of live millipedes (Polydesmida: Xystodesmidae). (Fig. 4 created in BioRender. Sengupta A (<https://BioRender.com/mtyj5ke>) is licensed under CC BY 4.0.)

For the *P. impressus* group, this test was done with a puddle (a small pool of water) made on the top of a 20.3 cm by 33.0 cm plastic lid. A 7 cm diameter puddle of variable depth was made by spraying tap water onto the lid. Individual millipedes were placed into the center of the puddle, left to walk out on their own, and then visually checked for any changes in powder retention. A UV flashlight was used to observe changes in powder retention and check for any powder that came off in the water.

For the *D. paynei* group, the puddle test was altered to be more replicable. A 10 cm diameter Petri dish was filled until the water was 1 cm deep. Each millipede was placed into the water and left completely submerged for 1.5 minutes. The millipedes were then removed and visually checked for any changes in powder retention (Fig. 6). A UV flashlight was used to observe changes in powder retention and check for any powder that came off in the water.

Field Experiment

The Field Experiment assessed powder retention and mortality in a natural setting. This also assessed the

possibility of powder transfer between marked and unmarked millipedes. Six 20 L buckets (rectangular with slightly rounded corners, 28 cm x 22.5 cm, 37 cm height), which were originally used for cat litter, were cleaned and modified to serve as mesocosms. This constrained the millipedes to a certain area while allowing them to experience natural conditions.

For *D. paynei*, three of the 20 L mesocosms were cleaned and 20 4 mm diameter holes were drilled into the bottom of each to allow for drainage, but to be small enough that *D. paynei* could not pass through. 20 cm deep holes were dug into the ground, the mesocosms were placed inside, and the soil (sieved to 4.75 mm) was placed into each mesocosm. Leaf litter from the holes was checked for other arthropods and placed back into the mesocosms. The soil in the mesocosms were watered liberally with a hose and then left for three days before putting millipedes in (Fig. 7A). This experiment took place at the location where *D. paynei* was collected.

The *D. paynei* used were a mixed group of freshly collected millipedes along with millipedes used from the previous IPR Experiment. Some freshly collected millipedes died

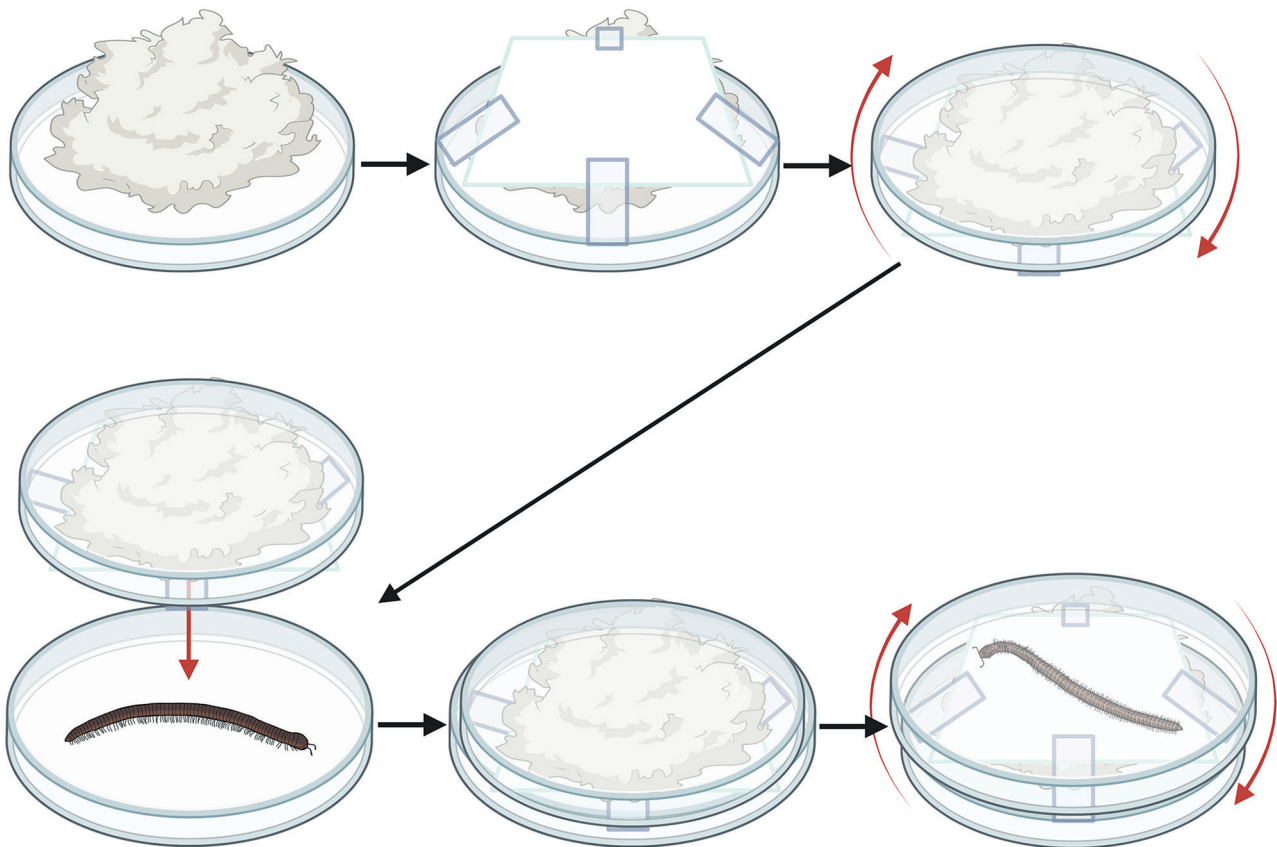


Fig. 5. Diagram showing method for facilitating ventral views of live millipedes (Julida: Parajulidae). (Fig. 5 created in BioRender. Sengupta A (<https://BioRender.com/mtvj5ke>) is licensed under CC BY 4.0.)



Fig. 6. Marked *Dicellarius paynei* underwater inside of Petri dish for Puddle Test.

before the beginning of the experiment, hence the usage of previously treated millipedes to better account for the disparity. In each mesocosm, there were equal amounts of marked and unmarked millipedes, so individuals that were previously used in the IPR Experiment were evenly distributed between the three mesocosms. Both unmarked and marked individuals from the IPR Experiment were re-treated following the same methods. Previously marked millipedes still retained some powder markings, having been marked approximately a month, and were retreated as marked millipedes. The same was for unmarked millipedes. Freshly collected millipedes were then marked using residual powder in the bag. Since the millipedes rolled up, they were dumped, with the powder, into a separate specimen container and allowed to uncurl as to evenly coat the ventral side with powder. Each group was kept in individual containers (marked old collection, marked new collection, unmarked old collection, unmarked new collection) and kept for three days in lab conditions before being released into the mesocosms, to allow ample time for excess loose powder to come off before being placed into the field.



Fig. 7. A, Mesocosms for *Dicellarius paynei* after being placed into the ground, filled with sieved soil, and watered; B, Mesocosms for *Uroblaniulus* sp. after installation.

The millipedes were then placed into each mesocosms by gently prodding them out of their containers. For *D. paynei* total of 10 millipedes were placed in each of two mesocosms, and eight were placed in the last (half marked, half unmarked in each mesocosm). The millipedes were then left for two weeks. After two weeks, millipedes were extracted. First, the leaf litter was sorted through to find millipedes at the surface. Remaining millipedes were found by wet sieving the soil through a 4.75 mm sieve. They were then placed into containers, one container of millipedes per mesocosm, and taken to the lab to be photographed and sexed under a microscope.

The Field Experiment was also conducted for Parajulidae, but with several modifications. First, The *P. impressus* group was replaced with *Uroblaniulus* sp. due to phenology and experiment timing. The experiment was conducted at Lake Laurel, near the area where the millipedes were collected.

The 20 L mesocosms had bottoms removed and were inserted 5–6 cm into the ground. The buckets were placed into the ground to make an outline, and shovels were used to dig a small trench so each mesocosm could slide into the soil. While digging, we were careful to not disturb the soil that would be within the mesocosm. After digging, we placed the mesocosm into the opening and used a board and mallet to hammer the mesocosm tightly into the soil (Fig. 7B). The leaf litter within the mesocosms was thoroughly searched to remove any millipedes and to check for any other organisms, such as centipedes or earthworms.

All millipedes were marked following the same method as the IPR Experiment. They were divided into six specimen

cups, with small amounts of soil and leaf litter, one per treatment group per mesocosm. They were kept in their respective specimen cups for approximately 24 hours to allow to excess powder to fall off, then released into the mesocosms by gently pushing them out with a probe. Each mesocosm had 10 millipedes, with half being marked with powder. They were kept in the field for two weeks. They were then extracted, first by using a UV flashlight to find any millipedes on the surface. Second, leaf litter was searched by hand within the mesocosm to find any other surface-active individuals. Last, leaf litter and surface soil were removed from the mesocosm and hand sorted on a tarp, until all millipedes were accounted for. For statistical purposes, millipedes that were not found after hand sorting were treated as not surviving the experiment. Millipedes were taken to the lab to be photographed and sexed under a microscope.

Data Analysis

A Wilcoxon Rank Sum Test, also called a Mann Whitney U test (Sheskin 2011), was conducted in R using the readxl package (R Core Team 2025, Wickham and Bryan 2025) between the mortality of the marked and unmarked group using the number of days each millipede survived for the IPR Experiment. For the Field Experiment, the test was run between the proportion of individuals of each group in each mesocosm that survived.

RESULTS

IPR Experiment

For *P. impressus*, there were two deaths in the marked group, and one death in the unmarked group (Fig. 8A). There was no significant difference between the survival of the marked millipedes as compared to the unmarked millipedes ($p = 0.6264$, $W = 45.5$, $n_1 = 10$, $n_2 = 10$). For *D. paynei*, no millipedes in either group died during the 20 days of treatment (Fig. 8B). Because of no variability between the two groups, the Wilcoxon Rank Sum Test could not create a p value ($p = n/a$, $W = 50$, $n_1 = 10$, $n_2 = 10$) (Sheskin 2011).

Most of the powder marking was rubbed off due to abrasion with moist soil. However, all marked individuals retained markings after 20 days for both *P. impressus* and *D. paynei*. For *P. impressus*, most of the markings were retained on or around the coxae, with a greater concentration of markings toward the anterior end of the body, especially surrounding the gonopods or gonopores (Fig. 9). For *D. paynei*, markings were instead mainly retained on the ventral and dorsal sides of the paranota, and occasionally on or around the coxae of the anterior legs (Fig. 10).

Puddle Test

For both species, exposure to water had no apparent impact on powder retention. No powder dissolved in the water or was rubbed off when exposed to water.

Field Test

After two weeks in the field, millipedes were extracted. For *D. paynei*, 25 of the 28 millipedes were able to be located on the surface of the soil and a total of 2 were extracted

through wet sieving the soil. There were a total of six mortalities, three from the unmarked group and three from the marked group. One unmarked individual was not recovered; 96.4% of millipedes were accounted for. A Wilcoxon Rank Sum Test found no significant difference between the proportion of marked individuals surviving and proportion of unmarked individuals surviving ($p = 0.6579$, $W = 6$, $n_1 = 3$, $n_2 = 3$) (Fig. 11A). There was one example of transfer in this group, with an unmarked millipede having a speck of powder on its body.

For *Uroblaniulus* sp., most millipedes could be found on the surface of the soil. Remaining individuals had to be located through hand sorting through the soil. There was only one mortality in one mesocosm and one millipede that had gone missing from another mesocosm, both being from the unmarked group; 96.7% of millipedes were accounted for. A Wilcoxon Rank Sum Test found no significant difference between the proportion of marked individuals surviving and proportion of unmarked individuals surviving ($p = 0.1876$, $W = 7.5$, $n_1 = 3$, $n_2 = 3$) (Fig. 11B). *Uroblaniulus* sp. retained markings in similar locations compared to *P. impressus*. Unmarked *Uroblaniulus* sp. remained completely free of powder.

DISCUSSION

Millipedes are difficult to mark due to their size, exoskeleton, and fossorial behavior. An ideal marking for animals is nontoxic, with no impact on health and mortality, durable, and inexpensive, unless performance is such that it justifies the costs (Hagler and Jackson 2001; Henderson 2021). Due to its retention abilities and no significant impact on mortality, fluorescent powder appears to be an effective method for marking millipedes. Across all experiments, all marked individuals retained markings and allowed them to

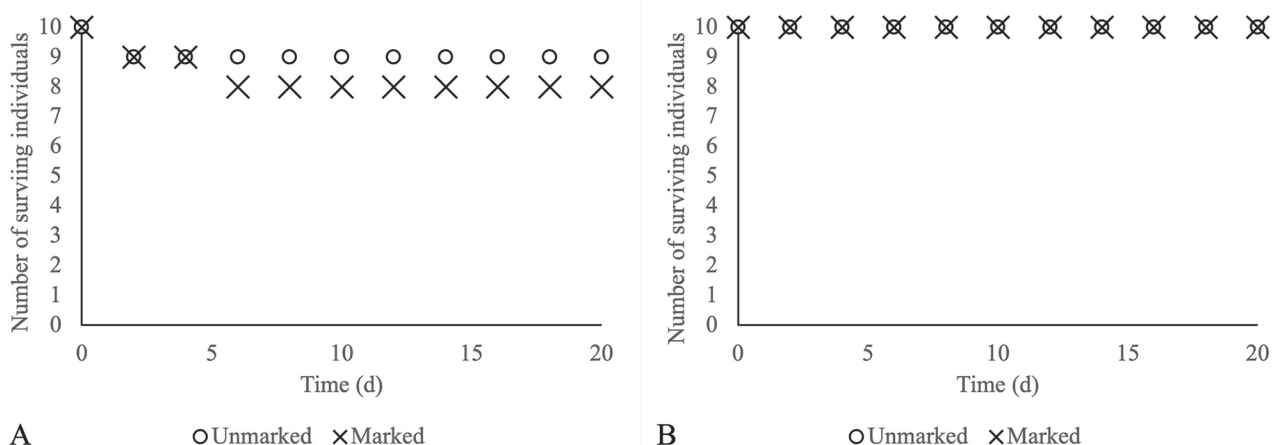


Fig. 8. Number of marked and unmarked surviving over time. A, *Ptyoiulus impressus*; B, *Dicellarius paynei*.

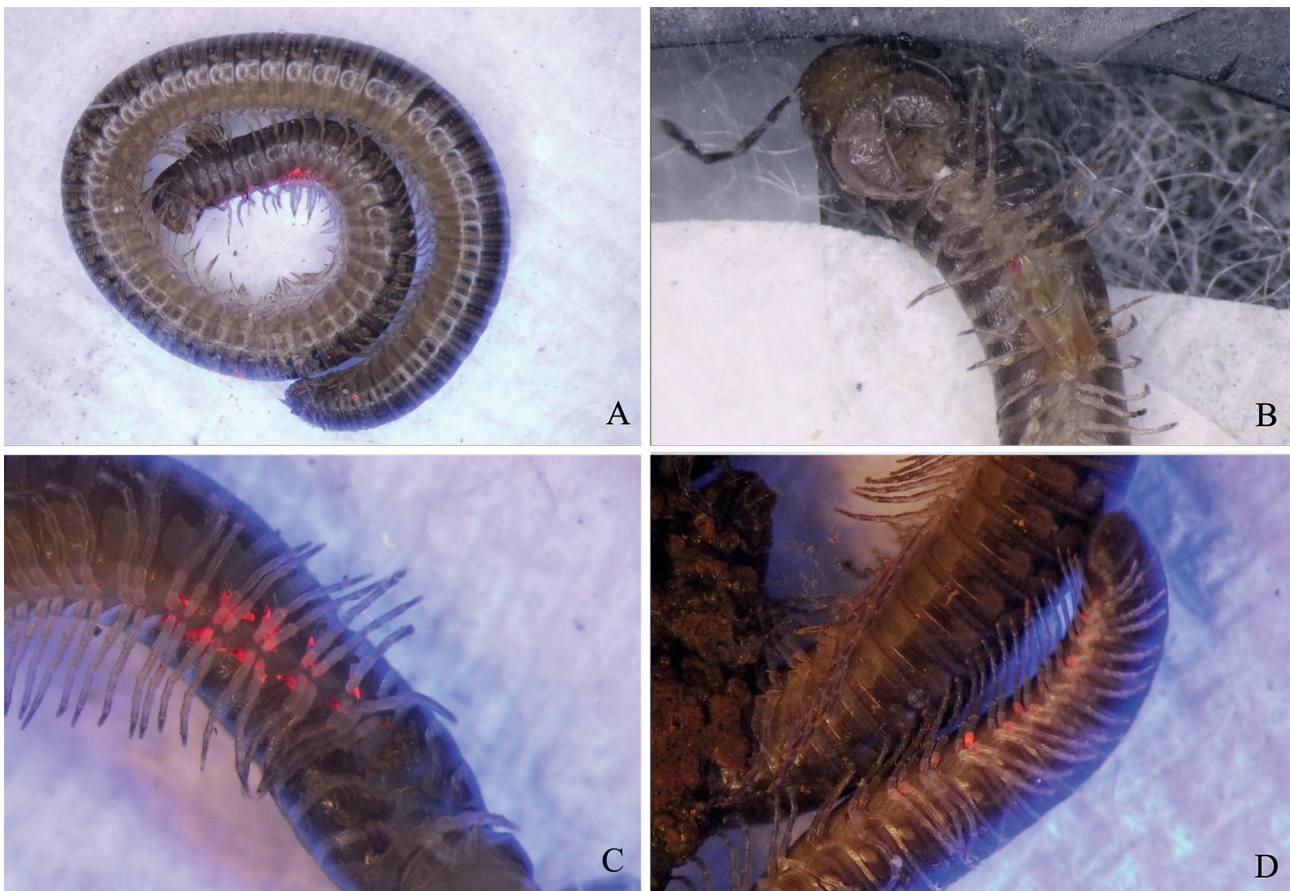


Fig. 9. Marked *Ptyoiulus impressus* 20 days after marking in the IFR Experiment, viewed with UV light assistance. **A**, Coiled lateral view; **B**, Anterior end ventral view; **C**, Anterior end ventral view; **D**, Posterior end ventral view.

be clearly distinguishable from unmarked individuals. With this, there is also little transfer between marked and unmarked individuals, with only one example of transfer occurring in the *D. paynei* portion of the Field Experiment. Even so, this example of transfer may have only occurred when the millipedes were removed from the mesocosms and put in the same container to be transported to the lab. The powder also did not come off during the Puddle Test. Although the fluorescent powder washes off of surfaces easily with soap and water, exposure to water, even in excessive amounts, does not impact retention on millipedes. Instead, abrasion against other surfaces impacts retention. This was also observed in the Field Experiment, as the marked millipedes lost most of their markings, but still retained some markings in less-abraded regions of the body, despite exposure to rain events. This indicates that these markings can last in natural environments despite risks of rain, flooding, and soil moisture. This is especially important in riparian, rainforest, or other habitats that experience frequent and heavy precipitation resulting in flooding or significant overland flow (Semenyuk 2018). Millipedes, and other soil fauna, must be adapted to these environments to survive frequent flooding (Tufová and

Tuf 2005; Marx et al. 2012). So, these markings should be able to withstand these sorts of environments.

Shaking the millipedes in the bag, even gently, did evoke stress responses for the millipedes (curling or thrashing), and could have been responsible for the quick deaths in the *P. impressus* portion of the IPR Experiment. Most limitations occurred during the Field Experiment. First, in the *D. paynei* portion of the experiment, the use of fresh and less fresh millipedes (from the previous study) was not ideal, as the less fresh millipedes had to be marked again and had endured more handling than the fresh millipedes. In this same study, we drilled holes at the bottom of the mesocosms to allow for drainage. However, the mesocosms still held a lot of water after multiple rain events. When the *D. paynei* were removed, there was a large amount of standing water in all of the mesocosms. Even so, both the use of different millipedes and the mesocosm design did not significantly impact mortality for the *D. paynei* group.

Overall, fluorescent powder functioned successfully to mark millipedes in the lab and field over periods of weeks. The powder has no significant impact on mortality of the millipedes, and works on millipedes that are and are not

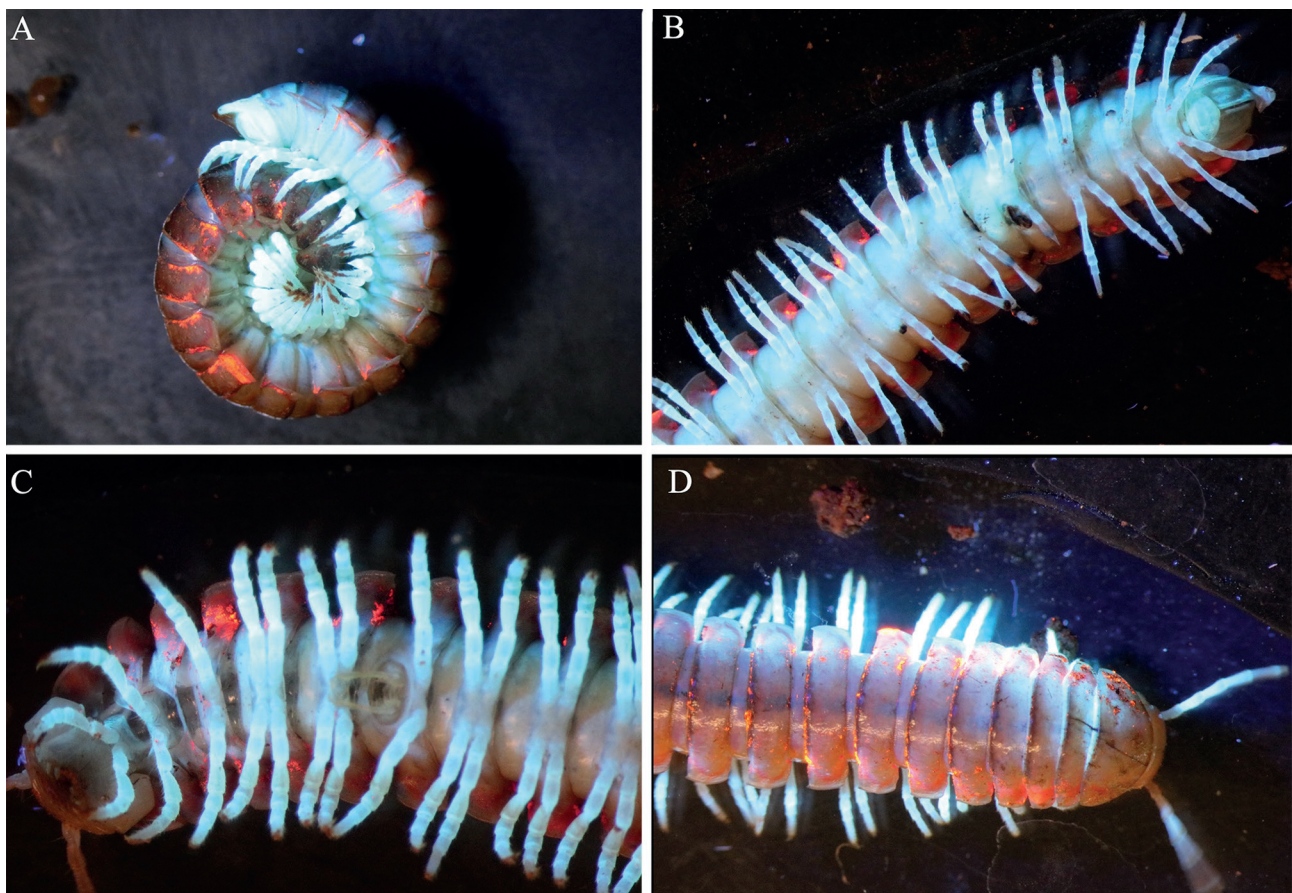


Fig. 10. Marked *Dicellarius paynei* 20 days after marking in the IFR Experiment, viewed with UV light assistance. **A**, Coiled lateral view; **B**, Posterior end ventral view; **C**, Anterior end ventral view; **D**, Anterior end dorsal view.

naturally fluorescent. There is still more to understand about the marking's impact on behavior, transfer during copulation, and long-term wear. Nonetheless, this marking method shows great potential to allow us to better study these animals.

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REFERENCES

- Andrew, L. 2025. First Checklist to the Diplopod Species of Georgia, USA with Notes on Distribution and a Key to Genus. Georgia College and State University Biology Theses. 41.
- Cárcamo HA, Abe TA, Prescott CE, Holl FB, Chanway CP. 2000. Influence of millipedes on decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. *Canadian Journal of Forest Research*. 30:817–826. <https://doi.org/10.1139/cjfr-30-5-817>.
- Chamberlin RV. 1951. On eight new southern millipeds. *The Great Basin Naturalist*. 6(1–2):19–26.
- Coleman DC, Callahan MA, Crossley DA. 2018. *Fundamentals of Soil Ecology*. 3rd ed. UK: Academic Press.
- Dangerfield JM. 1990. Abundance, biomass and diversity of soil macrofauna in savanna woodland and associates managed habitats. *Pedobiologia*. 34 (2):141–150.
- Drahokoupilová T, Tuf IH. 2011. Behavior of pill millipedes can be affected by external marking. *International Journal of Myriapodology*. 6:51–60. <https://doi.org/10.3897/ijm.6.2182>.
- Golovatch SI, Kime RD. 2009. Millipede (Diplopoda) distributions: A review. *Soil Organisms*. 81(3):565–597.
- Hagler JR, Jackson CG. 2001. Methods for marking insects: Current techniques and future prospects. *Annual Review of Entomology*. 46:511–543. <https://doi.org/10.1146/annurev.ento.46.1.511>.
- Henderson PA. 2021. Absolute Population Estimates Using Capture-Recapture Experiments. In: Southwood TRE. *Ecological Methods. With Particular Reference to the Study of Insect Populations*. 5th ed. New York: Chapman & Hall. p. 70–129.
- Hopkin SP, Read HJ. 1992. *The Biology of Millipedes*. UK: Oxford University Press.
- Iyer V, Najafi A, James J, Fuller S, Gollokota S. 2020. Wireless steerable vision for live insects and insect-scale robots. *Science Robotics*. 5(44):eabb0839. <https://doi.org/10.1126/scirobotics.abb0839>.
- Marx MT, Guhmann P, Decker P. 2012. Adaptations and predispositions

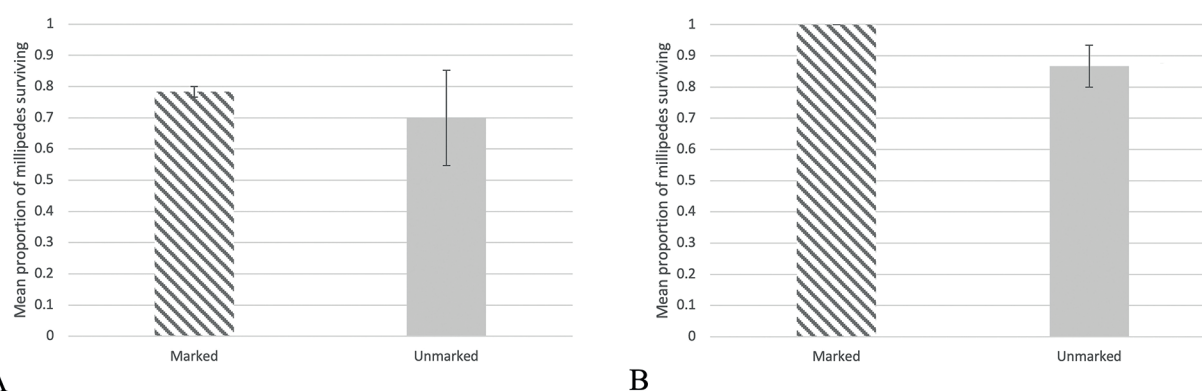


Fig. 11. Average proportion of millipedes in each group within each mesocosm surviving after two weeks with standard error bars. **A**, *Dicellarius paynei*; **B**, *Uroblaniulus sp.*

- of different Middle European arthropod taxa (Collembola, Araneae, Chilopoda, Diplopoda) to flooding and drought conditions. *Animals*. 2(4):564–590. <https://doi.org/10.3390/ani2040564>.
- Marek PE, Bond JE. 2009. A Müllerian mimicry ring in Appalachian millipedes. *Proceedings of the National Academy of Sciences of the United States of America*. 106(24):9755–9760. <https://doi.org/10.1073/pnas.0810408106>.
- Means JC, Hennen DA, Tanabe T, Marek PE. 2021. Phylogenetic systematics of the millipede family Xystodesmidae. *Insect Systematics and Diversity*. 5(2):1–26. <https://doi.org/10.1093/isd/ixab003>.
- Narissu JAL, Schell SP. 1999. A novel mark-recapture technique and its application to monitoring the direction and distance of local movements of rangeland grasshoppers (Orthoptera: Acrididae) in the context of pest management. *British Ecological Society*. 36(4):604–617.
- Nijima K, Nii M, Yoshimura J. 2020. Eight-year periodical outbreaks of the train millipede. *Royal Society Open Science*. 8:201399. <https://doi.org/10.1098/rsos.201399>.
- Perry KI, Wallin KF, Wenzel JW, Herms DA. 2017. Characterizing movement of ground-dwelling arthropods with a novel mark-capture method using fluorescent powder. *Journal of Insect Behavior*. 30(1):32–47. <https://doi.org/10.1007/s10905-017-9598-0>.
- R Core Team. 2025. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Say T. 1821. Description of the Myriapoda of the United States. *Journal of the Academy of Natural Sciences of Philadelphia, 1st series*. 3(1):102–114.
- Semenyuk, II. 2018. Myriapoda communities in a reforestation area and mature forest in Cat Tien National Park. *Tạp chí Khoa học và Công nghệ nhiệt đới*. 16(10):20–28. <https://doi.org/10.58334/vrtc.jtst.n16.03>.
- Sengupta A. 2026. Created in BioRender. <https://BioRender.com/mtjy5ke>.
- Shaw GG. 1968. Population size, ecology and mineral reservoir of the millipede, *Narceus annularis* (Raf). *Ecology*. 49(6):1163–1166.
- Shear WA. 2015. The chemical defenses of millipedes (Diplopoda): Biochemistry, physiology, and ecology. *Biochemical Systematics and Ecology*. 61:78–117. <https://doi.org/10.1016/j.bse.2015.04.033>.
- Shelley RM. 1984. A revision of the millipede genus *Dicellarius* with a revalidation of the genus *Thrinaxoria* (Polydesmida: Xystodesmidae). *Proceedings of the Biological Society of Washington*. 97(3):473–512.
- Shelley RM. 2002. *Thrinaxoria paynei*, a new species of Pachydesmine millipede from Georgia (Polydesmida: Xystodesmidae). *Entomological News*. 113(2):144–146.
- Shelley RM, Smith JM. 2016. Parajulid millipede studies XII: Initial assessment of *Ptyoiulus* Cook 1895 and neotype designations for *Julus impressus* Say 1821 and *J. montanus* Cope 1869 (Diplopoda: Julida). *Insecta Mundi*. 0522:1–21.
- Sheskin DJ. 2011. *Handbook of Parametric and Nonparametric Statistical Procedures*. 2nd ed. Florida: Chapman & Hall.
- Sierwald P, Decker P, Spelda J. 2025. Millibase. Accessed at <https://millibase.org> on 2025-08-28. <https://doi.org/10.14284/370>.
- Stašiov S, Vician V, Benčat T, Pätöprsty V, Lukáčik I, Svitok M. 2021. Influence of soil properties on millipede (Diplopoda) communities in forest stands of various tree species. *Acta Oecologica*. 113:103793. <https://doi.org/10.1016/j.actao.2021.103793>.
- Suriel C, Bueno-Villegas J, Jauregui-Haza UJ. 2025. Population density and diversity of millipedes in four habitat classes: comparison concerning vegetation type and soil characteristics. *Ecologies* 6:55. <https://doi.org/10.3390/ecologies6030055>.
- Techno Glow. 2025. [accessed 2025 November 10]. <https://www.technoglow-products.com/fluorescent-uv-powder/>.
- Tufová J, Tuf IH. 2005. Survival under water – comparative study of millipedes (Diplopoda), centipedes (Chilopoda) and terrestrial isopods (Oniscidea). In: Tajovský K, Schlaghamerský J, Pižl V, editors. *Contributions to Soil Zoology in Central Europe I*. Institute of Soil Biology AS CR, České Budějovice. p. 195–198.
- Wickham H, Bryan J. 2025. Readxl: Read Excel Files. R package version 1.4.5. <https://github.com/tidyverse/readxl>, <https://readxl.tidyverse.org>.
- Wong VL, Hennen DA, Macias AM, Brewer MS, Kasson MT, Marek P. 2020. Natural history of the social millipede *Brachycybe lecontei* Wood, 1864. *Biodiversity Data Journal*. 3:50770. <https://doi.org/10.3897/BDJ.8.e50770>.